Acuaria/Cosmocephalus/Dispharynx/Echinuria/Streptocara
(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 tylenchinids, rhabditinids and spirurinids. The latter contains the infraorder Spiruromorpha: an enigmatic clade linked by molecular characters, but all having indirect life-cycles involving one or more intermediate hosts, the first invariably being an arthropod. Most possess two trilobed lips (sometimes greatly reduced), a bipartite oesophagus (anterior muscular, posterior glandular) and non-bursate males with coiled tails and two dissimilar spicules. Several superfamilies are recognised: including acuarioids (with cephalic cordons) found in the oesophagus, proventriculus and gizzards of birds and are transmitted by water fleas, isopods, grasshoppers and beetles in which L3 develop. Numerous genera (*Acuaria, Cosmocephalus, Dispharynx, Echinuria, Streptocara*) have been associated with oesophagitis, proventriculitis and emaciation predominantly in waterfowl.

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:	Spirurina (mostly parasitic in vertebrate hosts)
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)
Family:	Acuariidae (cephalic cordons, grooved cuticular structures)
Genus:	*Acuaria* (parasitic in gizzard of birds)
Genus:	*Cosmocephalus* (parasitic in oesophagus of birds)
Genus:	*Dispharynx* (parasitic in proventriculus of birds)
Genus:	*Echinuria* (parasitic in oesophagus of birds)
Genus:	*Streptocara* (parasitic in gizzard of birds)
Species:	various species cause inflammation and emaciation in birds

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 (some monodelphic or polydelphic) with 2 ovaries, 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 IHs
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.

Molecular phylogenetic studies have grouped a variety of superfamilies into the infraorder Spiruromorpha whose members are parasites of vertebrates with indirect life-cycles involving larval development within invertebrate intermediate hosts. Most members were previously classified within the order Spirurida: either within the suborder Camallanina (worms with conspicuous phasmids, uninucleate oesophageal glands, larvae without cephalic hooks, usually with copepodid intermediate hosts); or the suborder Spirurina (worms with inconspicuous phasmids, multinucleate oesophageal glands, larvae with cephalic hooks or spines, usually with non-copepodid intermediate hosts). Ten spirurinid superfamilies are recognised: Gnathostomatoidea and Physalopteroidea (buccal cavity weakly cuticularized, 2 large lateral pseudolabia); Habronematoidea and Acuarioidea (buccal cavity well cuticularized, 2 large lateral pseudolabia); Filarioidea, Rictularioidea, Aproctoidea and Diplotriaenoidea (buccal cavity well cuticularized, without pseudolabia); Thelazioidea (long cylindrical buccal cavity well cuticularized, body without caudal alae); and Spiruroidea (short buccal cavity well cuticularized, body with caudal alae).

The superfamily Acuarioidea comprises medium-sized worms with 2 triangular pseudolabia and elaborate cephalic ornamentation consisting of grooved cuticular elevations (in the form of cordons, collarettes or ptilina) infecting the stomach of birds (rarely mammals) and using arthropods (aquatic crustaceans or terrestrial insects) as intermediate hosts for larval development, and sometimes fish and amphibians as paratenic hosts for larval transport. A single family (Acuariidae) is recognised with over 300 species classified in 40 genera in 3 subfamilies: Acuariinae with 4 cordons extending beyond the pseudolabia and males with 4 pairs of precloacal papillae (*Acuaria, Antechiniella, Aviculariella, Chandleronema, Cheilospirura, Chevreuxia, Chordatortilis, Chordocephalus, Cosmocephalus, Decorataria* (sometimes included in *Syncuaria*), *Desportesius, Dispharynx* (sometimes included in *Synhimantus*), *Echinuria* (syn. *Hamannia*), *Parachordatortilis, Paracuaria, Pectinospirura, Pelecanema, Pseudoavicularielle,*

Sexansocara, Skrjabinocara, Skrjabinocerca, Skrjabinoclava, Stammerinema, Syncuaria (sometimes included in *Echinuria*), *Synhimantus, Voguracuaria, Willmottia,* and *Xenocordon*); Seuratiinae with cephalic collarettes limited to the bases of the pseudolabia and males with 4 pairs of precloacal papillae (*Deliria, Ingliseria, Navonia, Proyseria, Pseudohaplonema, Rusguniella, Seuratia, Stegophorus, Streptocara* and *Tikusnema*); and Schistorophinae with 4 ptilina arising from the sublabia in the form of horns, lappets, blades or leaf-like structures, and males with 5 or more pairs of precloacal papillae (*Ancyracanthopsis, Molinacuaria, Quasithelazia* (sometimes included in *Schistorophus*), *Schistorophus, Sciadiocara,* and *Viktorocara*). Recent molecular phylogenetic studies have shown the family Acuariidae to be monophyletic with 2 major clades: one formed by members of the subfamily Schistorophinae (with ptilina), and the other composed of members of the subfamilies Acuariinae (with cordons) and Seuratiinae (with collarettes alternatively interpreted as cordons restricted to the cephalic region).

Genus	No. spp.	Definitive Hosts	Location	Adult worms	Eggs	Transmission
Subfamily: Acuariinae (cordons extend longitudinally)						
Acuaria	70	mainly passerine birds	gizzard	8-30 mm long, cordons long, vulva median	40-65 x 27-50 µm, ovoid, thick-shelled	indirect (L3 in insect IH)
Cosmocephalus	9	fish-eating birds	oesophagus, proventriculus	9-22 mm long, cordons looped, vulva median	31-40 x 18-22 µm, ovoid, thick-shelled	indirect (L3 in amphipod IH) [fish PH]
Dispharynx	15	passerine, galliform birds, some birds of prey	oesophagus, proventriculus	3-10 mm long, cordons curved, vulva posterior	22-42 x 17-26 µm, ovoid, thick-shelled	indirect (L3 in isopod IH)
Echinuria	16	water birds	proventriculus	4-21 mm long, cordons displaced ventrally, vulva posterior	28-37 x 17-23 µm, ovoid, thick-shelled	indirect (L3 in crustacean IH)
Subfamily: Seuratiinae (cordons forming collarette)						
Streptocara	8	water birds	gizzard	3-11 mm long, collarette serrated	32-65 x 18-50 µm, ovoid, thick-shelled	indirect (L3 in amphipod IH) [fish PH]

