

Camallanus

(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 camallanoids with well-developed buccal capsules (many containing two sclerotized valves) found in the intestines of fishes, amphibians and reptiles. Infections by *Camallanus* spp. are commonly found in the intestines of freshwater ornamental fish, red worms sometimes protruding from the anus.

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: Camallanoidea (conspicuous phasmids, L1 with dorsal prominence/tooth, ovoviviparous, L1-L3 in copepod)
Family: Camallanidae (buccal capsule well-developed, with pair sclerotized valves, male with caudal alae)
Genus: *Camallanus* (parasitic in intestines of fish)
Species: various species cause enteritis in fish

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)]
<i>Incertae sedis</i> 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). Two camallaninid superfamilies are recognised: Camallanoidea (buccal cavity well-developed, tiny internal labial papillae, gut parasites); and Dracunculoidea (buccal cavity weakly-developed, prominent internal labial papillae, tissue parasites).

The superfamily Camallanoidea contains small red nematodes with large buccal capsules (often orange in colour). They are gastrointestinal parasites of predaceous lower vertebrates (fish, amphibians and reptiles) usually within aquatic habitats (freshwater, estuarine or marine). Female worms are viviparous and birth live larvae (L1) which are released into the water column. Most species have indirect heteroxenous life-cycles involving larval development in crustacean intermediate hosts (copepods), although some species may utilize paratenic hosts (usually planktivorous fish) and a few species have been found to have direct homoxenous cycles with final hosts ingesting free-living larvae. Numerous genera have been described in the single family Camallinidae, principally on the basis of morphological differences in the prominent buccal capsule. However, it was recently noticed that buccal capsule morphology varied within several species, with male and female worms of the same species having different buccal structures. This led to several taxonomic revisions whereby many genera were synonymized and others were demoted to subgeneric status. At present, 12 genera are currently recognised in 3 subfamilies: Procammallaninae with rounded buccal capsules (*Batrachocomallanus*, *Malayocomallanus*, *Onchocomallanus*, *Platocomallanus*, *Procammallanus* (syn. *Indocomallanus*) (incl. subgenera *Denticammallanus*, *Isospiculus*, *Monospiculus*, *Procammallanus* (syn. *Spirocotyle*), *Punctocomallanus*, *Spirocammallanoides*, *Spirocammallanus*)); Camallaninae with buccal capsules divided by lateral valves into large anterior chamber and minute posterior chamber (*Camallanides*, *Camallanus* (incl. subgenera *Camallanus*, *Zeylanema*) *Neocammallanus* (syn. *Neozeylanema*), *Neoparacammallanus*,

Oncophora (syn. *Piscilania*), *Serpinema*); and Paracamallaninae with buccal capsules divided by lateral valves into anterior and posterior chambers almost equal in depth (*Paracamallanus* (incl subgenera *Paracamallanus*, *Dentocamallanus*)). The genus *Camallanus* is characterised by the possession of buccal capsules divided into 2 chambers by a pair of sclerotized valves (the second chamber being very small). The dorsoventral margins of the buccal capsule also have 3 posteriorly-directed rods (tridents) on each side. Over 110 species have been described, mostly in predatory fish, but some in amphibians and reptiles (esp. turtles). Many species are euryxenous and have a broad host range, although a few species appear to be stenoxenous or oioxenous and restricted to a few closely-related host species. Infections frequently occur in freshwater ornamental fish and are clearly evident when red adult worms protrude from the anus of their hosts.

