

Lernaea

(crustacean: copepod)

Overview

Arthropods are coelomate metameric invertebrate animals with a chitinous exoskeleton and jointed limbs. They undergo protostomial embryonic development and most grow by cuticular moulting (ecdysis). Three main subphyla are recognized: Chelicerata, Crustacea and Hexapoda. Crustaceans have a very strong cuticle strengthened by calcium salts; thus their growth must proceed through repeated moults. Most species are aquatic with internal or external gills, two pairs of antennae, mouthparts comprising one pair of mandibles and two pairs of maxillae, and each heteronomous body segment usually bears a pair of ventral biramous extremities (podia). Maxillopods lack appendages on abdominal segments and the nauplius larval stage has a unique maxillopodan eye. Copepods have an elongate segmented body (first few thoracic segments fused with head to form cephalothorax) and they undergo gradual metamorphosis with a series of copepodid instars succeeding naupliar instars. Many species are free-living, although some are ectoparasitic on fish. Cyclopoid copepods have short antennules with 10-16 articles and an open buccal cavity. Lernaeids have a free-swimming naupliar stage, five copepodid stages and the adults attach to aquatic hosts. Females insert anterior attachment organs into host tissues and develop paired egg sacs. Infestations by *Lernaea cyprinacea* may cause lesions and mortalities in a wide range of freshwater fishes, especially in aquaculture facilities.

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: Arthropoda (chitinous exoskeleton, segmented body, jointed limbs, haemocoel)
Subphylum: Crustacea (mandibular mouthparts, gills, two pairs antennae, biramous podia, larval nauplius/zoea)
Class: Maxillipoda (nauplius with maxillipodan eye)
Subclass: Copepoda (elongate body, series of copepodid instars succeeding naupliar instars, several ectoparasites)
Order: Cyclopoida (antennules short with 10-16 articles, buccal cavity open)
Family: Lernaeidae (attachment organ inserted into host, paired egg sacs)
Genus: *Lernaea* (parasitic on gills/skin of fish)
Species: *L. cyprinacea* causes lesions and mortalities in freshwater fishes

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). Arthropods have small segmented bodies encased in chitinous exoskeletons with articulated limbs. Most species are free-living in terrestrial and aquatic habitats, although a small range are ectoparasitic on other animals, some feeding on the blood or skin of vertebrates. Five subphyla are recognized: Chelicerata, Crustacea, Hexapoda, Myriapoda and Trilobita. Crustaceans have very strong cuticles strengthened by calcium salts, so they moult periodically as they grow and metamorphose through different types of larval stages before forming adults. Most species are aquatic and have internal or external gills, while terrestrial species have internal gills which are kept moist. Crustaceans have mouthparts with two pairs of maxillae (to handle food) and paired mandibles (with opposing biting and grinding surfaces). They have two sets of antennae and each body segment usually gives rise to a pair of ventral biramous appendages (podia). Six crustacean classes are recognized: Brachiopoda, Cephalocarida, Malacostraca, Maxillipoda, Ostracoda and Remipedia. Maxillopods usually have a body plan comprising 5 cephalic, 6 thoracic and 4 abdominal segments followed by a telson. The thoracic segments bear biramous (sometimes uniramous) limbs, but the abdominal segments lack appendages. The carapace is present or reduced, most feed using maxillae, and the nauplius larval stages have unique eyes with three cups, each with tapetal cells (= maxillopodan eye). Six maxillopodan subclasses are recognized: Branchiura, Cirripedia, Copepoda, Mystacocarida, Pentastomatida and Tantulocarida.

Major parasitic crustacean families	Biodiversity	Hosts	Parasitic stages	Pathogenesis	Disease transmission
Class: Maxillipoda					
Subclass: Copepoda (copepods)					
Order: Cyclopoida (open buccal cavity)					
Family: Lernaecidae (anchor worms)	19 genera, 114 spp.	freshwater fishes	copepodids and adults	skin lesions	direct (water)
Former order: Poecilostomatoida (slit-like buccal cavity)[now a "poecilostome" lineage within the Cyclopoida]					
Family: Ergasilidae (gill lice)	27 genera 61 spp.	freshwater and marine fish	adult ♀	gill/skin lesions	direct (water)
Subclass: Branchiura (head with flattened bilobed cephalic fold, carapace expands laterally)					
Order: Argulidea (discoid bodies, attach using hooks, suckers and barbs)					
Family: Argulidae (fish lice)	4 genera 150 spp.	marine and freshwater fish	juveniles, adults	skin lesions	direct (water)
Subclass: Pentastomatida (tongue worms, elongate annulated bodies, 2 pairs tiny anterior claws near mouth)					
Order: Porocephalida (mouth between/below anterior hooks)					
Family: Porocephalidae	5 genera, 10 spp.	snakes (rodent IH)	adults	lung lesions	indirect (via IH*)
Family: Linguatulidae	1 genus, 4 spp.	carnivorous mammals (mammal IH)	adults	naso-pharyngeal lesions	indirect (via IH*)