Many genera have been described from the upper digestive tracts of a wide range of passerine and non-passerine birds around the world, sometimes in association with inappetence, wasting and sometimes anaemia and death. Representative genera include *Acuaria* (cordons long, rectilinear and extending longitudinally (not recurrent or anastomosing), spicules equal or subequal, no tuft of spines on tail of female, vulva median), *Cosmocephalus* (cordons recurrent anteriorly and anastomose laterally, composed of inner row of plates (giving scalloped appearance) and an outer longitudinal ridge, female tail with terminal projection, vulva median), *Dispharynx* (cordons with descending arms forming several curves (not anastomosing), vulva posterior), *Echinuria* (cordons anastomose but not recurrent, 2 pairs of longitudinal rows of cuticular spines, vulva posterior), and *Streptocara* (circular cephalic collarette (sometimes described as cordons), limited to bases of paired pseudolabia, posterior border generally serrated or divided into several teeth, female tail short and rounded, vulva median-posterior).

Parasite species	Definitive hosts	Location [Clinical signs]	Intermediate hosts [plus Paratenic hosts (PH)]	Distribution
Subfamily Acuariinae				
Acuaria				
A. alii	Passeriformes: motacillid (grey wagtail), muscicapid (black redstart), sturnid (common mynah, common starling)			Eurasia
A. anthuris (syn. *A. corvicola, depressa*, *nebraskensis*, *scutata*)	Coraciiformes: coraciid (European roller); Passeriformes: alaudid (horned lark), campephagid (long-tailed minivet), cinclid (brown dipper, white-throated dipper), corvid (Eurasian magpie, Oriental magpie, black-billed magpie, red-billed blue magpie, blue jay, Eurasian jay, American crow, Cuban crow, house crow, large-	gizzard	Coleoptera: tenebrionid (darkling beetle, *Adesmia biseriata, Pisterotarsa gigantea*); Orthoptera: acridid (grasshopper, *Calliptamus italicus, Chorthippus longicornis, Locusta migratoria, Melanoplus femurrubrum*), gryllid (unidentified crickets); Malacostraca: gammarid	worldwide

	billed crow, hooded crow, fish crow, carrion crow, eastern carrion crow, rook, common raven, Chihuahuan raven, rufous treepie, Indian treepie, red-billed chough), motacillid (pipit), muscicapid (blue whistling thrush), oriolid (Indian golden oriole), passerid (sparrow), sturnid (common mynah, crested mynah, great mynah, common starling, black-collared starling, red-billed starling, vinous-breasted starling, rosy starling), vaganid (large wood shrike)		(amphipod, *Gammarus lacustris*)	
A. brevispicula	Passeriformes: muscicapid (bluethroat), sturnid (common mynah)			Europe
A. brumpti (syn. *A. attenuata*, *dollfusi, muscicapae*, *papillifera*, *paragalliardi*)	Passeriformes: acrocephalid (great reed warbler, icterine warbler), alaudid (crested lark, horned lark, calandra lark), corvid (hooded crow, rook, Eurasian jay), emberizid (red-headed bunting), hirundinid (common house martin, sand martin, barn swallow), laniid (brown shrike), motacillid (white wagtail, tree pipit), muscicapid (spotted flycatcher), phylloscopid (greenish warbler), sturnid (rosy starling), sylviid (common whitethroat, lesser whitethroat), turdid (common nightingale, thrush nightingale)			worldwide
A. caeruleus	Passeriformes: muscicapid (blue whistling thrush)			Eurasia
A. cettiae	Passeriformes: cettid (Manchurian bush warbler)			Asia
A. cincli	Passeriformes: cinclid (brown dipper)			Asia
A. cissae	Passeriformes: corvid (red-billed blue magpie)			Asia
A. coloradensis	Passeriformes: hirundinid (violet-green swallow)			North America
A. colluricinclae	Passeriformes: pachycephalid (western shrikethrush)			Australia
A. copsychusi	Passeriformes: muscicapid (Oriental magpie-robin)	gizzard		India
A. cordata	Passeriformes: alaudid (horned lark), corvid (common raven), dicrurid (black drongo, hair-crested drongo), laniid (red-backed shrike, great grey shrike, lesser grey shrike, long-tailed shrike, brown shrike), motacillid (water pipit, white wagtail, grey wagtail), muscicapid (black redstart), phylloscopid (dusky warbler), sturnid (rosy starling), turdid (common blackbird)			Eurasia
A. cordonspinosa	Passeriformes: vireonid (white-eyed vireo)	gizzard		Cuba

A. crami	Passeriformes: dicrurid (fork-tailed drongo)			Africa
A. crypsirinae	Passeriformes: corvid (grey treepie)			Asia
A. dicrura	Passeriformes: dicrurid (greater racket-tailed drongo), motacillid (white wagtail)			Africa
A. europaea	Piciformes: picid (Syrian woodpecker); Passeriformes: oriolid (Eurasian golden oriole)	gizzard		Europe
A. excubitori	Passeriformes: laniid (great grey shrike)	gizzard		India
A. flindersi	Falconiformes: falconid (brown falcon)			Australia
A. galliardi	Passeriformes: muscicapid (flycatcher)			Europe
A. gracilis	Passeriformes: corvid (Eurasian jay), motacillid (olive-backed pipit), oriolid (Eurasian golden oriole)			Eurasia
A. gruveli	Galliformes: phasianid (double-spurred spurfowl, grey partridge, Barbary partridge, chukar, red-legged partridge, Daurian partridge, common quail, Japanese quail, ring-necked pheasant, black grouse, Himalayan snowcock); Passeriformes: corvid (Eurasian jay); Strigiformes: strigid (Eurasian eagle-owl)	gizzard	Orthoptera: acridid (grasshopper, *Tylotropidus patagiatus*)	Africa, Eurasia
A. hamulosa (syn. *A. pavonis, Cheilospirura*)	Galliformes: phasianid (chicken, red junglefowl, Burmese peafowl, Indian peafowl, turkey, chukar, rock partridge, ring-necked pheasant, common quail), numidid (helmeted guineafowl); Anseriformes: anatid (domestic duck); Columbiformes: columbid (rock dove); Passeriformes: corvid (large-billed crow), pycnonotid (light-vented bulbul), sturnid (white-shouldered starling); Pelecaniformes: ardeid (whistling heron, yellow-crowned night heron)	gizzard [weight loss, anaemia]	Orthoptera: acridid (grasshopper, *Aeolopus tamulus, Melanoplus differentialis, femurrubrum, Oxya chinensis, nitidula, sinensis, Paroxya clavuliger, Prumna* (*Primnoa*) *ussriensis*), pyrgomorphid (*Atractomorpha ambigua*), tettigoniid (*Conocephalus sallator, Decticus verrucivorous, Gampsocleis sadahovi, Phaenoreptereus falcata, Stilpnochlora couloniana*); Malacostraca: talitrid (amphipod, *Orchestia platensis*); Coleoptera: curculionid (flower beetle, *Oxydema fisiforme, Sitophilus oryzae*), dermestid (skin beetle, *Dermestes ater*), hydrophilid (water scavenger beetle, *Dactylosternum abdominale*), mycetophagid (fungus beetle, *Litargus balteatus, Typhaea stercorea*), nitidulid (sap beetle, *Carpophilus dimidiatus*), scarabaeid (dung beetle, *Scarabaeus sacer*), tenebrionid (darkling beetle, *Adesmia biseriata, Epitragus*	worldwide