<i>Camallanus</i> species	Definitive Hosts	Location	Intermediate Hosts [Paratenic Hosts (PH)]	Distribution
<i>C. acaudatus</i>	Osteoglossiformes: osteoglossid (silver arowana)	intestines		South America
<i>C. alatae</i>	Anura: dicroglossid (Indian bullfrog)			India
<i>C. alii</i>	Cypriniformes: cyprinid (mud carp)	intestines		Asia
<i>C. amazonicus</i> (syn. <i>Serpinema</i>)	Testudines: kinosternid (scorpion mud turtle), podocnemidid (Arrau turtle)	intestines		South America
<i>C. anabantis</i> (anabantus) (syn. <i>Zeylanema</i>)	Anabantiformes: anabantid (climbing perch), channid (dwarf snakehead, spotted snakehead), osphronemid (Howong betta, three-spot gourami); Cypriniformes: cyprinid (filament barb, slender rasbora); Siluriformes: clariid (walking catfish); Synbranchiformes: mastacembelid (zig-zag eel)	intestines, caeca	Copepoda: cyclopid (<i>Mesocyclops leuckarti</i>)	Asia
<i>C. ancylodirus</i>	Cypriniformes: catostomatid (quillback); Perciformes: centrarchid (green sunfish, bluegill); Gadiformes: lotid (burbot)			North America
<i>C. aotea</i>	Perciformes: emmelichthyid (bigscale rubyfish); Scombriformes: scombrid (yellowfin tuna, bigeye tuna)			worldwide
<i>C. atridentus</i>	Anabantiformes: channid (spotted snakehead)			India
<i>C. atropusi</i>	Carangiformes: carangid (cleftbelly trevally)	intestines		Indo-Pacific
<i>C. aurangabadensis</i>	Anabantiformes: channid (striped snakehead)	intestines		India
<i>C. bahli</i> (syn. <i>Neozeylanema</i>)	Anabantiformes: anabantid (climbing perch)			Asia
<i>C. barilii</i>	Cypriniformes: cyprinid (trout barb)			India
<i>C. barragi</i> (syn. <i>Zeylanema</i>)	Synbranchiformes: mastacembelid (zig-zag eel)			
<i>C. baylisi</i>	Anura: bufonid (European green toad), dicroglossid (Indian bullfrog)			Eurasia
<i>C. beveridgei</i>	Testudines: chelid (northern snapping turtle)	intestines		Australia
<i>C. bispiculus</i>	Clupeiformes: chirocentrid (dorab wolf-herring); Anguilliformes: anguillid (European eel)	intestines		Indo-Pacific
<i>C. boomkeri</i>	Anabantiformes: channid (Ceylon snakehead)	swim bladder		Asia
<i>C. bufonis</i>	Anura: bufonid (toad)			
<i>C. cancelai</i> (<i>cancelai</i>)	Beloniformes: belonid (freshwater garfish)			Asia
<i>C. carangis</i> (syn. <i>C. paracarangis</i>)	Carangiformes: carangid (yellowtail scad, trevally); Scorpaeniformes: platycephalid (fringe-eye flathead); Perciformes: serranid (honeycomb grouper), leiognathid (toothpony, pony-fish), priacanthid (glasseye), trichiurid (largehead hairtail), terapontid (spiny-cheeked grunter), nemipterid (fork-tailed threadfin bream), mullid (yellow-striped goatfish, white-saddle goatfish); Scombriformes: scombrid (chub mackerel); Siluriformes: ariid (veined catfish)	intestines		Indo-Pacific

<i>C. ceylonensis</i> (syn. <i>Neoparacamallanus</i>)	Siluriformes: silurid (helicopter catfish)			Asia
<i>C. charsaddiensis</i>	Anabantiformes: channid (dwarf snakehead)			Asia
<i>C. chauhani</i>	Perciformes: trichiurid (smallhead hairtail)	intestines		Indo-Pacific
<i>C. chiralensis</i> (syn. <i>Zeylanema</i>)	Anabantiformes: channid (spotted snakehead)	intestines		India
<i>C. chelonius</i> (syn. <i>Serpinema</i> , <i>C. nithoggi</i>)	Testudines: pelomedusid (serrated hinged terrapin), chelid (broad-shelled river turtle, saw-shelled turtle, Krefft's turtle)	intestines		Africa, Australia
<i>C. chorinemi</i>	Carangiformes: carangid (double-spotted queenfish, barred queenfish); Clupeiformes: chirocentrid (dorab wolf-herring)			Indo-Pacific
<i>C. cinereusis</i>	Anguilliformes: muraenesocid (daggertooth pike conger)			worldwide
<i>C. corderoi</i>	Osmeriformes: galaxiid (peladilla, puye, tolo, common galaxias); Atheriniformes: atherinopsid (Chilean silverside, Patagonian freshwater pejerrey); Characiformes: characid (pocha); Salmoniformes: salmonid (rainbow trout, brown trout, brook trout); Perciformes: percichthyid (largemouth perch, Creole perch)			Americas
<i>C. cotti</i> (syn. <i>C. fotedari</i>)	Cyprinodontiformes: poeciliid (rainbow fish, shortfin molly, green swordtail, southern platyfish), nothobranchiid (blue lyretail); Cypriniformes: cyprinid (predatory carp, zebrafish, yellowcheek, Mongolian redbfin, sharpbelly, minnow, white Amur bream, barbel chub, pale chub, common snow trout), nemacheilid (Kashmiri kobertrulling); Gobiiformes: oxudercid (scribbled goby, Hawaii freshwater goby, Naniha goby), eleotrid (Hawaii sleeper); Siluriformes: sisorid (devil catfish), bagrid (Korean bullhead); Scorpaeniformes: cottid (utsusemi); Anabantiformes: osphronemid (paradise fish, paradise gourami), channid (northern snakehead); Salmoniformes: salmonid (masu salmon); Perciformes: percid (European perch), polynemid (Indian threadfin); Centrarchiformes: percichthyid (mandarin fish); Myliobatiformes: potamotrygonid (freshwater stingray)	intestines	Copepoda: cyclopid (<i>Macrocylops albidus</i> , <i>Cyclops</i>)	Eurasia, Africa
<i>C. ctenopomae</i>	Perciformes: anabantid (tailspot ctenopoma)			Africa
<i>C. cynophlyectis</i>	Anura: microglossid (skittering frog)			India
<i>C. dimitrovi</i>	Anura: alytid (painted frog)			Europe
<i>C. dollfusi</i>	Perciformes: trichiurid (ribbonfish, largehead hairtail); Pleuronectiformes: soleid (elongated sole)	intestines		Indo-Pacific
<i>C. emydidius</i>	Testudines: emydid (black-bellied slider)	intestines		South America
<i>C. equispiculus</i> (syn. <i>Neoparacamallanus</i>)	Siluriformes: heteropneustid (Asian stinging catfish)			Asia
<i>C. farooqii</i>	Perciformes: sciaenid (sin croaker), haemulid (saddle grunt); Carangiformes: carangid (giant queenfish, double-spotted queenfish, needle-scaled queenfish)			Indo-Pacific
<i>C. fernandoi</i>	Anabantiformes: channid (spotted snakehead, snakehead murrel)			India
<i>C. gibsonia</i>	Anabantiformes: channid (snakehead murrel)			India
<i>C. gomtii</i>	Anabantiformes: channid (spotted snakehead)			India
<i>C. guptae</i>	Siluriformes: ariid (veined catfish);	intestines		Indo-Pacific

