Oesophagostomum
(helminth: nematode)

Overview

Nematodes are triploblastic pseudocoelomate unsegmented worms that undergo protostomial embryonic cleavage and grow by cuticular moulting (ecdysis). Two groups identified by the presence/absence of sensory phasmids have partly been ratified by molecular studies recognising three subclasses: Enoplia and Dorylaimia (both without phasmids) and Chromadoria (most with phasmids). Many phasmidian parasites of vertebrates are grouped in the chromadorian order Rhabditida; including spirurinids, tylenchinids and rhabditinids. The latter contains the infraorder Rhabditomorpha which includes strongyloid nematodes characterised by an expansion of the tail of the male known as the copulatory bursa (clasper with one dorsal and two lateral lobes with muscular rays). Many families are recognised: including the chabertiids which have large buccal capsules and often form nodules in the large intestines of herbivores. They have direct life-cycles where eggs passed in faeces develop to L3 (L2 cuticle retained as a sheath). Hosts ingest L3 which exsheath, migrate into the mucosa and moult into L4 (some may undergo arrested development, termed hypobiosis) before they return to the lumen and moult into adults. *Oesophagostomum* spp. (nodule worms) are found in the large intestines causing diarrhoea and ulcerative colitis in ruminants and sometimes necrotic colitis in pigs worldwide.

Classification:

Domain:	Eukaryota (membrane-bound nucleus)
Supergroup:	Amorphea (unikonts with single flagellum, or nonflagellated amoebae)
Kingdom:	Metazoa (multicellular eukaryotes, heterotrophs, notably animals)
Group:	Protostomia (triploblastic, spiral cleavage)
Subgroup:	Ecdysozoa (cuticle moulted = ecdysis)
Phylum:	Nematoda (unsegmented, pseudocoelomate roundworms, tubular digestive tract, dioecious)
Class:	Chromadorea (spiral amphids, three oesophageal glands, usually annulated bodies, free-living and parasitic)
Order:	Rhabditida (Secernentea, Phasmidea) (secretors, with phasmids, bipartite oesophagus, single testis)
Suborder:	Rhabditina (free-living or parasitic in invertebrates/lower vertebrates)
Infraorder:	Rhabditomorpha (‘rod-shaped’ buccal cavity)
Superfamily:	Strongyloidea (bursate males, prominent buccal capsules, parasites of mammals, birds, reptiles)
Family:	Chabertiidae (nodular worms, two pairs of branches in dorsal ray)
Genus:	*Oesophagostomum* (parasitic in caecum/colon of ruminants/pigs/humans)
Species:	various species cause enteritis in ruminants and pigs

Parasite biodiversity and host range: Most Metazoa are multicellular triploblastic animals with differentiated tissues, many being bilaterally symmetrical with a body cavity. Most invertebrate animals are protostomes as their embryonic development involves spiral determinate cleavage. Those that moult their external cuticles during their life-cycles (process known as ecdysis) are grouped together in the unique clade Ecdysozoa, including the nematodes (roundworms), onychophorans (velvet worms), tardigrades (water bears) and arthropods (myriapods, chelicerates, crustaceans and hexapods, all with jointed limbs). Nematodes (roundworms) are unsegmented tubular worms with a fluid-filled body cavity (pseudocoelom) that acts as a hydrostatic skeleton. They have longitudinal muscles and typically exhibit a sideways thrashing motion. They have well developed digestive tracts with various partitions: the foregut comprising the mouth (often with lips and papillae), buccal capsule (sometimes with ridges, rods, plates, spears, stylets or teeth) and oesophagus (glandular, muscular or both); the midgut (nonmuscular absorptive section); and hindgut (rectum) emptying through a subterminal anus (cloaca in males). Most nematodes are dioecious and form separate sexes. Male worms have a single testis (sometimes 2), an elongate vas deferens often equipped with a seminal vesicle and ejaculatory duct (glandular and/or muscular), 1-2 copulatory spicules (sometimes with an accessory gubernaculum), and bursate species with elaborate posterior claspers. Female worms are usually didelphic with 2 ovaries (some monodelphic or polydelphic), 2 oviducts usually with spermatheca, 2 uteri opening into a common vagina and a vulva often equipped with a muscular ovejector. Female worms are oviparous or viviparous and produce numerous eggs or larvae, respectively. Larval stages undergo several moults (L1-L4) before maturing into adult worms. Some nematodes have direct life-cycles where eggs or larvae infect definitive hosts (per os or per cutaneous), but many have indirect cycles where larvae first develop in invertebrate intermediate hosts before infecting definitive hosts (by ingestion, injection or deposition). Many nematode species are free-living in terrestrial and aquatic habitats, while some species from diverse groups have become plant or animal parasites. Two nematode groups identified by the presence/absence of sensory phasmids have partly been ratified by molecular studies recognising three subclasses: Enoplia and Dorylaimia (both without phasmids) and Chromadoria (most with phasmids). Most Enoplia are free-living marine organisms but

some are found in freshwater, and on land as plant parasites. The Dorylaimia comprise numerous freshwater and terrestrial species, including major groups of plant and animal parasites. The Chromadoria is represented by many marine groups as well as a terrestrial group of plant and animal parasites. The taxonomic ranks of many nematode assemblages vary considerably depending on which classification system has been followed. Molecular phylogenetic studies, however, have supported the separate classification of most groups, particularly at the level of superfamily. Collectively, species from at least 16 superfamilies are considered to pose serious threats to human and animal health as infectious diseases.