			diremptus, Palorus ratzeburgi, Tenebroides nana, Tenturia gigas, Tribolium castaneum); Blattodea: blattid (cockroach); Diptera: ulidiid (picture-winged fly, *Euxestus*), Dermaptera: anisolabidid (earwig, *Carcinophora americana, Euborellia annulipes*), forficulid (*Doru taeniata*), labidurid (*Labidura bidens, reporia*), spongiphorid (*Marava unidentata*); Diplopoda: spirobolellid (millipede, *Microspirobolus*)	
A. kinsellai	Passeriformes: dicrurid (black drongo)			Asia
A. kungi	Passeriformes: muscicapid (Indian robin)			India
A. lanii	Passeriformes: laniid (long-tailed shrike)			Asia
A. lina	Passeriformes: icterid (western meadowlark), motacillid (grey wagtail)			North America
A. longicaudata	Passeriformes: corvid (large-billed crow, collared crow, Oriental magpie)			Asia
A. lophurae (syn. *Cheilospirura*)	Galliformes: phasianid (silver pheasant, ring-necked pheasant)			Asia
A. lucknowensis	Passeriformes: corvid (common green magpie)	gizzard		India
A. magpii	Passeriformes: corvid (blue magpie)	gizzard		India
A. mamillaris	Passeriformes: corvid (cayenne jay)	gizzard		South America
A. martinagliai	Passeriformes: ploceid (South African weaver)			Africa
A. mayori	Passeriformes: corvid (purplish jay, plush-chested jay), thraupid (double-collared seedeater, saffron finch), tyrannid (Nutting's fly catcher)			Americas
A. microecae	Passeriformes: petroicid (jacky winter)			Australia
A. microspinosa	Pelecaniformes: ardeid (yellow-crowned night heron)			Americas
A. minor	Passeriformes: icterid (western meadowlark)			North America
A. minuta	Passeriformes: icterid (common grackle)			North America
A. mirafrae	Passeriformes: alaudid (Horsfield's bush lark)			Australia
A. muelleri	Bucerotiformes: upupid (hoopoe); Passeriformes: passerid (sparrow)			Europe, Africa
A. ornata	Passeriformes: corvid (rook), sturnid (common starling, white-throated dipper)			Asia
A. paraguayensis	Passeriformes: tyrannid (sibilant sirystes)			South America
A. parorioli	Passeriformes: oriolid (Eurasian golden oriole)			Eurasia

A. pattoni	Passeriformes: icterid (western meadowlark)			North America
A. petterae	Passeriformes: artamid (pied butcherbird, black-faced woodswallow), campephagid (varied triller), cinclosomatid (cinnamon quail-thrush), meliphagid (red wattlebird, singing honeyeater, yellow-fronted honeyeater, spiny-cheeked honeyeater), monarchid (restless flycatcher), oreoicid (crested bellbird), petroicid (southern scrub robin)			Australia
A. phalacrocoracis	Suliformes: phalacrocoracid (European shag)	stomach		Russia
A. pseudicettiae	Passeriformes: hirundinid (common house martin)			Asia
A. ptilopachydis	Galliformes: phasianid (stone partridge)			Africa
A. quadriloba	Piciformes: picid (black woodpecker, European green woodpecker)	oesophagus		Europe, North America
A. quiscali	Passeriformes: corvid (Florida scrub jay), icterid (common grackle, great Antillean grackle); Piciformes: picid (hairy woodpecker)			North America
A. raillieti	Pelecaniformes: pelecanid (pelican)			
A. rectovaginata	Falconiformes: falconid (European kestrel)	stomach		Africa
A. resticula	Cuculiformes: cuculid (groove-billed ani)			Americas
A. rotundata	Passeriformes: laniid (lesser grey shrike)	oesophagus		Asia
A. sagittata	Pelecaniformes: ardeid (purple heron, black-crowned night heron); Ciconiiformes: ciconiid (black stork)	stomach		Europe
A. semei	Otidiformes: otidid (kori bustard)			Africa
A. sialia	Passeriformes: turdid (western bluebird)			North America
A. singhi	Passeriformes: sturnid (Brahminy starling)	gizzard		India
A. skrjabini (syn. *A. buttnerae*)	Passeriformes: alaudid (greater short-toed lark), corvid (Eurasian magpie), estrildid (long-tailed finch, plum-headed finch, red-throated parrotfinch, red-cheeked cordon-bleu, orange-cheeked waxbill, tricoloured munia), passerid (house sparrow, Spanish sparrow, Eurasian tree sparrow, Japanese tree sparrow), prunellid (alpine accentor), sturnid (white-cheeked starling, gray starling), thraupid (Cuban grassquit)	oesophagus, gizzard		Eurasia, Australasia
A. spinosa	Galliformes: phasianid (greater prairie chicken, sharp-tailed grouse)			North America
A. sturni	Passeriformes: sturnid (common starling, Caucasian starling, rosy			North America