*IH = intermediate host

Copepods are small aquatic crustaceans that are one of the most speciose metazoan groups in aquatic communities (over 13,000 morpho-species known). They inhabit a wide range of water sources, ranging from oceans and marine sediments, freshwater streams, rivers, lakes, subterranean cave pools, and even damp leaf litter and puddles in bromeliad leaves. Most species are free-living (important as both predators and prey in planktonic food chains) and some are symbiotic or internal/external parasites of other metazoa, including commercial fish species. Copepods lack a carapace and have elongate segmented bodies (first few thoracic segments fused with head to form cephalothorax) with a single pair of uniramous maxillipods and four pairs of biramous thoracic swimming appendages. They undergo gradual metamorphosis with a series of copepodid instars succeeding naupliar instars. Copepods have been classified within 2 superorders: Gymnoplea (prosome-urosome division posterior to fifth leg-bearing somite) with 2 orders (Calanoida and Platycopioidea) and Podoplea (prosome-urosome division anterior to fifth leg-bearing somite) with 9 orders (Canuelloidea, Cyclopoida (incl. Poecilostomatoida which is no longer recognised as a valid order as all its cognate families form a well-defined "poecilostome" lineage within the Cyclopoida), Gelyelloidea, Harpacticoida, Misophrioida, Monstrilloidea, Mormonilloidea, Platycopioidea and Siphonostomatoida). Members of the order Cyclopoida s.s. form adults with an open buccal cavity and have short antennules with 10-16 articles. Some 27 families are recognized: including the family Lernaecidae which contains 17 genera (*Afrolerna*, *Amazolerna*, *Areotrachelus*, *Bedsylerna*, *Cataphila*, *Dysphorus*, *Indolerna*, *Indopeniculus*, *Lamproglena*, *Lamproglenoides*, *Lerna*, *Lernaegiraffa*, *Minilerna*, *Opistholerna*, *Pillainus*, *Pseudolamproglena* and *Taurocheros*) assigned to 2 subfamilies, Lamprogleninae (prevalent in Palaearctic, Oriental and Afrotropical regions) and Lernaecinae (found in all zoogeographic regions except Antarctica). Lernaecids have free-swimming naupliar stages but all subsequent copepodid and adult stages are ectoparasitic on the skin and gills of freshwater fishes (in contrast, only the female adults of poecilostome ergasilids are parasitic). Adult females insert an anterior holdfast (attachment organ) into host tissues and develop paired egg sacs posteriorly. Those belonging to the genus *Lerna* form a unique holdfast resembling an anchor with antler-like processes. All *Lerna* spp. occur in freshwater systems, or those with low salinity levels. Early studies described over 100 nominal species, but the small number of morphological traits and their pleomorphy has confounded species discrimination, so over half the nominal species are considered synonymous with other species. At present, some 55 species are considered valid, with many recorded in cultured fish species (both ornamental and farmed), sometimes in association with morbidity and mortality.

<i>Lerna</i> species	Hosts	Distribution
<i>L. arcuata</i>	Cypriniformes: cyprinid (Java barb); Perciformes: osphronemid (Vaillant's chocolate gourami)	Asia
<i>L. argentinensis</i>	Siluriformes: pimelodid (spotted sorubim, barred catfish)	South America
<i>L. bagri</i>	Siluriformes: bagrid (kampango)	Africa
<i>L. barbicola</i>	Cypriniformes: cyprinid (smallmouth yellowfish); Siluriformes: malapterurid (electric catfish)	Africa
<i>L. barilii</i>	Cypriniformes: cyprinid (goldfish, lake salmon), danionid (bariline fish)	Africa, Asia
<i>L. barnimii</i> (syn. <i>Lernaecera barnimiana</i> , <i>temnocephala</i>)	Cypriniformes: cyprinid (largescale yellowfish, smallmouth yellowfish, ningu, moggel, rednose labeo, massas, redeye labeo, purple labeo, Orange River mudfish, Ethiopia barb, Zanzibar barb, Niger barb, chikasu, Ripon barbel); Cichliformes: cichlid (Mweru hump-backed bream, Victoria tilapia,	Africa