	Perciformes: trichiurid (smallhead hairtail)			
<i>C. guttatii</i>	Scombriformes: scombrid (Indo-Pacific king mackerel)			Indo-Pacific
<i>C. hampalae</i>	Cypriniformes: cyprinid (hampala barb)			Asia
<i>C. hypophthalmichthys</i>	Cypriniformes: cyprinid (bighead carp, silver carp, black carp)	intestines	Copepoda: cyclopid (<i>Mesocyclops leuckarti</i>)	Asia
<i>C. indicus</i>	Anura: dicroglossid (skittering frog); Carangiformes: carangid (barred queenfish)			Indo-Pacific
<i>C. inglisi</i>	Anura: dicroglossid (Indian bullfrog)			India
<i>C. intermedius</i> (syn. <i>Serpinema</i>)	Testudines: geomydid (Chinese pond turtle)			Asia
<i>C. intestinalus</i>	Anabantiformes: channid (spotted snakehead, snakehead murrel)			Asia
<i>C. jadhavae</i>	Anabantiformes: channid (spotted snakehead)	intestines		India
<i>C. jiyuensis</i>	Gobiiformes: oxudercid (shokihaze goby)	intestines		China
<i>C. jodhpurensis</i>	Anura: dicroglossid (skittering frog)			India
<i>C. jullundurensis</i>	Synbranchiformes: mastacembelid (zig-zag eel)			Asia
<i>C. kaapstaadi</i>	Anura: pipid (African clawed frog, Lake Victoria clawed frog, DeWitte's clawed frog, Marsabit clawed frog, Fraser's plantanna, Muller's plantanna)			Africa
<i>C. kachugae</i> (syn. <i>Serpinema</i>)	Testudines: geomydid (brown roofed turtle), kinosternid (scorpion mud turtle)			Asia, South America
<i>C. karachiensis</i>	Scombriformes: scombrid (Indian mackerel)			Asia
<i>C. khalili</i>	Cypriniformes: cyprinid (common snowtrout); Osteoglossiformes: notopterid (bronze featherback)			India
<i>C. kherai</i>	Anabantiformes: channid (spotted snakehead)			India
<i>C. kirandensis</i>	Rhinopristiformes: pristid (saw fish); Cypriniformes: cyprinid (barbel, rednose labeo, Nile carp)			Africa
<i>C. kollerensis</i>	Anabantiformes: channid (spotted snakehead), anabantid (climbing perch)			India
<i>C. kulasirii</i> (syn. <i>Zeylanema</i>)	Anabantiformes: channid (spotted snakehead)			India
<i>C. kumaoni</i>	Cypriniformes: cyprinid (korang, stoneroller)			India
<i>C. lacustris</i> (syn. <i>Echinorhynchus</i>)	Cypriniformes: cyprinid (common carp, sabre carp, common roach, common bream, white bream, vimba bream, common bleak, common dace, common minnow, Marmara chub, tench, rudd, zope, asp, ide); Perciformes: percid (European perch, ruffe, Eurasian ruffe, zander, Volga zander, common zingel); Anguilliformes: anguillid (European eel); Cichliformes: cichlid (bay snook, firemouth cichlid, blackgullet cichlid); Salmoniformes: salmonid (masu salmon, Atlantic salmon, grayling, rainbow trout, brown trout, Arctic char, European cisco, common whitefish, northern whitefish, Siberian taimen, beloribitsa); Scorpaeniformes: cottid (European bullhead, alpine bullhead, fourhorn sculpin); Esociformes: esocid (northern pike); Gasterosteiformes: gasterosteid (three-spined stickleback, nine-spine stickleback); Gobiiformes: gobiid (bighead goby, sand goby, tubenose goby); Gadiformes: lotid (burbot); Osmeriformes: osmerid (European smelt); Siluriformes: silurid (Wels catfish); Pleuronectiformes: pleuronectid (European	intestines	Copepoda: cyclopid (<i>Megacyclops viridis</i> , <i>Macrocyclus albidus</i> , <i>Acanthocyclops vernalis</i> , <i>Mesocyclops leuckarti</i> , <i>Eucyclops serrulatus</i> , <i>Cyclops strenuus</i> , <i>quadricornis</i>), canthocamptid (<i>Canthocamptus staphylinus</i>) [plus PH: nonpredatory cyprinids, cobitids]	worldwide