	starling)			
A. subula	Passeriformes: acrocephalid (thrush warbler), alaudid (red-capped lark, horned lark), bombycillid (Bohemian waxwing), campephagid (black-winged cuckooshrike), corvid (Eurasian jay, spotted nutcracker, Eurasian magpie, grey treepie), dicrurid (black drongo), emberizid (Ortolan bunting, pine bunting), fringillid (hawfinch), hirundinid (sand martin), laniid (brown shrike, great grey shrike, lesser grey shrike), motacillid (white wagtail, citrine wagtail), muscicapid (blue-and-white flycatcher, spotted flycatcher, European pied flycatcher, Siberian rubythroat, European robin, pied bush chat, western black-eared wheatear, Isabelline wheatear, northern wheatear, variable wheatear), passerid (house sparrow, Eurasian tree sparrow), sittid (Eurasian nuthatch), sturnid (common starling, white-cheeked starling), sylviid (great reed warbler, Blyth's reed warbler, Eurasian reed warbler, icterine warbler, willow warbler, common chiffchaff), turdid (scaly thrush); Apodiformes: apodid (white-throated needletail); Columbiformes: columbid (oriental turtle dove); Coraciiformes: coraciid (European roller); Piciformes: picid (white-backed woodpecker, black woodpecker, grey-headed woodpecker)	gizzard		Palearctic
A. sygmoidea	Accipitriformes: accipitrid (crested goshawk)			South America
A. tenuis	Galliformes: phasianid (chukar); Passeriformes: cinclid (brown dipper), muscicapid (whinchat)			Eurasia
A. triaenucha	Pelecaniformes: ardeid (American bittern)			North America
A. tuberculata	Coraciiformes: alcedinid (kookaburra)			Africa?
A. tyranna	Passeriformes: tyrannid (eastern kingbird)			North America
A. upupa	Bucerotiformes: upupid (Eurasian hoopoe)	gizzard		India
A. vanelli	Charadriiformes: charadriid (northern lapwing)			India
A. wangi	Passeriformes: thamnophilid (white-cheeked antbird, spotted antbird)			South America
Cosmocephalus				
C. aduncus	Charadriiformes: larid (great black-backed gull, Audouin's			Eurasia

	gull); Podicipediformes: podicipedid (great crested grebe)			
C. asturis	Pelecaniformes: ardeid (cattle egret)			
C. capellae	Anseriformes: anatid (northern shoveler, garganey); Charadriiformes: charadriid (northern lapwing), scolopacid (common snipe, broad-billed sandpiper, marsh sandpiper, red-necked phalarope, common redshank, spotted redshank)			Holarctic
C. faridi	Pelecaniformes: pelecanid (great white pelican)			Africa
C. imperialis	Charadriiformes: alcid (common murre)			Russia
C. jaenschi	Suliformes: phalacrocoracid (great cormorant)			Australia
C. obvelatus (syn. *C. alatus, argentinensis, diesingii, firlottei, papillosus, tanakai*)	Charadriiformes: alcid (common murre), larid (common gull, ring-billed gull, slender-billed gull, slaty-backed gull, black-headed gull, lesser black-headed gull, great black-backed gull, brown-backed gull, kelp gull, European herring gull, Mediterranean gull, Caspian gull, Vega gull, Audouin's gull, common tern, little tern, sandwich tern, gull-billed tern, black skimmer, black-legged kittihawk), scolopacid (sanderling, western willet, marbled godwit, Wilson's phalarope, lesser yellowlegs), stercocoriid (pomarine jaeger); Anseriformes: anatid (common eider); Ciconiiformes: ciconiid (wood stork); Gaviiformes: gaviid (common loon, black-throated loon, Pacific loon); Passeriformes: bombycillid (cedar waxwing); Pelecaniformes: ardeid (great egret, great blue heron), pelecanid (American white pelican, brown pelican), threskiornithid (roseate spoonbill); Podicipediformes: podicipedid (western grebe, horned grebe, great crested grebe, red-necked grebe, black-necked grebe); Sphenisciformes: spheniscid (southern rockhopper penguin, Magellanic penguin)	oesophagus, proventriculus	Amphipoda: gammarid (*Crangonyx laurentianus, Gammarus fasciatus*), hyalellid (*Hyalella azteca*); Malacostraca: mysid (opossum shrimp, *Neomysis americana*) [plus PH: Anguilliformes: anguillid (European eel); Atheriniformes: atherinid (bigscale sand smelt); Carangiformes: carangid (Atlantic horse mackerel); Clupeiformes: clupeid (twaite shad, Atlantic herring, European sprat), engraulid (European anchovy); Cypriniformes: cyprinid (goldfish, spottail shiner, creek chub, Danube bleak); Cyprinodontiformes: fundulid (mummichog); Gadiformes: merluccid (European hake); Gasterosteiformes: gasterosteid (three-spined stickleback, four-spined stickleback, nine-spined stickleback); Gobiiformes: gobiid (common goby, sand goby, monkey goby, round goby, grass goby); Labriformes: labrid (goldsinny wrasse); Mugiliformes: mugilid (so-iuy mullet); Osmeriformes: osmerid (rainbow smelt, European smelt); Perciformes: percid (ruffe, zander), sparid (two-banded seabream), zoarcid (viviparous eelpout); Pleuronectiformes: pleuronectid (European flounder), soleid (common sole); Salmoniformes:	worldwide