	Nile tilapia, Mozambique tilapia, longfin tilapia, blue-spotted tilapia, Singida tilapia, redbelly tilapia, blue Victoria mouthbrooder); Perciformes: latid (Nile perch)	
<i>L. bengalensis</i>	Anabantiformes: channid (spotted snakehead)	India
<i>L. bhadraensis</i>	Cypriniformes: cyprinid (rohu, Indian carp)	India
<i>L. bisticornis</i>	Cichliformes: cichlid (featherfin cichlid, giant cichlid, sinievahiekkahautoja, glanzmaulbruter)	Africa
<i>L. brachycera</i>	Ababantiformes: channid (northern snakehead)	China
<i>L. catostomi</i> (syn. <i>Lernaecocera catostomi</i> , <i>pectoralis</i> , <i>tortua</i>)	Siluriformes: ictalurid (brown bullhead, white bullhead); Cypriniformes: cyprinid (common shiner), catostomid (shorthead redhorse, northern hogsucker, lake chubsucker), leuciscid (weed shiner); Perciformes: centrarchid (bluegill)	North America
<i>L. chackoensis</i>	Cypriniformes: cyprinid (Indian carp); Anabantiformes: osphronemid (giant gourami)	India
<i>L. composita</i> (syn. <i>Lernaecocera weneri</i>)	Siluriformes: malapterurid (electric catfish), clariid (African sharptooth catfish); Characiformes: distichodontid (Nile distichodus)	Africa
<i>L. cruciata</i> (syn. <i>Lernaecocera</i>) (maybe conspecific with <i>L. cyprinacea</i> according to recent molecular studies)	Cypriniformes: cyprinid (goldfish), catostomid (shorthead redhorse); Cyprinodontiformes: poecilid (eastern mosquitofish); Perciformes: percid (sauger), moronid (white bass, white perch), centrarchid (largemouth bass, smallmouth bass, spotted bass, pale river bass, redspotted sunfish, warmouth, pumpkinseed, rock bass); Siluriformes: ictalurid (channel catfish)	Asia, Americas
<i>L. ctenopharyngodontis</i>	Cypriniformes: cyprinid (grass carp)	Asia
<i>L. cyprinacea</i> (syn. <i>L. carassii</i> , <i>elegans</i> , <i>ranae</i> , <i>tentaculis</i> , <i>Lernaecocera cyprinacea</i> , <i>gastrostei</i>) (incl. subspp. <i>brachycera</i> , <i>chakoensis</i> , <i>cyprinacea</i> , <i>elegans</i> , <i>macropodi</i> , <i>mastacembeli</i>) (anchor worm)	Acanthuriformes: sciaenid (freshwater drum); Amiiiformes: amiid (bowfin); Anabantiformes: anabantid (climbing perch), channid (northern snakehead, forest snakehead, giant snakehead, striped snakehead, spotted snakehead), helostomatid (kissing gourami), osphronemid (snakeskin gourami, threespot gourami, giant gourami, Siamese fighting fish, paradise fish, long-tailed paradise fish); Anguilliformes: anguillid (European eel, American eel, Japanese eel); Atheriniformes: atherinopsid (pejerrey); Beloniformes: adrianchthyid (Japanese rice fish); Blenniiformes: blenniid (woundfin); Characiformes: anostomid (piava), characid (pike characin, twospot astyanax), prochilodontid (streaked prochilod); Cichliformes: cichlid (Mozambique tilapia, Victoria tilapia, redbelly tilapia, Singida tilapia, black tilapia, blue tilapia, Mozambique tilapia, Nile tilapia, redbreast tilapia, southern mouthbrooder); Clupeiformes: clupeid (Allis shad); Cypriniformes: catostomid (razorback sucker, golden redhorse, bluehead sucker, Sonora sucker, largescale sucker, Sacramento sucker, white sucker, desert sucker, lake chubsucker, creek chubsucker, northern hogsucker, quillback, smallmouth buffalo, bigmouth buffalo, black buffalo), cobitid (pond loach, spined loach), cyprinid (goldfish, silver crucian carp, crucian carp, Japanese crucian carp, grass carp, common carp, koi carp, Mossul bleak, Kinneret bleak, Sellal bleak, bit, silver carp, black carp, Eurasian carp, Indian carp, bighead carp, bigeye carp, predatory terling, gudgeon, field gudgeon, Suwa gudgeon, barbell steed, topmouth gudgeon, Japanese dace, dark chub, pale chub, Yunnani silemokk, Java barb, common shiner, silver labeo, rednose labeo, Orange River mudfish, purple labeo, redeye labeo, largescale yellowfish, largemouth yellowfish, shabout, asp, dali poorpuntius, barbell, yellow barbell, common barbel, yellowfin barbel, Italian barbel, Jordan barbel, Jordan himri, Mesopotamian himri, mangar, binni, ogaramul, Levantine scraper, sharpray, common nase, brond-snout, kangal fish, idanaploug, hiina nappoug, red garra, sharpbelly, hitch, ide, common roach, Tigris asp, peppered chub, Wuchang bream, black Amur bream, Moapa dace, black sharkminnow, hardhead, golden shiner, threelips, Sacramento blackfish, hardlipped barb, Moltrecht's minnow, suckermouth minnow, common minnow, southern redbelly dace, bluntnose minnow, fathead minnow, bullhead minnow, stone moroko, pehmeium-soorhuul, Siambarbe, tinfoil barb, gold barb, European bitterling, rosy bitterling, common roach, common rudd, tench), leuciscid (big-scaled redbfin, Mesopotamian pike chub, eastern blacknose dace, longnose dace, speckled dace, northern pikeminnow, Colorado squawfish, satinfin shiner, rosefin shiner, redffin shiner, emerald shiner, river shiner, minnilus, Arkansas River shiner, spottail shiner, red	worldwide