	flounder), scophthalmid (turbot); Acipenseriformes: acipenserid (dwarf sturgeon); Serpentes: colubrid (dice snake)			
<i>C. lissemysus</i> (syn. <i>Serpinema</i>)	Testudines: trionychid (Indian flapshell turtle)			India
<i>C. longicaudatus</i>	Cypriniformes: cyprinid (Assuan labeo)			Africa
<i>C. longitridentatus</i> (syn. <i>Neoparacamallanus</i>)	Siluriformes: clariid (walking catfish)	intestines		Asia
<i>C. luchnowensis</i>	Anabantiformes: channid (striped snakehead)			India
<i>C. macrocephalus</i>	Anura: pipid (Marsabit clawed frog)			Africa
<i>C. maculatus</i>	Cyprinodontiformes: poeciliid (southern platyfish)			South America
<i>C. magathi</i> (syn. <i>Serpinema</i> , <i>C. parvus</i>)	Testudines: kinosternid (Mexican mud turtle)	intestines		Americas
<i>C. magna</i> (<i>magnus</i>) (syn. <i>Zeylanema</i> , <i>Paracamallanus</i>)	Synbranchiformes: mastacembelid (barred spiny eel, zig-zag eel)			Asia
<i>C. magnavaginus</i> (syn. <i>C. cinereusis</i>)	Anguilliformes: muraenesocid (daggertooth pike conger)			Asia
<i>C. magnorugosus</i>	Testudines: emydid (ornate slider)			North America
<i>C. marinus</i>	Carangiformes: carangid (yellowtail scad, white-tipped mackerel scad, oxeye scad); Scombriformes: nomeid (cubehead), scombrid (narrow-barred Spanish mackerel); Scorpaeniformes: platycephalid (fringe-eye flathead); Perciformes: leiognathid (toothpony), trichiurid (largehead hairtail)	intestines		Indo-Pacific
<i>C. mastacembeli</i> (syn. <i>Zeylanema</i>)	Synbranchiformes: mastacembelid (zig-zag eel)			Asia
<i>C. melanocephalus</i>	Scombriformes: scombrid (bluefin tuna, bullet tuna, Atlantic bonito, Atlantic chub mackerel)			Atlantic
<i>C. microcephalus</i> (syn. <i>Serpinema</i>)	Testudines: geomydid (Caspian turtle), emydid (pond slider, painted turtle, map turtle, Blanding's turtle), chelydrid (snapping turtle)	stomach, intestines		North America, Europe
<i>C. monospiculatus</i> (syn. <i>Serpinema</i>)	Testudines: chelid (common toad-headed turtle, tuberculate toad-headed turtle, Geoffroy's toad-headed turtle)			South America
<i>C. moraveci</i>	Cyprinodontiformes: poeciliid (millionfish); Cichliformes: cichlid (freshwater angelfish)			South America
<i>C. mujibia</i> (syn. <i>Zeylanema</i>)	Anura: microglossid (skittering frog)			Asia
<i>C. multilineatus</i>	Cypriniformes: catostomid (highfin carpsucker)			Asia
<i>C. multiruga</i>	Anura: ranid (West African frog)	intestines		Africa
<i>C. mustelus</i>	Carcharhiniformes: triakid (smooth-hound)			Pacific
<i>C. myopsi</i>	Aulopiformes: synodontid (bluntnose lizardfish)			Atlantic
<i>C. nandai</i>	Anabantiformes: nanid (Gangetic leaf-fish)			Asia
<i>C. nigrescens</i>	Anura: microglossid (green pond frog)	intestines		Europe
<i>C. nigriscens</i>	Testudines: geomydid (Indian roofed turtle)			India
<i>C. nodulosus</i>	Anura: microglossid (skittering frog)			Asia
<i>C. octorugatus</i> (syn. <i>Serpinema</i>)	Testudines: geoemydid (Amboina box turtle)	intestines		Asia
<i>C. ophichthi</i>	Anguilliformes: ophichthid (rice paddy eel)	intestines		Asia
<i>C. ophiocephali</i> (<i>ophicepahli</i>) (syn. <i>Neocamallanus</i> , <i>C. adamsi</i>)	Anabantiformes: channid (snakehead murrel, striped snakehead, spotted snakehead, bullseye snakehead); Siluriformes: silurid (helicopter catfish)	intestines	Copepoda: cyclopid (<i>Mesocyclops leuckarti</i> , <i>Thermocyclops</i>)	India