			salmonid (rainbow trout); Scorpaeniformes: cottid (shorthorn sculpin); Syngnathiformes: syngnathid (lesser pipefish); Trachiniformes: ammodytid (great sand eel); Sauria: lacterid (sand lizard); Serpentes: colubrid (dice snake)]	
C. pelecani	Pelecaniformes: pelecanid (Australian pelican)			Australia
C. podicipis	Podicipediformes: podicipedid (great crested grebe, black-necked grebe)			Asia
Dispharynx				
D. aduncus	Charadriiformes: larid (common gull, yellow-legged gull)			Europe
D. aegyptica (syn. *Acuaria*)	Pelecaniformes: ardeid (cattle egret)			Africa
D. affinis	Strigiformes: strigid (barn owl)			Americas
D. buteonis	Accipitriformes: accipitrid (roadside hawk)			South America
D. capitata	Accipitriformes: accipitrid (greater spotted eagle, tiny hawk)			Europe, Americas
D. emberizae	Passeriformes: sturnid (common mynah)			Asia
D. karachii	Accipitriformes: accipitrid (black kite)			India
D. laplantei	Passeriformes: corvid (Eurasian jay)			Eurasia
D. magnilabiata	Pelecaniformes: threskiornithid (roseate spoonbill)			South America
D. malvyae	Accipitriformes: accipitrid (black kite)			Africa
D. mathevossianae	Falconiformes: falconid (Eurasian kestrel)			Eurasia
D. nasuta (syn. *A. spiralis, D. spiralis*)	Galliformes: phasianid (chicken, greater prairie chicken, red junglefowl, turkey, peacock, Indian peafowl, ruffed grouse, hazel grouse, dusky grouse, sharp-tailed grouse, common quail, northern bobwhite quail, California quail, chukar, rock partridge, grey partridge, Barbary partridge, golden pheasant, ring-necked pheasant, Bianchi's pheasant), numidid (helmeted guineafowl), cracid (plain chachalaca); Accipitriformes: accipitrid (black kite, swallow-tailed kite, American kestrel); Anseriformes: anatid (garganey); Charadriiformes: charadriid (northern lapwing, killdeer, European golden plover), jacanid (African jacana), larid (slender-billed gull, Mediterranean gull, black-headed gull, common tern, sandwich tern, gull-billed tern); Columbiformes: columbid (pigeon, rock dove, common	proventriculus oesophagus, [weight loss, anaemia]	Malacostraca: armadillid (woodlouse, *Armadillidium vulgare, Cubaris*), porcellionid (woodlouse, *Porcellio fedtschencoi, laevis, scaber, Porcellionides pruinosus*), trachelipodid (woodlouse, *Hemilepistus pectinatus, reductus*)	worldwide

	ground dove, white-winged dove, mourning dove, Luzon bleeding-heart dove); Coraciiformes: coraciid (European roller); Cuculiformes: cuculid (smooth-billed ani); Falconiformes: falconid (kestrel hawk, Eurasian hobby); Gruiformes: gruid (whooping crane, sandhill crane); Passeriformes: acrocephalid (great reed warbler, Eurasian reed warbler), alaudid (Eurasian skylark), cardinalid (northern cardinal, rose-breasted grosbeak, black-faced grosbeak), corvid (blue jay, Florida scrub jay, Eurasian magpie, American crow, Cuban crow, carrion crow, fish crow, rook), emberizid (common reed bunting, red-headed bunting, yellow hammer), icterid (red-winged blackbird, common grackle, boat-tailed grackle, greater Antillean grackle, brown-headed cowbird), mimid (northern mockingbird, gray catbird), motacillid (tree pipit), oriolid (Eurasian golden oriole), parulid (prairie warbler, Blackburnian warbler, Tennessee warbler, grey-crowned yellowthroat), passerellid (eastern towhee), passerid (sparrow), polioptilid (trilling gnatwren), sturnid (common mynah, common starling, Caucasian starling, golden-breasted starling), thraupid (blue-gray tanager), troglodytid (Carolina wren), turdid (common blackbird, clay-coloured robin, American robin, red-throated thrush, eastern bluebird), tyrannid (least flycatcher); Piciformes: picid (red-bellied woodpecker, red-headed woodpecker, yellow-shafted flicker, yellow-bellied sapsucker, northern flicker); Psittaciformes: psittaculid (princess parrot, Alexandra's parrot); Rheiformes: rheid (greater rhea); Strigiformes: strigid (little owl, eastern screech owl, Eurasian scops owl)			
D. noctuae	Strigiformes: strigid (little owl)			Europe
D. pipilonis	Passeriformes: passerellid (red-eyed towhee)			North America
D. stonae	Passeriformes: troglodytid (Carolina wren)			North America
Echinuria				
E. australis	Anseriformes: anatid (Pacific black duck)			New Zealand
E. borealis	Anseriformes: anatid (long-tailed			Holarctic

	duck, surf scoter, common eider, king eider, ruddy shelduck)			
E. cincli	Passeriformes: cinclid (brown dipper)			Asia
E. gilsoni	Charadriiformes: scolopacid (ruff)	oesophagus		Africa
E. heterobrachiata	Charadriiformes: larid (little gull, slender-billed gull), scolopacid (western sandpiper)			North America
E. hypognatha	Anseriformes: anatid (common scoter, surf scoter)			North America
E. jugadornata	Anseriformes: anatid (duck)			
E. minor	Anseriformes: anatid (knob-billed duck)			Africa
E. pamirica (syn. *E. leiperi*)	Anseriformes: anatid (common shelduck, ruddy shelduck)			Eurasia
E. parva	Anseriformes: anatid (bufflehead, Canada goose)			North America
E. phoenicopteri	Phoenicoptiformes: phoenicopterid (greater flamingo)			Africa
E. skrjabiniana	Anseriformes: anatid (mute swan)	proventriculus		Asia
E. skrjabiniensis	Charadriiformes: scolopacid (dunlin, curlew sandpiper, white-rumped sandpiper, Baird's sandpiper, sanderling, little stint, Wilson's phalarope), recurvirostrid (pied avocet)			Eurasia, Americas
E. singhi	Anseriformes: anatid (common pochard)	proventriculus		India
E. squamata (syn. *Acuaria*)	Suliformes: phalacrocoracid (great cormorant)			Australia
E. uncinata (syn. *A. uncinata, E. querquedulae*)	Anseriformes: anatid (domestic duck, mallard, muscovy duck, ring-necked duck, falcated duck, spectacled duck, white-eyed duck, mottled duck, white-winged duck, yellow-billed duck, blue duck, tufted duck, harlequin duck, ruddy duck, American black duck, African black duck, Pacific black duck, Philippine duck, comb duck, wood duck, Hartlaub's duck, Mandarin duck, black-bellied whistling duck, white-faced whistling duck, fulvous whistling duck, West Indian whistling duck, gadwall, garganey, redhead, lesser scaup, greater scaup, common pochard, red-crested pochard, rosy-billed pochard, common shelduck, ruddy shelduck, canvasback, bufflehead, common eider, king eider, northern shoveler, northern pintail, white-cheeked pintail, yellow-billed pintail, ringed teal, blue-winged teal, cape teal, chestnut teal, cinnamon teal, silver teal, Eurasian teal, Eurasian wigeon, American wigeon, Chiloe wigeon, brant, common merganser, cotton pygmy goose, African pygmy goose, domestic	proventriculus, oesophagus [weight loss, anaemia]	Cladocera: daphniid (*Ceriodaphnia, Daphnia magna, pulex*, *Simocephalus vetulus*); Amphipoda: gammarid (*Gammarus*); Isopoda: asellid (*Asellus aquaticus*); Ostracoda: cypridid (*Heterocypris incongruens*); Branchiopoda: lynceid (*Lynceus brachyurus*)	Africa, Asia, Americas