CLASSIFICATION* OF SUPERFAMILIES OF PARASITIC NEMATODES
Class: Enoplea (Aphasmidea, Adenophorea) (gland-bearers, cylindrical oesophagus, no phasmids, setae, two testes)
Subclass: Dorylaimia (five or more oesophageal glands, buccal stylet (odontostyle), free-living or parasitic)[clade I(2)]
Order: Trichinellida (Trichocephalida, Trichurida) (single spicule, stichosome oesophagus, L1 with buccal stylet)
Superfamily: Trichinelloidea (oesophagus with short anterior muscular and long posterior glandular portions)
Class: Chromadorea (spiral amphids, 3 oesophageal glands, usually annulated bodies, free-living and parasitic)
Order: Rhabditida (Secernentea, Phasmidea) (secretors, phasmids present, amphids anterior, bulbous oesophagus)
Suborder: Rhabditina (free-living or parasitic in invertebrates/lower vertebrates)[clade V(9)]
Infraorder: Rhabditomorpha (‘rod-shaped’ buccal cavity)
Superfamily: Rhabditoidea (open tube stoma, excretory system with lateral canals)
Superfamily: Strongyloidea (bursate males, prominent buccal capsules, parasites of mammals, birds, reptiles)
Suborder: Spirurina (animal parasites, many use invertebrate intermediate hosts (IH))[clade III(8)]
Incertae sedis Superfamily: Dracunculoidea (elongate parasites of vertebrate tissues, freshwater crustacean IH)
Infraorder: Ascaridomorpha (large roundworms, three large lips, numerous caudal papillae)
Superfamily: Ascaridoidea (ascarids, eggs thick-shelled, larvae may undertake hepato-pulmonary migration)
Superfamily: Heterakoidea (preanal sucker anterior to cloaca in males, direct cycle, infection by egg ingestion)
Infraorder: Gnathostomatomorpha (‘jaw-mouthed’ due to unique bulbous armed heads)
Superfamily: Gnathostomatoidea (first IH copepod, often use paratenic hosts)
Infraorder: Oxyuridomorpha (pinworms, pointed tails, oesophagus with terminal bulb, males with single spicule)
Superfamily: Oxyuroidea (common in mammals, birds, reptiles, amphibians)
Infraorder: Spiruromorpha (enigmatic clade linked by molecular characters, indirect cycles with IHs)
Superfamily: Acuarioidea (small parasites mostly of birds, with cephalic cordons, ptilina or serrated shields)
Superfamily: Camallanoidea (conspicuous phasmids, L1 with dorsal tooth, ovoviviparous, L1-L3 in copepod)
Superfamily: Filarioidea (tissue-dwelling filarial parasites, lack lips, infect tissues/vessels, arthropod IH)
Superfamily: Habronematoidea (unique head structures with small pseudolabia and median lips)
Superfamily: Physalopteroidea (stomach worms in mammals, insect IH)
Superfamily: Spiruroidea (pseudolabia, bipartite oesophagus, infect birds (crop/gizzard), arthropod His
Superfamily: Thelazioidea (eye-worms of birds and mammals, transmitted by insects)
Suborder: Tylenchina (fungal, plant and animal parasites)[clade IV(10,11,12)]
Infraorder: Panagrolaimomorpha (free-living or parasitic (insects, reptiles, amphibians, mammals))
Superfamily: Strongyloidoidea (dauer stages, lip region without processes, striated cuticle)

*Contemporary genotypic classification schemes recognize strong monophyletic clades at the level of superfamily and infraorder, while previous phenotypic classification schemes had ranked many as separate orders.

The superfamily Strongyloidea comprises a range of worms often with prominent buccal capsules and specialised oral structures well-suited to their feeding habits on host tissues and/or fluids. Adults of most species are parasitic in the gastrointestinal tracts of mammals and some birds, while larval stages feed on bacteria in the external environment, although some larvae may infect invertebrates as intermediate or paratenic hosts. The adult worms are sexually dimorphic, the smaller males characterised by an expansion of the tail (bursa) which is used as a copulatory clasping organ. Many classification schemes group these ‘bursate’ nematodes into one or more superfamilies in the order Strongylida (with suborders containing the strongyles, trichostrongyles, hookworms and lungworms), although the families essentially remain the same. Many families are recognised on the basis of parasite morphology, biology, life-cycle, host specificity and tissue tropism; including the following which contain many notorious parasites of vertebrates.