			<i>crassus</i>)	
<i>C. oxycephalus</i>	Perciformes: moronid (white bass), percid (yellow perch, common logperch, walleye, scaly sand darter, Iowa darter), centrarchid (small-mouth bass, large-mouth bass, rock bass, spotted bass, redbreast sunfish, green sunfish, long-ear sunfish, red-ear sunfish, red-spotted sunfish, spotted sunfish, pumpkinseed, warmouth, bluegill, black crappie), sciaenid (freshwater drum); Cypriniformes: cyprinid (spotfin shiner, emerald shiner, golden shiner), catostomid (quillback); Cyprinodontiformes: fundulid (banded killifish); Osmeriformes: osmerid (rainbow smelt); Clupeiformes: clupeid (alewife); Amiiformes: amiid (bowfin); Characiformes: characid (Mexican tetra); Cichliformes: cichlid (Texas cichlid); Esociformes: esocid (northern pike); Siluriformes: ictalurid (blue catfish); Gadiformes: lotid (burbot); Salmoniformes: salmonid (coho salmon, sock-eye salmon)	intestines	Copepoda: cyclopid (<i>Cyclops bicuspidatus, vernalis</i>) [plus PH: Cypriniformes: cyprinid (spotfin shiner, emerald shiner); Osmeriformes: osmerid (rainbow smelt); Perciformes: sciaenid (freshwater drum); Clupeiformes: clupeid (alewife)]	North America
<i>C. oxygasterae</i>	Cypriniformes: cyprinid (large razorbelly minnow)			North America, India
<i>C. papillifer</i>	Acipenseriformes: acipenserid (European sturgeon)			Europe
<i>C. patani</i>	Synbranchiformes: mastacembelid (zig-zag eel)			Asia
<i>C. pearsei</i> (syn. <i>Zeylanema</i>)	Anabantiformes: anabantid (climbing perch), channid (dwarf snakehead, striped snakehead); Cypriniformes: cyprinid (slender rasbora)			Asia
<i>C. pentkoti</i>	Clupeiformes: chirocentrid (dorab wolf-herring); Perciformes: sparid (gold-lined seabream), mullid (ubakan); Aulopiformes: synodontid (bluntnose lizardfish);	intestines		Indo-Pacific
<i>C. pernandoi</i>	Anabantiformes: channid (spotted snakehead)			Asia
<i>C. polyodontis</i>	Acipenseriformes: polyodontid (American paddlefish)			North America
<i>C. polypteri</i>	Siluriformes: clariid (mudfish), mochokid (wahrindi); Polypteriformes: polypterid (Nile bichir)			Africa
<i>C. prashadi</i>	Anura: dicroglossid (Indian bullfrog)	intestines		India
<i>C. praveeni</i>	Cypriniformes: cyprinid (ticto barb)	ovary		India
<i>C. psettodi</i>	Pleuronectiformes: psettodid (Indian halibut)			India
<i>C. puriensis</i>	Siluriformes: ariid (veined catfish)	intestines		Asia
<i>C. qadrii</i>	Perciformes: sciaenid (black-spotted croaker)			Indo-Pacific
<i>C. ranae</i>	Anura: dicroglossid (skittering frog, Indian bullfrog)			Asia
<i>C. salmonae</i>	Salmoniformes: salmonid (salmon)			India
<i>C. satyapali</i>	Cypriniformes: cyprinid (vagra baril)			India
<i>C. sauridai</i>	Synbranchiformes: mastacembelid (zig-zag eel)	intestines		India
<i>C. scabrae</i>	Testudines: dermatemydid (hickatee)			South America
<i>C. siluranae</i>	Anura: pipid (western clawed frog)			Africa
<i>C. spinosa</i> (syn. <i>Zeylanema</i>)	Anabantiformes: osphronemid (spotted betta)	intestines		Malaya
<i>C. sprenti</i>	Testudines: chelid (saw-shelled turtle, Krefft's turtle)	intestines		Australia
<i>C. surmai</i> (syn. <i>C. goaensis</i>)	Scombriformes: scombrid (Indo-Pacific king mackerel)			Indo-Pacific
<i>C. sweeti</i>	Anabantiformes: channid (spotted snakehead,	intestines	Copepoda: cyclopid	Asia