	<p>shiner, spotfin shiner, sand shiner, mimic shiner, steelcolor shiner, Allegheny pearl dace, Mississippi silvery minnow, chiselmouth, Tigris bream, asp, central stoneroller, creek chub, Utah chub, roundtail chub), xenocypridid (barbel chub, kulter niulansky, sale niglask, predatory carp);</p> <p>Cyprinodontiformes: cyprinodontid (Arabian toothcarp, Zagros pupfish), goodeid (White River springfish), fundulid (northern studfish, mummichog, plains killifish, northern plains killifish, blackstripe topminnow), poeciliid (southern platyfish, dusky millions fish, molly, short-finned molly, Yucatan molly, guppy, rainbow fish, livebearer, eastern mosquitofish, western mosquitofish); Esociformes: esocid (chain pickerel, northern pike, redfin pickerel), umbrid (central mudminnow, eastern mudminnow); Gadiformes: lotid (burbot); Galaxiiformes: galaxiid (western galaxias, mountain galaxias);</p> <p>Gasterosteiformes: gasterosteid (three-spined stickleback, ninespine stickleback); Gobiiformes: gobiid (monkey goby, round goby), odontobutid (sleeper), oxudercid (mudskipper); Mugiliformes: mugilid (greenback mullet, liza, flathead grey mullet, thinlip mullet, Abu mullet); Osmeriformes: retropinnid (Australian grayling); Osteoglossiformes: osteoglossid (Asian arowana, pirarucu); Perciformes: centrarchid (white crappie, black crappie, longear sunfish, orange-spotted sunfish, warmouth, green sunfish, rock bass, bluegill, largemouth bass, pumpkinseed, smallmouth bass, spotted bass, largemouth bass, Sacramento perch), channid (snakehead), cichlid (freshwater angelfish), gobiid (edohaze, jyuzukakehaze, dusky tripletooth goby), moronid (white bass), percichthyid (Creole perch, southern pygmy perch, Macquarie perch, Murray cod, trout cod, nightfish, western pygmy perch, river blackfish), percid (walleye, blackside darter, redfin perch, mud darter, johnny darter, orangethroat darter, banded darter, Eurasian ruffe), sinipercid (mandarin fish), terapontid (silver perch); Salmoniformes: plecoglossid (ayu), salmonid (trout, rainbow trout, brown trout, brook trout, chinook salmon); Scombriformes: stromateid (silver pomfret); Scorpaeniformes: cottid (banded sculpin, European bullhead); Siluriformes: bagrid (Tigris mystus, cut-tailed bullhead, semutundu), heptapterid (South American catfish), heteropneustid (Asian singing catfish), plotosid (freshwater cobbler, eel-tailed catfish), silurid (Amur catfish, wels catfish, Tigris catfish), ictalurid (brown bullhead, black bullhead, channel catfish); Synbranchiformes: mastacembelid (lesser spiny eel); Tetraodontiformes: tetraodontid (pufferfish); Caudata: salamandrid (Japanese fire belly newt); Anura: ranid (tadpoles)(American bullfrog, northern leopard frog, marsh frog, green frog, foothill yellow-legged frog)</p>	
<i>L. devastatrix</i>	Characiformes: characid (tetra), erythrinid (wolf fish); Cypriniformes: cyprinid (Eurasian carp); Siluriformes: heptapterid (South American catfish)	South America
<i>L. diceracephala</i> (syn. <i>Lernaeocera</i>)	Siluriformes: clariid (African sharptooth catfish, vundu)	Africa
<i>L. dolabrodes</i>	Perciformes: centrarchid (bluegill)	America
<i>L. gambusiae</i>	Cyprinodontiformes: poecilid (western mosquitofish)	India
<i>L. gamitanae</i>	Characiformes: serrasalmid (tambaqui)	South America
<i>L. gobioptera</i>	Gobiiformes: godiid (macrolepis mosquitofish)	Eurasia
<i>L. gonionoti</i>	Cypriniformes: cyprinid (Java barb)	Asia
<i>L. haplocephala</i> (syn. <i>Lernaeocera bichiri</i>)	Cypriniformes: cyprinid (smallmouth yellowfish); Polypteriformes: polypterid (saddled bichir, barred bichir, Congo bichir, ornate bichir, gray bichir)	Africa
<i>L. hardingi</i>	Cichliformes: cichlid (Nile tilapia, redbelly tilapia, mango tilapia, happy, tigerfish, snaileater); Characiformes: alestid (nurse tetra); Siluriformes: claroteid (monde), mochokid (spotted squeaker)	Africa
<i>L. hesaragattensis</i>	Cyprinodontiformes: poecilid (guppy)	India
<i>L. incisor</i>	Perciformes: centrarchid (bluegill)	North America
<i>L. inflata</i>	Cypriniformes: cyprinid (rosefin barb)	Africa
<i>L. lagenula</i> (syn. <i>Lernaeocera</i>)	host unknown	South America
<i>L. lavareti</i> (maybe <i>Ergasilus sieboldi</i>)	Salmoniformes: salmonid (whitefish)	Europe
<i>L. longa</i>	Perciformes: latid (Nile perch)	Africa
<i>L. lophiara</i>	Cichliformes: cichlid (redbelly tilapia, redcheek, golden mola hap, happy,	Africa