Representative Strongyloidea (cf. Strongylida) [with bursate males]				
Family	**Characters**	**Definitive Hosts**	**Transmission***	**No. genera**
Strongylina (strongyles)				
Chabertiidae (nodule worms)	large buccal capsules, leaf crown of labial collar, L3 sheathed	artiodactyls, primates	ingestion of L3	22
Strongylidae (strongyles)	large buccal capsule often armed with teeth, leaf crown around mouth	mammals, reptiles, birds	ingestion of L3	32
Syngamidae (gapeworm)	cup-shaped buccal capsule, armed with teeth, male attached to female	birds, mammals	ingestion of L3 or invertebrate PH	7
Stephanurinae (kidneyworm)	buccal capsule armed with teeth, leaf crowns and external epaulettes	suids	transdermal penetration or ingestion of L3 or PH	1
Trichostrongylina (trichostrongyles)				
Trichostrongylidae (trichostrongyles)	reduced buccal capsule, ridged synlophe, oesophagus lacking bulb, thin-shelled eggs	artiodactyls, birds	ingestion of L3	50
Molineidae (stomach/intestinal worms)	reduced buccal capsule, cephalic vesicle, female tail with spine or cusps, oviparous/viviparous	mammals, birds, reptiles	ingestion of L3	61
Heligmonellidae (hookworm-like)	body coiled, cephalic vesicle, ridged synlophe, bursa asymmetrical	mammals, birds	transdermal penetration of L3	56
Ancylostomatina (hookworms)				
Ancylostomatidae (hookworms)	large buccal capsule bent dorsally, armed with teeth/cutting plates	primates, carnivores, artiodactyls	transdermal penetration of L3 (sometimes *per os*)	20
Metastrongylina (lungworms)				
Metastrongylidae (lungworms)	small buccal capsule, 2 trilobed lips, bursa with reduced dorsal lobe	suids	ingestion of IH carrying L3	1
Protostrongylidae (lungworms)	small buccal capsule, bursa with large lobes, gubernaculum	artiodactyls	ingestion of IH carrying L3	17
Angiostrongylidae (lungworms)	no or reduced buccal cavity, short club-shaped oesophagus	carnivores, rodents	ingestion of IH or PH carrying L3	28
Dictylocaulidae (lungworms)	small buccal capsule, bursa with large lobes, short stout spicules	ungulates, reptiles	ingestion of L3	5
Filaroididae (lungworms)	small buccal capsule, reduced male bursa, infective L1	carnivores	ingestion of L1	4

*IH = intermediate host, PH = paratenic (transport) host, L1 = first-stage larva, L3 = third-stage larva

Strongyle worms are characterised by their prominent buccal capsules with lips, leaf crowns or labial collars at the mouth opening, sometimes with teeth or cutting plates. They are parasitic in a variety of organ systems in a range of animals, including the large intestines of mammals (ruminants, suids, elephants, perissodactyls, rodents, marsupials and primates), tortoises and ratite birds, the forestomach of marsupials, the trachea of birds and mammals, and the renal system of suids. Four families are recognised: Strongylidae (buccal capsule globular or cylindrical, oral opening circular, dorsal ray with 6 terminal branchlets, 32 genera in large intestines of mammals, reptiles and birds); Chabertiidae (buccal capsule globular or cylindrical, oral opening circular or oval, with leaf crown or labial collar, with up to 3 teeth at base of buccal capsule, dorsal ray with 4 terminal branchlets, 22 genera in gastrointestinal tract of mammals); Syngamidae (buccal capsule subglobular, oral opening hexagonal, numerous teeth at base of buccal capsule, dorsal ray with 4 terminal branchlets, 7 genera in respiratory, urinary and digestive tracts of mammals and birds); and Deletrocephalidae (oral opening hexagonal, dorsal ray with 6 terminal branches, 2 genera in large intestines of birds). The family Chabertiidae contains 4 subfamilies: Chabertinae (globular buccal capsule with leaf crowns, J-shaped ovejector, 11 genera in large intestines of ruminants, rodents, marsupials and primates); Oesophagostominae (cylindrical buccal capsule with leaf crowns and often cervical collar, J-shaped ovejector, 11 genera in large intestines of ruminants, suids, rodents and primates); Cloacinae (cylindrical buccal capsule with leaf crowns, J-shaped ovejector, 39 genera in stomach of marsupials); and Phascolostrongylinae (cylindrical or globular buccal capsule without leaf crowns but with teeth or cutting plates, Y-shaped ovejector, 6 genera in stomach and intestines of marsupials).

Genus	No. spp.	Definitive Hosts	Location	Adult worms	Worm eggs
Oesophagostominae (nodule worms)					
Oesophagostomum (nodule worms)	52	artiodactyls, primates	large intestines	6-25 mm, white-grey body, cylindrical buccal capsule, prominent leaf crown, cervical collar, larvae provoke nodule formation	58-89 x 34-51 µm, ovoid, thin-shelled
Chabertiinae (bowel worms)					
Chabertia (large-mouthed bowel worm)	5	artiodactyls	large intestines	10-26 mm long, stout white body, prominent bell-shaped buccal capsule curved ventrally, vestigial leaf crown in 2 rows, bifurcate dorsal gutter	90-105 x 50-55 µm, ellipsoidal, thin-shelled

The subfamily Oesophagostominae contains 11 genera of nodular worms which are classified within 3 tribes: Oesophagostominea (*Oesophagostomum, Daubneyia, Wuia*) with the transverse cervical groove confined to ventral side, parasitic in ruminants, rodents and suids; Bourgelatioidinea (*Bourgelatioides*, *Neorhabditostomum*, *Rhabditistomum*) with the transverse cervical groove completely encircling body, parasitic in ruminants and tragulids; and Bourgelatinea (*Bourgelatia*, *Kuntzistrongylus*, *Lemurstrongylus*, *Phacochoerostrongylus*, *Trachypharynx*) lacking a transverse cervical groove, parasitic in suids, rodents and primates. Over the years, various workers proposed the division of the genus *Oesophagostumum* into various subgenera (*Oesophagostomum, Proteracaecum*, *Hysteracrum*, *Conoweberia, Ihlea, Lerouxiella*, *Bosicola, Hydsonia* and *Pukuia*), but many considered such divisions to be based primarily on host records and not on characteristics of the parasites themselves. At present, the genus *Oesophagostomum* contains over 50 species which occur worldwide in domestic and wild artiodactyls, primates and some rodents. The species *O. radiatum* and *O. columbianum* infect ruminants mainly in tropical or subtropical areas, with heavy parasite burdens seen during periods of high (often summer) rainfall. The species *O. venulosum* also occurs in ruminants but mainly in regions with cooler climates and winter rainfall. The species *O. dentatum* is found in pigs worldwide, but only in free-range animals (and not in intensive feedlot piggeries) as the presence of soil is necessary for larval development. The species *O. bifurcum, O. aculeatum* and *O. stephanostomum* infect primates (including humans) mostly in South-East Asia and western Africa.