(syn. <i>Paracamallanus</i>)	dwarf snakehead), anabantid (climbing perch)		(<i>Mesocyclops leuckarti</i> , <i>hyalinus</i>) [plus PH: Cypriniformes: cobitid (spotted loach), cyprinid (redside barb, twospot barb); Cyprinodontiformes: poeciliid (gambusia)]	
<i>C. testudineusi</i>	Anabantiformes: anabantid (climbing perch)			Asia
<i>C. thapar</i>	Anura: dicroglossid (Indian bullfrog)			Asia
<i>C. thaparus</i>	Anabantiformes: channid (snakehead murrel)			Asia
<i>C. therapsi</i>	Centrarchiformes: terapontid (large-scaled terapon)	intestines		Indo-Pacific
<i>C. tholukodensis</i>	Siluriformes: bagrid (Gangetic mystus)			India
<i>C. tigrinis</i>	Anura: dicroglossid (Indian bullfrog)			Asia
<i>C. trichiuris</i> (<i>trichiurusi</i>)	Perciformes: trichiurid (largehead hairtail, smallhead hairtail); Siluriformes: ariid (veined catfish)	intestines		Indo-Pacific
<i>C. tridentatus</i> (syn. <i>Cucullanus</i>)	Osteoglossiformes: osteoglossid (silver arowana), arapinnid (pirarucu); Perciformes: percichthyid (large-mouth perch, creole perch); Salmoniformes: salmonid (rainbow trout, brook trout)			Americas
<i>C. trispinosus</i> (syn. <i>Serpinema trisponosum</i>)	Testudines: emydid (red-eared slider, pond slider, painted turtle), chelydrid (snapping turtle)	stomach, intestines	[plus PH: Gastropoda: lymnaeid (<i>Lymnaea stagnalis</i>)]	North America
<i>C. truncatus</i> (syn. <i>Cucullanus</i>)	Perciformes: percid (common perch, yellow perch, European perch, ruffe, striped ruffe, Eurasian ruffe, European chub, ide, zander, Volga zander, zingel); Cypriniformes: cyprinid (sabre carp, common bream, gudgeon, white-finned gudgeon, asp); Gadiformes: lotid (burbot); Salmoniformes: salmonid (European whitefish); Scorpaeniformes: cottid (European bullhead); Esociformes: esocid (northern pike); Siluriformes: bagrid (mystus), silurid (wels catfish); Osmeriformes: osmerid (European smelt); Pleuronectiformes: pleuronectid (flounder); Salmoniformes: salmonid (Atlantic salmon, Arctic char, brown trout); Anguilliformes: anguillid (European eel)		Copepoda: cyclopid (<i>Mesocyclops leuckarti</i> , <i>Acanthocyclops viridis</i> , <i>Macrocyclus albidus</i> , <i>Cyclops strenuus</i> , <i>Megacyclus viridis</i>) [plus PH: amphibians, fish]	Eurasia
<i>C. tuckeri</i>	Testudines: chelid (northern red-faced turtle, sandstone snake-necked turtle)	intestines		Australia
<i>C. undulatus</i> (syn. <i>Serpinema</i> , <i>C. viviparus</i>)	Testudines: geoemydid (Chinese pond turtle)	intestines		Asia
<i>C. unispiculus</i>	Synbranchiformes: mastacembelid (zig-zag eel); Anura: dicroglossid (skittering frog)			Asia
<i>C. vachaii</i>	Siluriformes: schilbeid (schilbid catfish)			Asia
<i>C. varanasiensis</i>	Siluriformes: bagrid (rita)			Asia
<i>C. viastimili</i>	Anura: dicroglossid (skittering frog)			Asia
<i>C. waelhreow</i>	Testudines: chelid (eastern short-necked turtle, broad-shelled river turtle, Krefft's turtle)	intestines		Australia
<i>C. xenentodoni</i> (syn. <i>C. cancelai</i>)	Beloniformes: belonid (freshwater garfish); Synbranchiformes: mastacembelid (lesser spiny eel)		Copepoda: cyclopid (<i>Mesocyclops crassus</i> , <i>leuckarti</i>)	Asia
<i>C. xenopodis</i> (syn. <i>Procamallanus</i> , <i>Spirocamallanus</i>)	Anura: pipid (African clawed toad, Marsabit clawed frog)	stomach	Copepoda: cyclopid (<i>Thermocyclops infrequens</i> , <i>Mesocyclops leuckarti</i>)	Africa

<i>C. yehi</i>	Anabantiformes: channid (striped snakehead)	intestines		Asia
<i>C. zacconis</i>	Cypriniformes: cyprinid (dark chub); Anguilliformes: anguillid (Japanese eel)		Copepoda: cyclopid (<i>Mesocyclops leuckarti</i>)	China

In addition to commonly accepted synonyms (given in the Table above), several recent review papers have endeavoured to synonymize many *Camallanus* spp. on the basis of their pleomorphic structural features and similar host ranges and distributions; in particular; *C. anabantis* (= *testudineusi*, *unisiculus*, *bahli*, *jullundurensis*); *C. atroposi* (= *dollfusi*, *chauhani*, *guptae*, *ophichthyi*, *pentkotai*, *puriensis*, *therapsi*, *trichiuris/trichiurusi*); *C. aurangabadensis* (= *ophiocephali*); *C. chorinemi* (= *ophichthyi*, *indicus*); *C. cotti* (= *fotedari*, *jiyuensis*, *incognitus*, *moravecii*, *zacconis*); *C. lacustris* (= *wolgensis*, *Cucullanus alatus*, *anguillae*, *armatus*, *cernuae*, *coronatus*, *elegans*, *lucii*, *luciopercae*, *papillosus*, *percae*, *tincae*, *viviparus*); *C. microcephalus* (= *confusus*, *testudinis*, *seurati*, *Cucullanus dumerilii*); *C. nodulosus* (= *inglisi*, *thapari*); *C. sweeti* (= *testudineusi*, *ophiocephali*); and *C. trispinosus* (= *americanus*, *chelydrae*, *cyathocephalus*, *elegans*, *floridiana*, *magnarugosus*, *microcephalus*, *pipientis*, *scabrae*, *troosti*), but further studies are warranted due to imperfect or inconsistent descriptions.