	tigerfish, saguga, ndunduma, chisawasawa, utaka, Lake Malawi cichlid); Cypriniformes: cyprinid (redeye labeo, ngumbo); Siluriformes: clariid (mudfish), malapterurid (electric catfish)	
<i>L. minima</i>	Salmoniformes: salmonid (salmon)	Europe
<i>L. multiobosa</i>	Cypriniformes: cyprinid (large razorbelly minnow)	Pakistan
<i>L. octocornua</i>	Abantiformes: channid (spotted snakehead)	China
<i>L. oryzophila</i>	Cypriniformes: cyprinid (Eurasian carp, Java barb); Gobiiformes: gobiid (goby)	Asia
<i>L. osphronemi</i>	Anabantiformes: osphronemid (giant gourami)	Asia
<i>L. palati</i>	Cichliformes: cichlid (happy (white blaze))	Asia
<i>L. papuensis</i>	Osteoglossiformes: osteoglossid (northern saratoga)	Papua New Guinea
<i>L. parasiluri</i>	Siluriformes: silurid (Amur catfish)	Asia
<i>L. phoxinacea</i> (syn. <i>Lernaeocera</i>)	Cypriniformes: leuciscid (common minnow)	Eurasia
<i>L. pirapitingae</i>	Characiformes: serrasalmid (pirapitinga)	South America
<i>L. piscinae</i>	Cypriniformes: cyprinid (bighead carp)	Asia
<i>L. polymorpha</i>	Cypriniformes: cyprinid (Eurasian carp)	Europe
<i>L. pomotidis</i> (syn. <i>Lernaeocera</i>)	Perciformes: centrarchid (bluegill, flier)	North America
<i>L. quadrinucifera</i>	Cypriniformes: cyprinid (grass carp)	Asia
<i>L. rhodei</i>	Cypriniformes: cyprinid (rosy bitterling)	China
<i>L. senegali</i> (syn. <i>Lernaeocera</i>)	Polypteriformes: polypterid (gray bichir)	Africa
<i>L. taipila</i>	Cichliformes: cichlid (Mozambique tilapia, chambo, lingara)	Africa
<i>L. tenuis</i> (syn. <i>Lernaeocera</i>)	Acanthuriformes: sciaenid (freshwater drum)	North America
<i>L. tilapiae</i>	Cichliformes: cichlid (lingara, chambo, lidole)	Africa
<i>L. tuberosa</i>	Cypriniformes: cyprinid (Lake Malawi sardine)	Africa
<i>L. variabilis</i> (syn. <i>Lernaeocera</i>)	Perciformes: centrarchid (bluegill)	Americas

Numerous species have also been reclassified to other genera: including *L. abyssicola* = *Lernaeocera abyssicola*; *L. adunca*, *L. pinnarum*, *L. uncinata* and *L. uncinata* = *Clavella adunca*; *L. anomala* and *L. insolens* = *Clavella anomala*; *L. asellina* = *Lernentoma asellina*; *L. brachialis* and *L. lumpi* = *Lernaeocera branchialis*; *L. cirrhosa* = *Pennella filosa*; *L. clavata* = *Hatschekia clavata*; *L. cornuta* = *Acanthochondria cornuta*; *L. cyclopterina* = *Haemobaphes cyclopterina*; *L. dalmanni* = *Charopinus dalmanni*; *L. diodontis* = *Pennella sagitta*; *L. elongata* = *Ommatokoita elongata*; *L. encrasicholi* = *Lernaeenicus encrasicholi*; *L. esocina* = *Lernaeocera esocina*; *L. exocoeti* = *Pennella exocoeti*; *L. gobina* = *Diocus gobinus*; *L. godfroyi* = *Trifur godfroyi*; *L. hemirhamphi* = *Lernaeolophus sultanus*; *L. huchonis* = *Basanistes huchonis*; *L. laterobrachialis* = *Opistholernaea laterobrachialis*; *L. longa* = *Opistholernaea longa*; *L. lotellae* and *L. rigida* = *Trifur tortuosus*; *L. lusci* = *Lernaeocera lusci*; *L. merlucii* and *L. merlangi* = *Chondracanthus merlucii*; *L. minuta* = *Lernaeocera minuta*; *L. nodosa* = *Chondracanthus nodosus*; *L. pectoralis* = *Lepeophtheirus pectoralis*; *L. radiata* = *Chondracanthodes radiatus*; *L. salmonea* = *Salmincola salmonea*; *L. sieboldi* = *Lernaeolophus sultanus*; *L. cyclophora*, *L. ocularis*, *L. surrirai* and *L. spratta* = *Lernaeenicus sprattae*. another 3 species are considered *species inquirenda* (*L. basteri*, *L. lotae* and *L. squamicola*), and 2 as *nomen nudum* (*L. luciopercae* and *L. ninnii*).