	goose, greylag goose, red-breasted goose, greater white-fronted goose, bar-headed goose, snow goose, swan goose, barnacle goose, Canada goose, Hawaiian goose, Orinoco goose, Egyptian goose, emperor goose, brant, smew, black swan, trumpeter swan, black-necked swan, whooper swan, mute swan); Charadriiformes: larid (Pallas's gull), scolopacid (sanderling, semipalmated sandpiper, Baird's sandpiper, willet, ruff, marbled godwit, Wilson's phalarope, horned grebe, great crested grebe, red-necked grebe, black-necked grebe, little grebe)			
Subfamily Seuratiinae				
Streptocara				
S. californica (syn. *S. dogieli*)	Anseriformes: anatid (mallard, long-tailed duck, velvet scoter, surf scoter, white-winged scoter, greater scaup, common eider, canvasback, Burrow's goldeneye, common merganser, red-breasted merganser)			Eurasia, North America
S. cirrohamata (= *Ingliseria*)	Suliformes: phalacrocoracid (Kerguelen shag, Auckland shag)			sub-Antarctic islands
S. crassicauda (syn. *S. pectinifera*)	Anseriformes: anatid (domestic duck, mallard, muscovy duck, mottled duck, ruddy duck, ring-necked duck, long-tailed duck, tufted duck, harlequin duck, fulvous whistling duck, plumed whistling duck, common shelduck, ruddy shelduck, blue-winged teal, cinnamon teal, European teal, Baikal teal, lesser scaup, greater scaup, red-crested pochard, ferruginous pochard, northern shoveler, northern pintail, gadwall, garganey, canvasback, European wigeon, American wigeon, common eider, king eider, redhead, bufflehead, common goldeneye, Barrow's goldeneye, common merganser, red-breasted merganser, hooded merganser, common scoter, surf scoter, velvet scoter, white-winged scoter, black scoter, smew, greylag goose, Japanese goose, Hawaiian goose, swan goose, tundra swan, whooper swan, trumpeter swan); Charadriiformes: alcid (pigeon guillemot, common murre, razorbill, horned puffin), charadriid (Kentish plover, snowy plover, northern lapwing), haematopodid (Eurasian	gizzard	Malacostraca: gammarid (amphipod, *Gammarus lacustris, locusta, maeoticus, pulex, triacanthus, Rivulogammarus pulex*), hyalellid (amphipod, *Hyalella azteca*) [plus PH: Clupeiformes: clupeid (Brashnikow herring); Cypriniformes: cyprinid (crucian carp, lake minnow, common rudd, common roach, Albanian roach, common minnow), nemacheilid (stone loach); Gobiiformes: gobiid (monkey goby, round goby, grass goby); Salmoniformes: salmonid (brown trout); Serpentes: colubrid (dice snake)	worldwide

	oystercatcher), larid (common tern, gull-billed tern, sandwich tern, Caspian tern, slender-billed gull, little gull, black-headed gull, Thayer's gull, European herring gull), recurvirostrid (pied avocet, American avocet), scolopacid (common sandpiper, spotted sandpiper, wood sandpiper, Terek sandpiper, ruff, common greenshank, common redshank, ruddy turnstone); Ciconiiformes: ciconiid (great bittern); Falconiformes: falconid (peregrine falcon); Galliformes: phasianid (chicken, red junglefowl, chukar, see-see partridge, ring-necked pheasant, black grouse, sharp-tailed grouse), numidid (helmeted guineafowl); Gaviiformes: gaviid (common loon, black-throated loon, red-throated loon, Arctic loon); Gruiformes: rallid (Eurasian coot); Passeriformes: sturnid (common starling); Pelecaniformes: phalacrocoracid (great cormorant), Podicipediformes: podicipedid (western grebe, horned grebe, great crested grebe, red-necked grebe, black-necked grebe, little grebe, hoary-headed grebe, Australasian grebe); Procellariiformes: procellariid (Manx shearwater)			
S. formosensis (syn. *S. somateriae*)	Anseriformes: anatid (mallard, muscovy, ring-necked duck, long-tailed duck, tufted duck, ferruginous duck, bufflehead, greater scaup, common goldeneye, Barrow's goldeneye, common merganser, red-breasted merganser, hooded merganser, common eider, velvet scoter, surf scoter, white-winged scoter, black scoter); Gaviiformes: gaviid (common loon)			Eurasia
S. formosus	Gaviiformes: gaviid (common loon)			Asia
S. incognita	Anseriformes: anatid (mallard, ruddy duck, Barrow's goldeneye, swan goose, Japanese goose); Phoenicopteriformes: phoenicopterid (Chilean flamingo)	gizzard	water flea	Americas
S. indica	Galliformes: phasianid (chicken)			India
S. penihamata	Strigiformes: strigid (variable screech-owl, western barn owl, black-banded owl)	stomach		Americas
S. recta	Gaviiformes: gaviid (red-throated loon, black-throated loon); Podicipediformes: podicipedid			Holarctic, Australia

	(horned grebe, little grebe, great crested grebe, black-necked grebe, Japanese black-necked grebe, hoary-headed grebe, Australasian grebe)			
S. triaenucha (= *Synhimantus*)	Pelecaniformes: ardeid (great blue heron, American bittern)			Americas
S. tridentata (= *Paracuaria*)	Charadriiformes: larid (European herring gull)			Europe