***Oesophagostomum* species**	**Definitive Hosts**	**Location [Clinical signs]**	**Distribution**
O. (*Conoweberia*) *aculeatum*	Primates: cercopithecid (rhesus macaque, Japanese macaque, crab-eating macaque, Togue macaque, Francois' leaf monkey, golden snub-nosed monkey, northern plains grey langur), hominid (human)		Asia
O. aethiopicum	Artiodactyla: suid (bushpig, warthog)		Africa
O. africanum	Artiodactyla: bovid (springbok)		Africa
O. apiostomum	Primates: cercopithecid (rhesus macaque), hominid (human)		
O. (*Hysteracrum*) *asperum*	Artiodactyla: bovid (sheep, bharal, goat, Himalayan goral, nilgai), cervid (sambar deer, Reeve's muntjac, moose), suid (pig)	large intestines [diarrhoea]	Asia, Americas
O. (*Conoweberia*) *bifurcum*	Primates: cercopithecid (grivet, mona monkey, Campbell's mona monkey, crab-eating macaque, rhesus macaque, stump-tailed monkey, olive baboon, yellow baboon, chacma baboon, gray-footed chacma baboon, patas monkey), hominid (chimpanzee, human); Artiodactyla: bovid (goat), suid (pig)	large intestines	Africa, South-East Asia, South America
O. (*Conoweberia*) *blanchardi*	Primates: hylobatid (gibbon), hominid (orangutan)		Asia
O. brevicaudum	Artiodactyla: suid (pig)	large intestines [diarrhoea]	Europe, North America
O. (*Conoweberia*) *brumpti*	Primates: cercopithecid (macaque), hominid (orangutan, human)		Asia
O. cervi	Artiodactyla: cervid (roe deer, fallow deer, red deer, sambar deer, white-tailed deer)		worldwide
O. (*Proteracaecum*) *columbianum*	Artiodactyla: bovid (cattle, sheep, argali, goat, impala, black wildebeest, blue wildebeest, common tsessebe, sable antelope, waterbuck, steenbok, Sharpe's grysbok, southern reedbuck, Limpopo	intestines [diarrhoea]	worldwide, esp. tropics

	bushbuck, common duiker), cervid (white-tailed deer), camelid (bactrian camel, dromedary, alpaca); Rodentia: caviid (guinea pig)		
O. curvatum	Artiodactyla: cervid (sambar deer, Indian muntjac)		Asia
O. dentatum (syn. *O. subulatum*)	Artiodactyla: suid (pig, Indian boar, Sardinian wild boar), tayassuid (collared peccary, white-lipped peccary)	large intestines [diarrhoea]	worldwide
O. dentigerum	Primates: hominid (chimpanzee)		Africa
O. (*Daubneyia*) *eurycephalum*	Artiodactyla: suid (desert warthog), bovid (roan antelope)		Africa
O. farchai	Artiodactyla: suid (desert warthog)		Africa
O. georgianum	Artiodactyla: suid (pig)	large intestines [diarrhoea]	North America
O. (*Daubneyia*) *goodeyi*	Artiodactyla: suid (warthog)		Africa
O. granatensis	Artiodactyla: suid (pig)	large intestines [diarrhoea]	Europe
O. hylochoeri	Artiodactyla: suid (giant forest hog)	colon	Africa
O. lechwei	Artiodactyla: bovid (kafue lechwe)		Africa
O. longicaudatum	Artiodactyla: suid (pig)	large intestines [diarrhoea]	Europe
O. longicaudum	Artiodactyla: suid (pig)	large intestines [diarrhoea]	Europe
O. macacae	Primates: cercopithecid (rhesus macaque)		Africa
O. mocambiquei	Artiodactyla: suid (desert warthog)		Africa
O. mpwapwae	Artiodactyla: suid (desert warthog); Proboscidea: elephantid (African bush elephant)		Africa
O. multifoliatum	Artiodactyla: bovid (sheep, goat, steenbok, Sharpe's grysbok, common duiker)	large intestines [diarrhoea]	Africa
O. (*Hysteracrum*) *muntiacum*	Artiodactyla: cervid (Indian muntjac, Reeve's muntjac)		Asia
O. (*Daubneyia*) *mwanzae*	Artiodactyla: suid (desert warthog), bovid (roan antelope, Livingstone's eland); Proboscidea: elephantid (African bush elephant); Perissodactyla: equid (plains zebra)		Africa
O. okapi	Artiodactyla: giraffid (okapi)		Africa
O. (*Daubneyia*) *oldi*	Artiodactyla: bovid (roan antelope), suid (warthog)		Africa
O. (*Conoweberia*) *ovatum*	Primates: hylobatid (gibbon),		Asia
O. (*Conoweberia*) *pachycephalum*	Primates: cercopithecid (red-tailed monkey)		Africa
O. quadrispinulatum	Artiodactyla: suid (pig, wild boar)	large intestines [diarrhoea]	worldwide
O. radiatum (syn. *Bosicola radiatum, tricollaris, O. inflatum, dilatum, bovos, biramosum, vesiculosum*)	Artiodactyla: bovid (cattle, Bali cattle, zebu, water buffalo, American bison, European bison, sheep, goat, chamois, kob, steenbok, Livingstone's eland), cervid (roe deer, fallow deer, red deer, Javan rusa deer, sambar deer)	intestines [diarrhoea]	worldwide
O. (*Conoweberia*) *raillieti*	Primates: hylobatid (gibbon),		Asia
O. roscoei	Artiodactyla: bovid (blue duiker)		Africa
O. (*Daubneyia*) *roubaudi*	Artiodactyla: suid (warthog)		Africa
O. santosdiasi	Artiodactyla: suid (warthog)		Africa
O. (*Conoweberia*) *selfi* (syn. *Kuntzistrongylus*)	Rodentia: murid (Coxing's white-bellied rat)		Taiwan
O. sikae	Artiodactyla: cervid (roe deer, fallow deer, red deer), tragulid (Java mouse-deer)		Asia
O. (*Daubneyia*) *simpsoni*	Artiodactyla: suid (warthog), bovid (roan antelope); Proboscidea: elephantid (African bush elephant)		Africa
O. (*Ihlea*) *stephanostomum* (incl. subspp. *stephanostomum*, *thomasi*)	Primates: hominid (eastern lowland gorilla, chimpanzee, eastern chimpanzee, human)		Africa, Asia,, South America
O. (*Lerouxiella*) *suzannae*	Rodentia: pedetid (springhare)		Africa
O. (*Protaeracum*) *synceri*	Artiodactyla: bovid (African buffalo)		Africa
O. traguli	Artiodactyla: tragulid (Java mouse-deer)		Asia