Parasite morphology: Camallanid nematodes form 2 different types of stages in their developmental cycles: larvae; and adult worms. Gravid females are ovoviviparous and produce eggs which hatch *in utero* releasing first-stage larvae (L1). The larvae are elongate and slender, measuring from 260-650 µm in length depending on species, and have rounded heads with a small dorsal cuticular tooth and attenuated tails. Infective third-stage larvae (L3) are usually orange in colour and elongate, measuring from 420-910 µm in length depending on species, but stouter. They have tapering tails armed with a few terminal spines (mucrons) and already have well-developed buccal cavities characteristic of camallanids. Adult worms are small (measuring from 2-16 mm in length) but are readily recognizable by their red body colour (often discoloured to white in fixed samples) and their prominent orange-brown buccal capsules (often discoloured to yellow in fixed samples). The buccal capsules of camallanid worms may be rounded without valves (subfamily Procammallaninae) or segmented with 2 sclerotized valves (subfamily Camallininae). The interior of the capsule may be smooth, ridged or granular, and the capsule margins may be clear or supported by posteriorly-directed rod(s) and sometimes lateral tridents. The mouths of *Camallanus* spp. appear slit-like due to the presence of 2 valves and the larger anterior chamber of the buccal capsule is ridged or granular and supported by a pair of tridents. Adult worms possess a bipartite oesophagus (with a short anterior muscular and a longer posterior glandular section) connected to the tubular intestines and rectum terminating in a posterior subterminal anus. Worms are covered by a thin flexible cuticle often with fine transverse striations and they have conspicuous anterior and posterior papillae. Adult worms are sexually dimorphic, female worms being larger than males. Mature males have coiled tails rolled ventrally and they have small caudal alae, 2 dissimilar unequal spicules (no gubernaculum) and a single anterior testis (often twisted or reflexed). Mature females have a single ovary, a posterior uterus and a vulva opening near the middle of the body, sometimes with elevated vulvar lips. In gravid females, the uterus is filled with small eggs (30-40 µm in diameter) which hatch internally releasing L1 (coiled *in utero* but over 260 µm long).

Site of infection: Adult camallanid worms infect the gastrointestinal tracts of their vertebrate definitive hosts, some infecting the stomach, some the small intestines and some the large intestines. Many species in small freshwater fish may often be seen protruding from the anus of their hosts. Larval stages develop in the haemocoel of copepodid intermediate hosts. Various species have also been found to infect paratenic hosts (amphibians and planktivorous fish), being found as L3 in the gut or sometimes encapsulated as L3 or L4 in host tissues (usually the mesenteries).

Pathogenesis: Even though adult worms penetrate the intestinal mucosa and feed on host tissues and fluids (incl. blood), most infections remain asymptomatic as only a few worms are involved. Heavy infections, however, may cause significant intestinal irritation and inflammation, haemorrhage, ulceration and abscess formation resulting in reduced appetite, anorexia, abdominal bloating, weight loss and wasting, diarrhoea (sometimes with melena) and secondary bacterial infections. Clinical infections have been recorded in fish and turtles, especially those living in crowded and confined situations such as aquaria and breeding ponds.

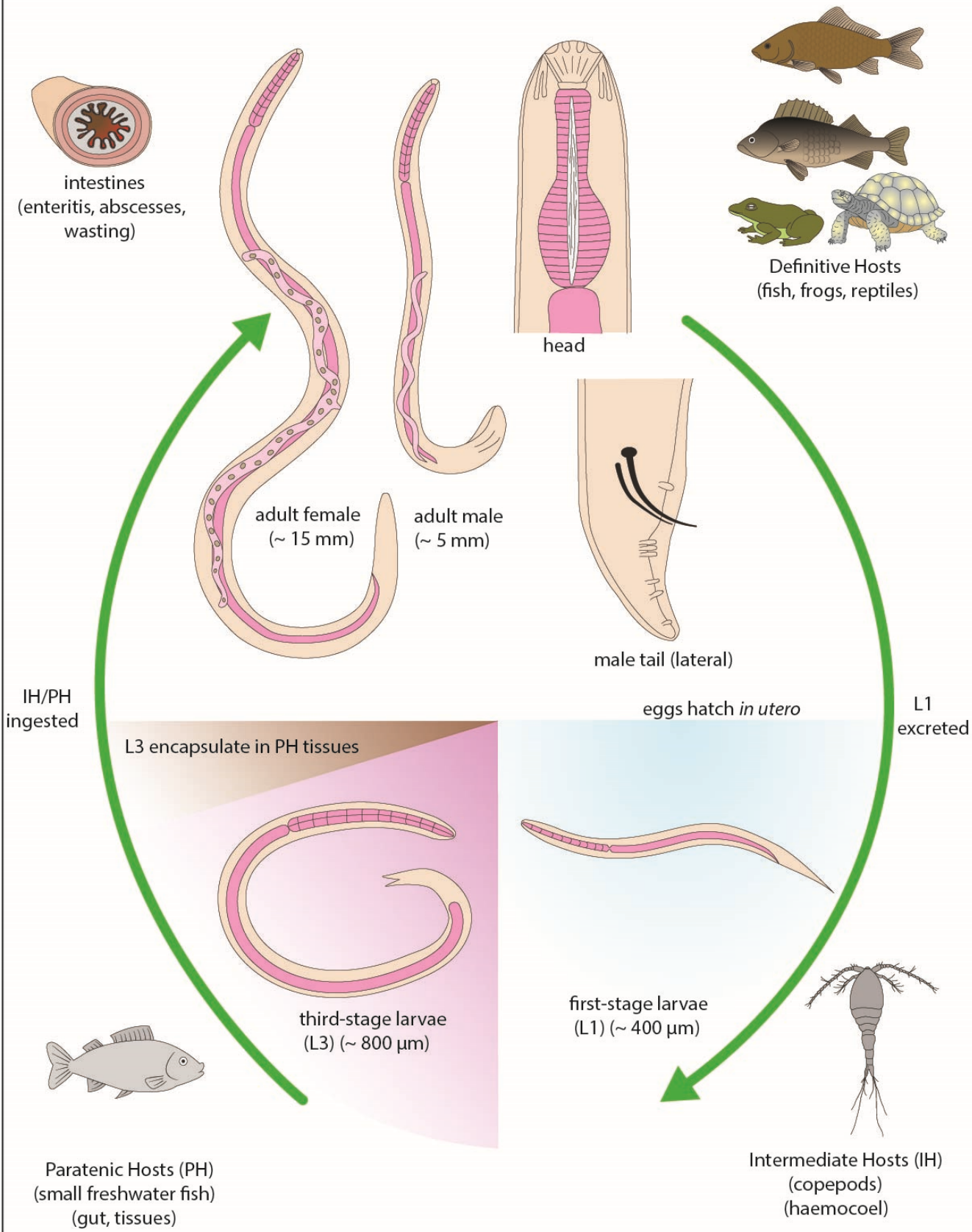
Developmental cycle and mode of transmission: These nematodes have indirect heteroxenous life-cycles involving the cyclic transmission of adult worms in aquatic or amphibious vertebrates (definitive hosts) and larval stages in aquatic invertebrates (intermediate hosts). Female worms produce eggs which hatch *in utero* releasing L1 which are either passed into water with host faeces or when gravid females protrude from the anus and rupture on contact with water. The larvae swim around in the water column or wriggle around while attached to submerged substrates by their tails. Their vigorous activity attracts copepodid crustaceans which devour them and act as intermediate hosts for larval development. L1 survival in water is related to temperature with many surviving up to 10 weeks at 5°C but only for 4 weeks at 20°C, although their infectivity for copepods was lost after 1-2 weeks. When infective L1 are ingested by suitable copepods, they penetrate the gut wall and invade the haemocoel where they moult into L2 in 3-4 days and then to L3 in 6-7 days. Infective L3 lay coiled and dormant in the haemocoel until the copepod is eaten by a suitable (permissive) definitive host (lower predaceous vertebrate). The L3 infect the gut mucosa and moult to L4 in 9-10 days and then to adults in 17-91 days (males develop first). After mating, female worms produce eggs which hatch *in utero* releasing