Parasite morphology: Acuariid nematodes form 3 different types of morphological stages during their development: namely, eggs, larvae (4 consecutive stages encoded L1 to L4), and adult worms. The eggs are bound by smooth thick shells and are oval-elliptical in shape ranging in size from 22-65 x 17-50 µm but varying according to genus (e.g. *Echinuria* 28-37 x 17-23 µm, *Dispharynx* 22-42 x 17-26 µm, *Cosmocephalus* 31-40 x 18-22 µm, *Acuaria*, 40-65 x 27-50 µm, *Streptocara* 32-65 x 18-50 µm). The eggs are fully embryonated when laid and contain a first stage larva (L1). Freed L1 are elongate and cylindrical, measuring 165-260 µm long, with rounded heads containing an indistinct subterminal cephalic hook, a rhabditoid oesophagus, and long conical tails, sometimes terminating in a delicate mucron. L2 are transient stages formed in intermediate hosts, while L3 are persistent stages found in their haemocoels or coiled up in their tissues. L3 vary in size from 0.5-3.7 mm depending on the parasite species and their maturity. They have well-developed buccal capsules, 2 triangular pseudolabia, lateral alae, a bipartite oesophagus, and short conical tails that are unarmed or ornamented with cuticular processes (spines or tubercles). L4 are transient parasitic stages in birds and they have begun to develop characteristic anterior ornamentations and genital primordia. Adults are small-medium white worms with stout cylindrical filiform bodies measuring from 3-30 mm long. They are bound by tough cuticles with fine or well-developed transverse striations and some species have lateral alae (e.g. *Cosmocephalus*) and others have 2 rows of cuticular spines (e.g. *Echinuria*). The mouth opening is flattened laterally and has 2 large pseudolabia involving the whole cephalic surface. The worms, however, are easily recognised by the possession of anterior cuticular ornamentations in the form of longitudinal elevations (called cordons). In the subfamily Seuratiinae, the cordons are restricted to the cephalic region forming a collarette just posterior to the pseudolabia. The collarette may be interrupted dorsally and ventrally, or laterally, or take the form of continuous serrated ring (e.g. *Streptocara*). In the subfamily Acuariinae, the cordons are expanded on the cervical region but extending longitudinally down the body, sometimes up to 2/3rd the body length. They arise at the mouth between the 2 pseudolabia and extend posteriorly as 4 sublateral structures which may be straight (e.g. *Acuaria*), curved/sinuous (e.g. *Dispharynx*), recurrent (e.g. *Cosmocephalus*) or anastomosing (e.g. *Echinuria*). Each cordon forms a longitudinal canal (gutter) bound either by a single row of cuticular plates and an outer longitudinal ridge (e.g. *Cosmocephalus*) or 2 rows of rectangular plates (e.g. *Acuaria, Echinuria*) or one lamellar row and one mosaic (mamillated) row (e.g. *Dispharynx*). The buccal cavity is well-developed and often cylindrical and the oesophagus is clearly divided into an anterior muscular and a posterior glandular section. Adult worms are sexually dimorphic, with males being smaller than females (*Acuaria* 8-19 cf. 9-30 mm, *Cosmocephalus* 9-14 cf. 11-22 mm, *Dispharynx* 3-7 cf. 3-10 mm, *Echinuria* 4-13 cf. 10-21 mm, *Streptocara* 3-8 cf. 8-11 mm). Mature females are didelphic with 2 ovaries and uteri connecting to a common vulva located around the median or posterior body. They may have short rounded tails (in the case of *Streptocara*) but usually have long conical tails, sometimes with a terminal projection (in the case of *Cosmocephalus*). Female worms are oviparous and lay embryonated eggs that contain fully developed L1. Mature males have coiled tails with caudal alae varying in length and width (and a precloacal ridge in *Cosmocephalus*), 9-10 pairs of caudal papillae, and 2 spicules, often dissimilar (left spicule being long and slender, right spicule being short and curved).

Site of infection: Adult worms infect the upper alimentary tract of their avian definitive hosts, with many species being found in the gizzard (*Acuaria, Streptocara*), some in the proventriculus (*Dispharynx*) and oesophagus (*Cosmocephalus*), and a few extending from the oesophagus to the small intestines (*Echinuria*). Larval stages develop in the haemocoel or tissues of invertebrate intermediate hosts (aquatic and terrestrial arthropods), and are sometimes carried in the tissues of small vertebrate paratenic hosts (amphibians, fish).

Pathogenesis: Most infections are light and remain subclinical, but heavy infections may cause morbidity and mortality in both wild and domestic birds. The severity of disease depends on parasite virulence (some species very pathogenic), host susceptibility (young birds most susceptible), the intensity of infection (numbers of parasites) and the stage of infection (with chronic disease development often following seasonal breeding). Adult worms feed on host tissues and blood and are found tunnelling or with their heads embedded in the mucosa, those in the gizzard being found under the koilin (tough keratinized layer) but sometimes penetrating to muscle layers. The parasites cause local tissue trauma, petechial haemorrhages, catarrhal inflammation, mucosal hypertrophy and thickening, oedema and nodule formation (soft yellow-red nodules). Worms become almost covered by proliferative tissue, the organ lumen becomes significantly narrowed, and lesions are predisposed to secondary bacterial infections, abscess formation, and sometimes granulomas. The keratinized layer of the gizzard may be progressively destroyed, sometimes resulting in organ rupture. Numerous parasite species have been associated with oesophagitis, proventriculitis and emaciation, especially in waterfowl. Clinical signs include listless, weakness, dysphagia, diarrhoea, dyspnoea, anaemia, untidy plumage, awkward gait, inability to fly, anorexia, reduced growth, weight loss, emaciation and death.