O. (*Ihlea*) *ventri*	Carnivora: felid (wild cat)		
O. (*Hysteracrum*) *venulosum* (large bowel worm) (syn. *Strongylus follicularis, O. acutum, inflatum var. ovis, vigintimembrum*)	Artiodactyla: bovid (cattle, zebu, European bison, sheep, argali, mouflon, goat, mountain goat, chamois, nilgai), cervid (roe deer, fallow deer, red deer, Iberian red deer, sika deer, chital deer, water deer, Reeve's muntjac, mule deer, Columbian black-tailed deer, white-tailed deer, boreal woodland caribou, moose), camelid (bactrian camel, dromedary, llama)	large intestines [diarrhoea]	worldwide
O. walkeri	Artiodactyla: bovid (impala, sable antelope, Sharpe's grysbok, common eland, Livingstone's eland)		Africa
O. (*Lerouxiella*) *xeri*	Rodentia: sciurid (African ground squirrel)		Africa
O. (*Daubneyia*) *yorkei*	Artiodactyla: suid (desert warthog); Proboscidea: elephantid (African bush elephant)		Africa
O. (*Conoweberia*) *zukowskyi*	Primates: cercopithecid (baboon)		Africa

Parasite morphology: *Oesophagostomum* spp. form 3 different types of morphological stages in their developmental cycles: eggs; larvae (4 stages designated L1-L4); and adult worms (males and females). Eggs are oval to elliptical in shape measuring 58-89 x 34-51 µm and contain a morula at the 8-32 cell (blastomere) stage with a clear space between the developing embryo and the very thin eggshell. L1 and L2 are free-living stages with long narrow buccal capsules, a muscular rhabditiform oesophagus (flask-shaped with 2 projections), intestines comprising several cells and long tapering tails. L3 are ensheathed stages that have retained the L2 cuticle as a protective covering. They are elongate stages measuring 600-923 µm in length and have broad squared heads, cylindrical buccal capsules, a strongyliform (club-shaped) oesophagus, intestines comprising 18-22 triangular cells, and tapering rounded tails encased in long tail sheath extension (122-207 µm) of which the terminal 50% is filamentous. Adult worms have stout white-grey bodies 6-25 mm long that are often slightly curled. The anterior oral opening is circular and often forms a high mouth collar (appearing as a truncate cone). The mouth is surrounded by a corona radiata with 9-24 elements in the external leaf crown (ELC) and usually double that number (18-48) in the internal leaf crown (ILC), although their composition varies between species. For example, *O. dentatum* and *O. quadrispinulatum* have 9-12 ELC but poorly developed ILC elements, *O. georgianum* and *O. longicaudum* have 9 ELC elements and 18 ILC elements, *O. brevicaudum* has 14-16 ELC elements and 28-32 ILC elements, *O. venulosum* has 18-20 ELC elements and 36-40 ILC elements, *O. columbianum* has 20-24 ELC elements and 40-48 ILC elements, while *O. radiatum* has 30-40 ILC elements but those of the ELC are highly reduced to small regular protuberances. All *Oesophagostomum* species have a small cylindrical thin-walled buccal cavity which opens forward (as opposed to the large globular buccal capsule of *Chabertia* which is bent ventrally). The head of adult worms then has a distinct anterior inflation of the cuticle (cephalic vesicle) located anteriorly from a transverse constriction (cervical groove) [which in the case of the oesophagostomines is confined to the ventral side]. The location of the lateral cervical papillae (spiny sensory protrusions) varies according to species, but most are located just posterior to the ventral groove. An excretory pore (stoma) is also present in the ventral groove at the level of the oesophagus (thus giving the genus its name). Some species also have well-developed lateral cervical alae arising behind the ventral groove (e.g. *O. columbianum*). Adult worms are sexually dimorphic, with females generally slightly larger than males (6-25 cf. 5-17 mm). Mature males have a bell-like copulatory bursa with 2 lateral lobes supported by 5 rays (comprising muscular elements following nerve channels to terminal papillae) whereby the 2 ventral rays are closely-associated but separate from the 3 lateral rays (with the middle anterolateral ray shorter and separate from the others), and a dorsal lobe supported by a ray with 4 terminal branches. Males also have a gubernaculum and telamon with 2 equal filiform spicules measuring 0.7-1.2 mm in length. Mature females are didelphic with 2 ovaries and 2 uteri connected by J-shaped ovejectors to a common vulva that opens near the anus along the tapering tail. Females are oviparous and lay partially embryonated thin-walled eggs.