Parasite morphology: *Lernaea* spp. form 5 different types of morphological stages during their developmental cycles: namely, eggs; nauplii (3 free-living instars); copepodids (5 parasitic instars); cyclopoids (free-living pre-metamorphic males and females); and adults (parasitic females only). Females carry eggs in 2 posterior elongate egg sacs that may measure up to 2 mm long. The eggs are small (0.07-0.08 mm), multiseriate, often dark in colour and variable in shape (elongate-conical-ovoid) depending on their age. They hatch to release the first larval stages known as nauplii (singular nauplius) which are free-living stages that are transparent or light-green in colour. *Lernaea* spp. form 3 naupliar instars (N1-3) whereas free-living copepods may form up to 6 naupliar stages. The nauplii are small measuring 0.7-1.0 mm wide, oval-elliptical in shape and have a unique maxillopodan eye located anteriorly. They typically have unsegmented bodies possessing only 3 pairs of functional appendages (antennules, antennae and mandibles) with reduced setation (the antennae also lack the feeding processes on the coxae found in free-living taxa). This anatomy is typical for parasitic copepods which have lecithotrophic nauplii that rely on yolk stores for nutrients (rather than planktotrophic copepods (like ergasilids) which feed on other planktonic organisms). Copepodid stages are then formed with elongate segmented bodies that are parasitic on fish, mostly on the gills. They develop through 5 copepodid instars (Co1-5) with one body somite added at each moult. Their body segments are divided between 2 major body tagmata, an anterior prosome and a posterior urosome. All stages have a full complement of cephalic appendages but a variable number of thoracic limbs (as early stages have fewer pedigerous somites) and no abdominal limbs (all maxillopods lack appendages on abdominal segments). Their body segmentation conforms to the basic maxillopodan plan, with 5 cephalic, 6 thoracic and 4 abdominal somites, but the first 5 thoracic segments are fused with

the head to form the prosome. Parasitic copepods usually have this 'podoplean' body plan with 4 pairs of legs and the division of the prosome and urosome located posterior to the fourth leg-bearing somite (whereas free-living copepods have a 'gymnoplean' body plan with 5 pairs of legs and the division located posterior to the fifth leg-bearing somite). The anterior prosome thus comprises the cephalosome made up of 5 cephalic somites (bearing antennules, antennae, mandibles, maxillules and maxillae, respectively - typical for all crustaceans) plus 5 thoracic somites (first thoracic somite bearing maxillipeds, then another 4 thoracic somites bearing legs 1-4), while the posterior urosome comprises the sixth thoracic somite plus the genital somite and 4 free abdominal somites. The mouthparts are gnathostome (open mouths with short broad hooked mandibles) rather than poecilostome (slit-like mouths with sickle-shaped mandibles) or siphonostome (tubular mouth with stylet-like mandibles). Larvae attached to hosts are unable to swim because their swimming legs are reduced to short stumps and their setae are lost, but when they moult between stages, they reform their appendages and are able to swim. The last copepodid stage moults to form free-swimming pre-metamorphic males and females (cyclopoid-like). The cephalothorax has a transverse chitinous bar dividing it into anterior and posterior sections, and the furcal rami have dorsal, lateral (plumose) and 3 apical setae. They have short antennules with 10-16 articles and open buccal cavities. Both males and females have 4 pairs of swimming legs, but the first legs of males have larger claws and small inner spines. Females have 5-segmented antennules while males have 6-segmented antennules and shorter antennae with larger claws. Mating occurs during this free-swimming cyclopoid stage of development. Males then die while females become parasitic by burrowing their heads into the flesh of fishes with their elongate bodies dangling as threads from the skin. Females grow from 5-23 mm in length and have distinctive bulbous heads joined by a slender neck to a cylindrical trunk (bearing eggs sacs when mature). The female cephalothorax has an anterior knob-like head with broad lateral margins containing 1-2 pairs of simple or forked cephalic horns (anchors) acting as attachment or holdfast organs (hence the common name of anchor-worm). The holdfast usually comprises 2 pairs (one pair in *L. cruciata*) of antler-shaped processes arranged perpendicular to the long axis of the body. The processes may extend laterally for 1.5-4.0 mm and can exhibit a high degree of inter- and intra-specific variation, usually comprising 2 larger bifurcate dorsal processes (branching at the tips to become T- or Y-shaped) plus 2 smaller (unbranched) ventral processes. Smaller specimens often have undivided dorsal processes (or sporting incipient bumps) and ventral processes being no more than conical pegs. Some mid-sized specimens appear X-shaped with 4 simple short processes approximately equal in size. The structure of the anterior mouthparts is unclear as they are clustered together and deeply embedded in host flesh. A small projection acts as an upper lip covering part of the mouth and the mandibles, while a larger separate projection acts as a lower lip and closes the oral space behind the maxillae. The neck and trunk sometimes exhibit body torsion (either sinistral or dextral) as they dangle from the host. The trunk carries 4 pairs of swimming legs which are conspicuous on juveniles, but highly reduced on mature females. The legs are small and biramous, with each branch having 3 segments. Legs 1 are located just behind the holdfast while legs 2-4 are widely spaced along the body. Some authorities report the presence of a fifth pair of legs located near the pregenital prominences but they are apparently highly reduced to rudimentary stumps. The abdomen is short and rounded with 3 inconspicuous segments terminating in a pair of small segmented caudal rami. As the females mature, the trunk develops a bilobed or double pregenital prominence in front of the vulva, from which projects a pair of elongate egg sacs (similar to other podoplean copepods). Egg sacs may contain from 100-500 eggs which are released into the water column to hatch.