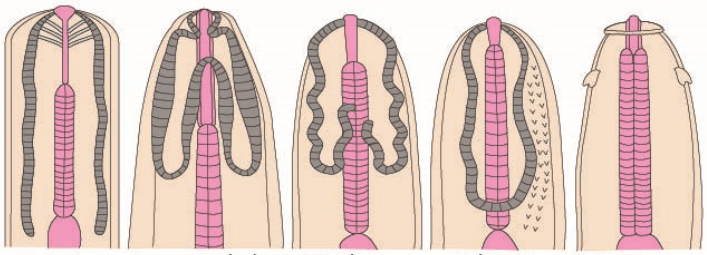
Developmental cycle and mode of transmission: Acuariid worms have indirect heteroxenous life-cycles involving the formation of adult worms in avian definitive hosts and larval development in invertebrate intermediate hosts. Infections have become well adapted to hosts occupying aquatic or terrestrial habitats, with parasites in sea and wetland birds (ducks, gulls, petrels, waders, herons, grebes, fishers, pelicans) developing in aquatic crustaceans (cladocerans, amphipods, ostracods, fiddler crabs), and those in terrestrial birds (mostly insectivorous passerines, birds of prey, some galliforms) developing in terrestrial arthropods (grasshoppers, beetles, diplopods, isopods, weevils, earwigs). Parasite species vary considerably in their host range and specificity, but many appear to stenoxenous and infect numerous closely-related host species. Gravid female worms lay embryonated eggs which are excreted with host faeces into the external environment where they may survive for 2-3 months (most susceptible to dessication and solar radiation). Eggs ingested by invertebrate intermediate hosts hatch in the gut releasing L1 which invade the haemocoel and moult twice to form L3 within 9-40 days. Infective L3 may remain free in the haemocoel or encapsulate in host tissues where they may survive for long periods (facilitating over-wintering in some arthropods). Studies have also shown that the L3 of some species may be transferred to small arthropod-eating vertebrates (fish, frogs) where they re-encapsulate in the intestines or mesenteries without further development. These vertebrates thus act as paratenic (transport) hosts, particularly for parasites infecting fish- or frog-eating final hosts. Birds therefore become infected when they consume L3 contained within intermediate or paratenic hosts. Ingested L3 do not undertake any somatic or extra-intestinal migration, but develop directly in the alimentary tract through 2 moults to adult worms, often in the proventriculus before moving to the oesophagus or gizzard. The prepatent period (time from infection to first egg excretion) generally ranged from 30-50 days, although that for some *Streptocara* spp. was as short as 9 days. Adult worms are thought to have short lifespans, living only for several months or seasons.

Differential diagnosis: Infections do not present with any distinctive clinical signs, but generally involve malaise and emaciation. The diagnosis of infections therefore relies on the direct detection of parasites, either worm eggs in faecal samples collected antemortem, or adult worms in tissue samples taken at necropsy. Eggs are best concentrated from faecal samples by floatation in heavy metal salt solutions with high specific gravities, but their identification by morphometrics is difficult as many acuariid genera and species produce eggs similar in size and appearance. Adult worms are best detected by close visual examination of the mucosal surface after rinsing off excess mucus and teasing apart nodular lesions. Modern molecular biological techniques have recently been used to explore parasite phylogenetic relationships by polymerase chain reaction (PCR) amplification and sequencing nuclear genes (predominantly 28S ribosomal RNA).

Treatment and control: While few detailed chemotherapeutic studies have been conducted, clinical infections by several species in domestic birds have responded reasonably well to treatment with several anthelmintics, including benzimidazoles (mebendazole) and macrocyclic lactones (ivermectin, moxidectin), but there are frequent reports of poor responses to other conventional anthelmintics. Preventive measures in farmed and aviary birds have included improved sanitation (removal and disposal of faeces), better hygiene (regular cleaning of holding facilities, providing clean food and water), vector control (using exclusion screens, barriers and possibly some surface insecticides) and bird management (preventing foraging, grazing or access to open pastures or pools). Note that the indiscriminate use of insecticides in the general environment is not encouraged, and may even be illegal, due to many concerns about their toxic impacts on ecosystem health.

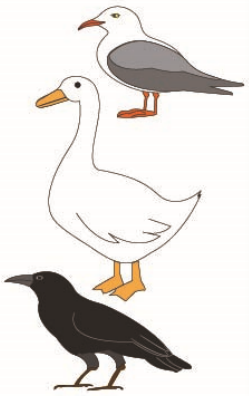
Acuariid nematodes

heads



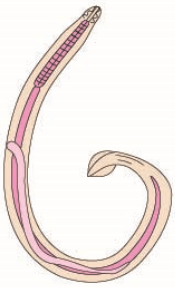
Acuaria *Cosmocephalus* *Dispharynx* *Echinuria* *Streptocara*

oesophagus, proventriculus, gizzard (nodules, inflammation, emaciation)

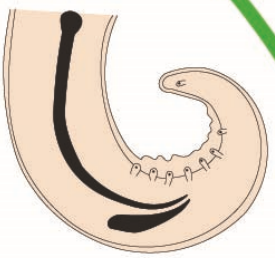


Definitive Hosts (terrestrial and aquatic birds)

adult female (~ 20 mm)



adult male (~ 10mm)

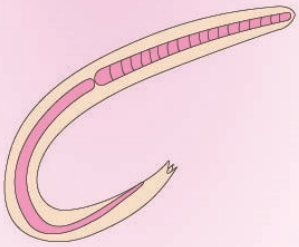


male tail

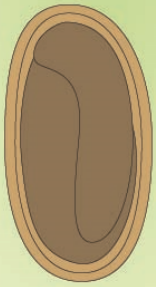
eggs excreted in faeces

PH/IH/L3 ingested

L3 encapsulate in PH



third-stage larvae (L3) (~ 2 mm)



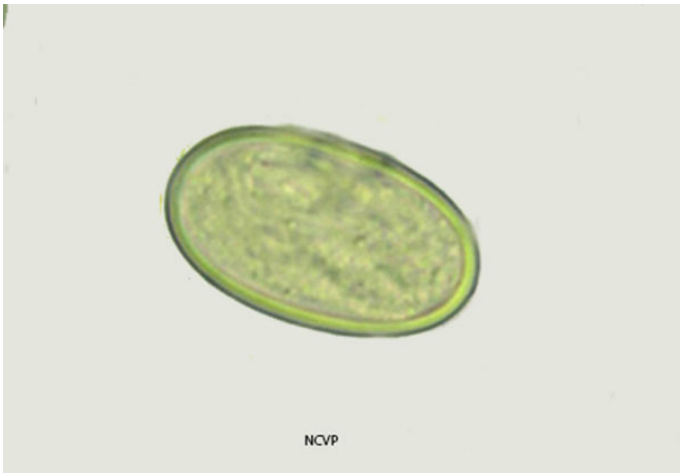
eggs (~ 50 µm)

Paratenic Hosts (IH) (amphibians, fish) (intestines, mesenteries)

eggs ingested by IH

Intermediate Hosts (IH) (terrestrial insects, aquatic crustaceans) (haemocoel, tissues)

Acuaria adult worm



Dispharynx worm egg

Cosmocephalus adult worm, head

Dispharynx adult worm, head