Site of infection: Adult worms infect the large intestines (caecum and colon) of their definitive hosts (ruminants, suids, rodents, primates), while developing larval stages (L3 and L4) are found in nodules in the walls of both the small and large intestines. Free-living larval stages (L1, L2 and sheathed L3) are found in the external environment where they contaminate soil and pastures.

Pathogenesis: Infections by several *Oesophagostomum* spp. have been associated with mild to severe disease in ruminants, suids and primates. The severity of disease depends on parasite virulence, the intensity of infection, host susceptibility, and prior exposure. While most infections are light and remain subclinical, heavier infections (> 800 worms in cattle, > 200 worms in sheep) may cause transient diarrhoea and illthrift. Adult worms reside in the lumen of the large intestines and are plug-feeders (ingest host tissues), often causing chronic infections where the intestinal mucosa becomes hyperaemic, mucoid and thickened. In contrast, earlier larval stages may cause acute disease when they damage the intestinal wall. Infective L3 penetrate deep into the wall of the small and large intestines where they become encapsulated in small subserosal nodules (1-2 mm) by host fibroblastic reactions (the exception is *O. venulosum* which does elicit nodule formation). The histotrophic stages develop to L4 which elicit stronger host reactions so the nodules become larger (1-2 cm) and start to mineralize becoming filled with caseous material that may eventually calcify. Nodular lesions render the gut wall unsuitable for use as sausage casings. While L4 may be retained in nodules for long periods, eventually they emerge leaving ulcerative lesions which ooze and bleed, with ecchymoses and petechial haemorrhages leading to fluid, protein and blood loss. It is estimated that worms may cause daily blood loss of 0.1 ml/worm so heavy infections

may result in anaemia and hypoproteinaemia (esp. hypoalbuminaemia). Tissue trauma and inflammation alters intestinal function (reduced digestion, absorption and peristalsis) resulting in blood-stained mucoid to projectile fetid diarrhoea, with dehydration, intestinal discomfort, anorexia, unthriftiness, progressive weight loss, retarded growth, general weakness, exhaustion, and starvation. Inflammatory nodular disease may also involve diphtheritic jejunitis, typhlitis and colitis with perforations and adhesions, intussusception, abscess formation and peritonitis. Acute disease involving diarrhoea, dehydration, colic and fever is seldom observed in sheep, as larval challenge elicits strong local protective immune responses in the colon resulting in worm expulsion. Nonetheless, persistent infections may produce chronic disease with intermittent diarrhoea (foul-smelling mucopurulent green faeces), anorexia, weight loss and occasionally intussusception. Cattle also develop strong protective immune responses after 8-12 months of age, but calves older than 7 weeks may develop acute disease with diarrhoea, anaemia, oedema, anorexia and cachexia. Most infections in pigs do not cause overt disease, but rather contribute to ill-thrift with occasional diarrhoea, particularly in older animals in which worm burdens increase with age. However, *O. dentatum* and *O. quadrispinulatum* may cause severe wasting disease in young pigs, with ulcerative colitis, enteritis, widespread haemorrhages, diphtheritic membrane formation and regional lymphadenopathy. In humans, emergent larvae may cause nodule remnants to become ulcerative and haemorrhagic, but in many cases, L4 do not emerge but cause dark pustular abscesses containing numerous eosinophils and macrophages. Oesophagostomiasis in humans may be uni-nodular, with single large nodules (2-11 cm in diameter) projecting from the colon causing hard painful abdominal masses (regionally known as Dapaong disease), or multi-nodular, with numerous tiny nodules forming along the colon causing mild diarrhoea, dysentery or constipation, anaemia, bowel obstructions, anorexia, nausea, fever and malaise. Infections have also been associated with peritonitis, appendicitis, hepatosplenomegaly, cardiomegaly, emaciation, and occasionally skin lesions.