L1 to complete the cycle. In some species, L3 may apparently move up the food chain using paratenic hosts. When eaten by an unsuitable (non-permissive) host (such as planktivorous fishes), L3 may persist in the gut or become encapsulated in tissues (usually mesenteries), only occasionally growing to L4. When these paratenic (transport) hosts are eaten by predatory definitive hosts, the larvae infect the gut mucosa and develop into adults. An exception to this indirect transmission was found for a few species (such as *C. cotti*) which appear to also be capable of direct transmission when definitive hosts ingest free-living L1 directly from the water column (without copepods being involved).

Differential diagnosis: Few infections cause clinical disease and even when present, clinical signs are relatively non-specific. Infections are generally diagnosed ante-mortem by the detection of red thread-like worms emerging from the anus of the host in heavy infections, or serendipitously upon post-mortem. Coprological techniques do not facilitate diagnosis as the worms release larvae (and not eggs) which are relatively fragile in the chemicals and conditions used for faecal concentrations.

Treatment and control: Clinical infections in fishes have been successfully treated with anthelmintics; including benzimidazole-methylcarbamates (fenbendazole) and imidazothiazoles (levamisole). Infections in aquaria and intensive culture facilities have been associated with over-crowding, poor water quality, and using live crustaceans as food sources. Strategies designed to break transmission cycles should redress these conditions, but remembering that some parasite species can undergo direct transmission (effectively fish-to-fish).

Camallanus

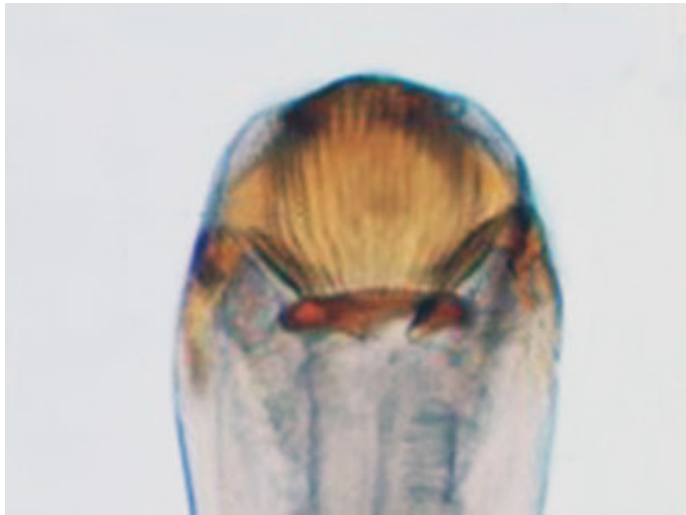




Camallanus adult worm removed from fish vent



Camallanus adult worms



Camallanus adult worm, head