Site of infection: Anchor-worm parasites live in freshwater systems, or those with low salinity levels (0.07-1.7%) consistent with the designation 'sweet water' (in contrast, the salinity of seawater is 3.5%). The parasites are therefore found not only on freshwater fishes but also on some estuarine or anadromous species. The naupliar stages are free-living, while the copepodid stages are parasitic mostly on the gills, and the adult females are parasitic mainly on the skin. Different *Lernaea* spp. were thought to exhibit some tissue tropism (site specificity), but heavy infections have been found over most body surfaces, including the inside of the buccal cavity and gill chambers, and occasionally on gill filaments or even the eyes. Most parasite species have exhibited a broad host specificity involving a large range of host species. Infections have been detected on many small Cypriniformes, but also on fish from another 27 orders, as well as on some salamandrids (newts) and ranids (frogs, and their tadpoles). Infections have been found throughout the world in wild and cultured fishes, including aquarium fishes. The parasites develop best in warm conditions, with temperatures between 23-30°C reported as the most favourable.

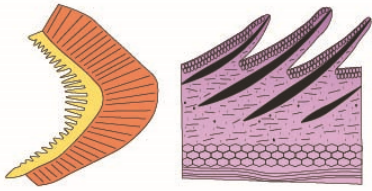
Pathogenesis: Disease (lernaeosis) may be produced by copepodid stages and adult females, both causing tissue trauma with inflammation and ulceration. Copepodid stages are often found on the gills where they attach to gill filaments and feed on host tissue. Light infestations may go unnoticed but large numbers can kill small fish by damaging their gills causing respiratory distress and hypoxia. After mating, immature females penetrate fish hosts by attaching their heads and mouthparts to body surfaces and burrowing deep into the underlying tissues to embed their anterior anchors. Hosts react by trying to isolate the invading parasite by forming ingrowths (tongues) of epidermal cells and sheaths of fibres and cellular infiltrates (fibroblasts and leucocytes) around areas of penetration. The tissues show extensive epidermal hyperplasia and metaplasia, degradation of subepidermal connective tissues, fibrous nodules, muscular breakdown and de-differentiation, all accompanied by progressive inflammation and erythema, with occasional haemorrhages, ulceration and necrosis. Fish may exhibit frequent rubbing or flashing, breathing difficulties and general lethargy with traumatic damage to the skin, scales, fins and underlying muscles (fin damage may also lead to sterility in fish species whose males lose use of their sexual fins). Invasion sites are also prone to secondary bacterial infections (e.g. *Aeromonas hydrophila*) and fungal infections, which worsen and contribute to loss of condition, reduced appetite, poor growth and reproductive performance, and sometimes death. Infections can build to high levels in cultured fish populations leading to severe disease and production losses due to disfigurement and death, particularly in small fishes.

Developmental cycle and mode of transmission: Like all copepods, *Lernaea* spp. undergo gradual metamorphosis where they slowly change from larval naupliar stages (several instars) to subadult copepodid stages (several instars) and then to adults which mate with females producing egg strings. Unlike many copepods, not all stages are free-living in aquatic environments, as some developmental stages have become parasitic on fish hosts: in this case, all copepodid instars and adult females. Eggs released by gravid females hatch in water in 1-3 days releasing free-swimming nauplii larvae, which develop through 3 instars (N1-3) over 3-16 days depending on species and temperature (most species faster in warmer waters). The nauplii do not feed on plankton but are lecithotrophic and are nourished by yolk stores. N3 then moult to copepodid stages which are parasitic and actively seek fish hosts, attaching to the gills or body with attrition of their swimming legs to short stumps. They are obligate parasites as no further development will occur if they do not find a host. The parasite develops through 5 copepodid instars (Co1-5) over 7-12 days. With each moult, the copepodids reform their appendages regaining the ability to swim. They move about but quickly re-attach, usually to the same host but sometimes to other hosts. The final copepodid moult produces pre-metamorphic males and females which are free-swimming cyclopoid-like stages. Mating occurs at this time, with males subsequently dying (within 24 hours) but fertilized females actively seeking fish hosts (the same or new hosts). Females use their heads and mouthparts to penetrate the host skin and permanently attach by developing the characteristic large anterior holdfast (anchor). Their bodies also elongate and transform into cylindrical worm-like threads hanging from the fish's body. The swimming legs remain but quickly atrophy and any body segmentation becomes inconspicuous. They develop long paired posterior egg sacs as early as 24 hours after attachment. The first egg sacs produced are small with approximately 100 eggs, while new eggs sacs are produced every 3-7 days while the female is reproductively active (usually for around 4 weeks). Subsequent egg sacs may contain up to 500 eggs for 3-4 cycles before slowly diminishing to exhaustion. The entire life-cycle may be completed in as little as 18-25 days under optimal conditions (temperatures from 25-30°C), but juveniles cannot complete development at temperatures below 20°C and female will not produce egg sacs at temperatures under 14°C. However, females can overwinter on fish hosts and resume egg production when temperatures rise in the spring. Parasites are usually multivoltine in tropical and subtropical regions producing several generations each year, but univoltine in colder temperate regions with only one generation per year. Infections are more common on fishes in stagnant and slowly-moving water bodies. Because the parasitic stages (copepodids and adult female) do not necessarily occur on the same individual fish, some early authorities suggested that copepodid infections should be recorded as occurring on intermediate hosts while adult females parasitize definitive hosts. This has not gained great acceptance as piscine intermediate and definitive hosts tend not to differ, particularly in small closed systems, and infections by both stages have been recorded on many fish. Transmission between fish is direct via free-swimming stages in water, and is readily achieved in confined spaces or in crowded populations.