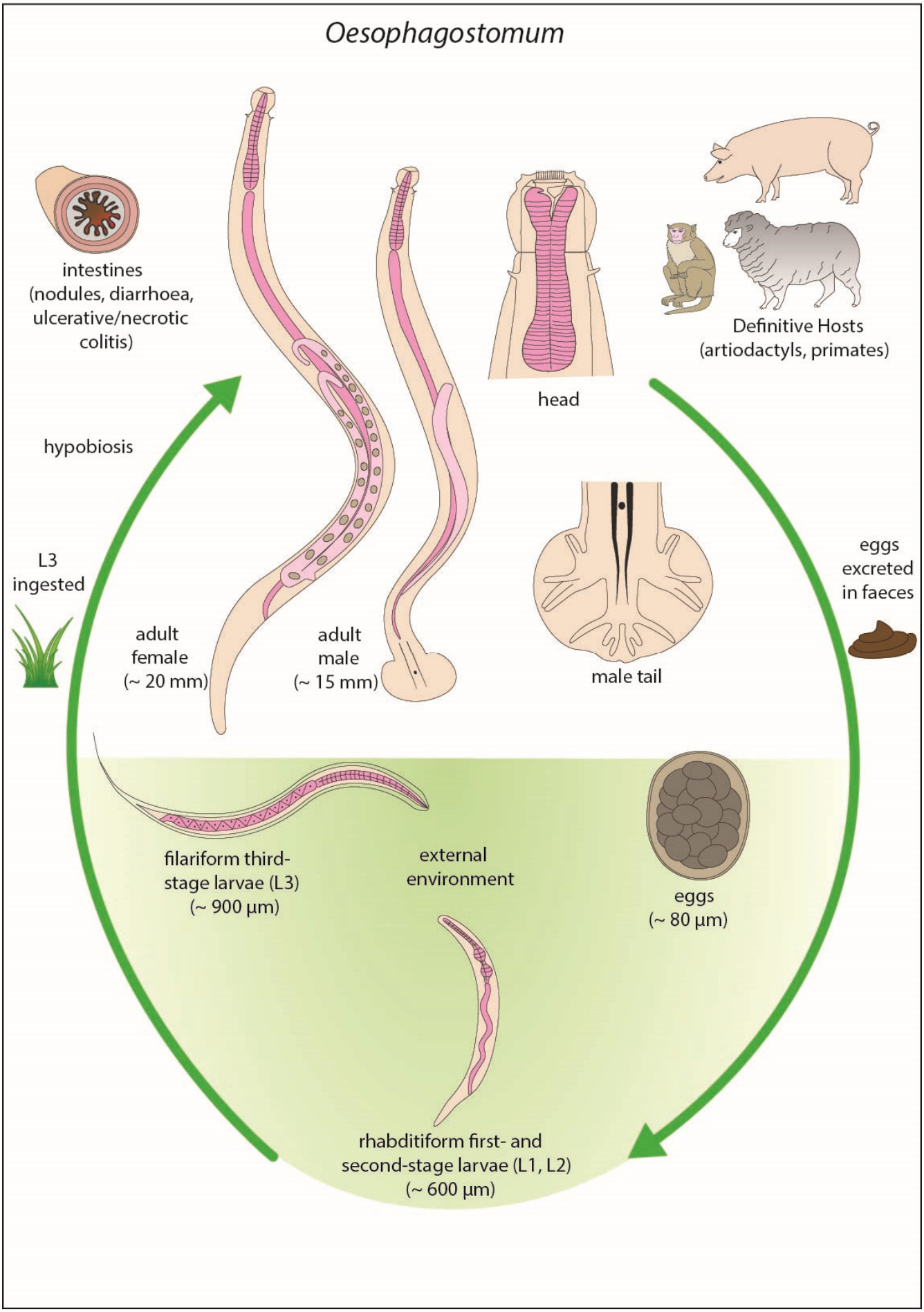
Developmental cycle and mode of transmission: *Oesophagostomum* spp. have simple direct monoxenous life-cycles involving the faecal-oral transmission of infections between individuals. Gravid female worms lay eggs (several thousand per day) which are excreted in host faeces to contaminate the external environment. In moist shady warm conditions, the eggs hatch after 2 or more days releasing free-living L1 which feed on faecal bacteria before moulting to form free-living L2 which also feed on bacteria. These stages then moult to form L3 which retain the L2 cuticle as a protective sheath and are thus unable to feed. Depending on prevailing environmental conditions, it usually takes several weeks for L3 to develop from eggs. While free-living larvae prefer hot moist conditions found in tropical and subtropical regions (particularly those with summer rainfall), the larvae of some species appear to be very resistant to desiccation and/or freezing, and are able to survive for several months (up to 14 months). Moisture stimulates L3 to migrate horizontally (dispersing from faecal pats) as well as vertically (ascending vegetation during the day but descending during cold nights). Hosts become infected by ingesting infective L3 in contaminated food, water or soil. Ingested L3 exsheath in the gut and penetrate the mucosa of the small or large intestines within a few hours. Here they undergo histotrophic development forming nodules over 6-20 days in which they moult to L4 (the larvae do not undertake any extra-intestinal migration). At this stage, some larvae may exhibit inhibited or arrested development (known as hypobiosis) for several weeks/months before resuming development. There is good evidence for L4 hypobiosis occurring in sows from colder regions, with resumption of development around farrowing resulting in a periparturient rise in egg production. In either case, L4 eventually emerge from the gut wall into the lumen and migrate to the colon where they moult to young adults (sometimes called L5) which feed, mature and mate. The prepatent period (time from infection to first excretion of eggs) ranges from 30-40 days for first infections, increasing to several months for subsequent infections (prior sensitization of the host apparently exacerbates nodule formation and the retention of L4 in the intestinal wall).

Differential diagnosis: Infections may be suspected on the basis of clinical symptomatology (diarrhoea, illthrift) but many other conditions may cause similar signs of disease (especially gastroenteric nematodes). Coprological techniques are conventionally used to detect worm eggs in faecal samples, either in wet mounts or smears but usually following their concentration by sedimentation in water and/or floatation in saturated sugar or heavy metal salt solutions. Regrettably, the thin-shelled eggs deteriorate quickly in floatation media, and they are also remarkably similar in morphology to those of other strongylid nematodes, particularly trichostrongyles (like *Hyostrongylus* in pigs) and hookworms. In addition, faecal egg counts often do not correlate well with the occurrence of clinical signs, as developing larval stages may cause disease before adult worms have matured and begun egg production. Faecal samples may be incubated in moist chambers in order to harvest L3 for morphological identification, but most coproculture techniques take over a week to perform and are frequently contaminated by fungal overgrowths. *Oesophagostomum* L3 are ~ 500 μm long and have broad rounded heads, intestines comprising 32 cells, and tapering tails with long filamentous tail sheaths. These characteristics are similar to those of *Chabertia* L3 but the latter are shorter and have shorter tail sheaths, whereas *Hyostrongylus* L3 are ~ 700 μm and have squared heads, intestines comprising 16 cells, tapering tails with a digitiform process, short tail sheaths, and are highly active (often exhibiting a swimming motion). Modern medical imaging techniques (particularly ultrasound) have also been used to detect intestinal and abdominal wall nodules in humans, sometimes in association with laparoscopy. Uni-nodular (Dapaong) tumours have defined but poorly-reflective walls and echo-free lumens, while multi-nodular disease revealed numerous small colonic lesions and pseudokidney intussusceptions. Investigative surgery has also been used to differentiate colonic carcinoma, amoebiasis or inflammatory bowel disease from oesophagostomiasis by the subsequent microscopic detection of parasites in biopsied nodules. Infections may also be diagnosed post-mortem in domestic animals by the detection of adult worms in the colon. Several enzyme immunoassays have been developed to detect specific host serum antibodies against parasite antigens, but many demonstrated cross-reactivity problems with other nematodes, especially hookworms. Modern molecular biological techniques have been used to characterize adult and larval stages of various species following the polymerase

chain reaction (PCR) amplification of parasite DNA, including restriction fragment length polymorphism (RFLP) analyses, rapid amplified polymorphic DNA (RAPD) analyses, single strand conformation polymorphism (SSCP) analyses or partial gene sequencing (nuclear ribosomal DNA and internal transcribed spacer regions, and mitochondrial cytochrome c oxidase subunit I).

Treatment and control: Infections by adult worms have been successfully treated with a variety of anthelmintics, including macrocyclic lactones (abamectin, doramectin, ivermectin), benzimidazoles (albendazole, thiabendazole, fenbendazole, flubendazole), imidazothiazoles (levamisole), tetrahydropyrimidines (pyrantel) and diethylenediamines (piperazine). However, the drugs were less effective against developing or hypobiotic larval stages encapsulated within nodules in the intestinal walls, so treatment needs to be repeated to counter emerging stages as well as re-infections. There have been increasing reports of drug resistance in worm populations, particularly against benzimidazole drugs. Veterinary authorities recommend monitoring for drug resistance using faecal egg count reduction tests, cycling between different drug classes, and using systematic or strategic dosing protocols to treat susceptible and/or infected animals, particularly following rainy seasons when infections are most prevalent. Surgical intervention has been used to incise and drain uni-nodular (Dapaong) tumours as well as to relieve bowel obstruction complications in human patients. Various control strategies can be used to reduce transmission rates, mostly by limiting faecal contamination of the environment and providing clean food and water supplies free of infective larvae. Where possible, faeces should be collected for treatment or sanitary disposal, and should not be used to fertilise edible foods. Strict hygiene should be maintained in intensive farming situations, with regular cleaning and disinfection of holding facilities, especially farrowing pens. Pasture management practices involve controlled rather than free-range grazing, reducing stocking rates, quarantining new livestock, rotational or mixed grazing, draining pastures of excess moisture, or leaving them ungrazed for a season. In human communities at risk, vegetables and fruits should be washed thoroughly in clean treated water or cooked properly before consumption. Education campaigns may also be used to create public awareness and suggest suitable interventions.

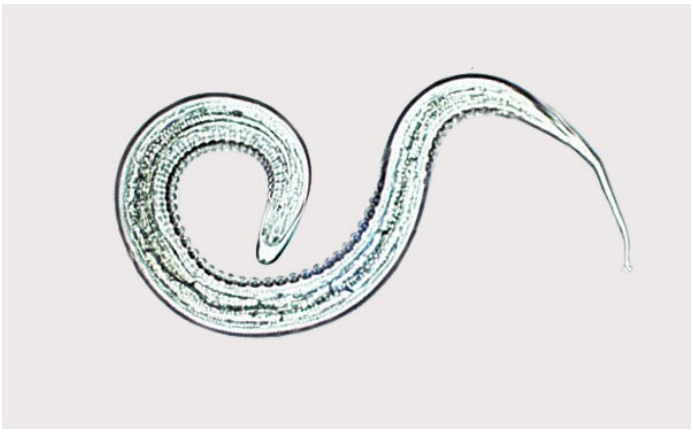
Oesophagostomum



Oesophagostomum adult worms

Oesophagostomum adult worm, head

Oesophagostomum worm egg



Oesophagostomum third-stage larva