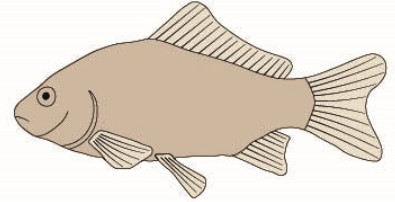
Differential diagnosis: Infections may be diagnosed by the direct detection of adult female parasites dangling from host surfaces as small thin threads or hairs around 20 mm long. They often appear as tiny white-green or red worms embedded in small patches of inflamed tissues. Under magnification, adult female worms are readily identified by their embedded anchors, tubular bodies and paired posterior egg sacs. At necropsy, infections by copepodid stages may be detected by microscopy of wet mounts of gill filaments, skin or fins. Molecular biological studies have been conducted to characterize species by polymerase chain reaction (PCR) amplification of nuclear (ribosomal DNA) and mitochondrial (cytochrome oxidase 1) gene sequences.

Treatment and control: Infections by a few anchor worms in a few fish can be treated by manual extraction using tweezers or forceps, although the worms may tear leaving the embedded anchors to fester. Fish should be regularly monitored for wounds by careful observation, and optimal water quality should be maintained to minimize the risk of secondary infections. *Lernaea* spp. develop best at warmer temperatures (especially above 25°C) and parasite populations can escalate quickly under those conditions. While water temperatures in small aquaria may be lowered to limit parasite numbers, thermal regulation in larger culture systems and outdoor ponds and streams is nigh on impossible. Chemical treatments, however, can be used to suppress parasite populations, but they must be repeated at regular intervals (several weeks) as the embedded adult females are quite resistant to many treatments. The most commonly applied treatment, which is approved for use on food fish species, is the application of salt in the form of salinity baths. Good results have been recorded using 0.5% salinity (1/7 that of seawater) for up to 30 days in those fish species that can tolerate such exposure. Many studies have experimented with concentration-time variations (ranging from low salinity for long periods to high salinity for short periods) depending on host tolerances. Alternatively, traditional treatments with quicklime, potassium permanganate and formalin baths have yielded variable results, but none of these are suitable for food fish species. Ornamental fishes have been successfully treated with several pesticides incorporated into baths; including organophosphates (trichlorfon), pyrethroids (fenvalerate) and insect growth regulators (diflubenzon). There is some anecdotal evidence to suggest that fish that have been successfully treated may be more resistant to subsequent infections. Indeed, fish that have recovered from infection without treatment appear to be somewhat resistant to subsequent infection. Health checks should be instigated before and after fish translocations, with quarantine measures being adopted when new stocks are introduced into culture facilities.

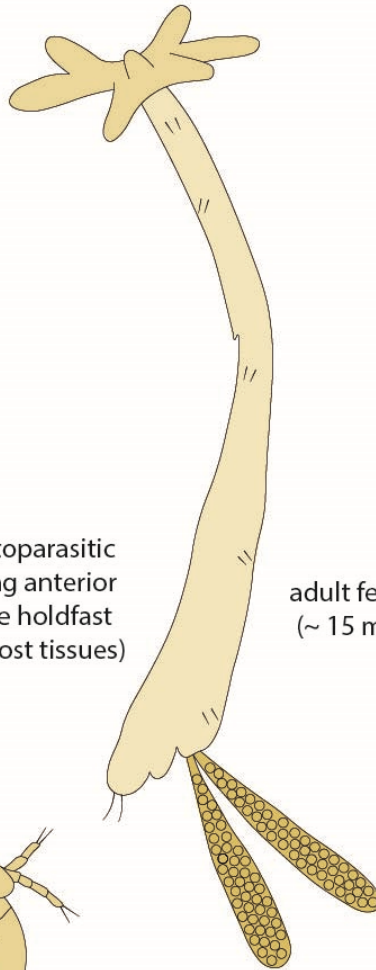
Lernaea



skin, gills
(trauma, lesions, inflammation,
ulceration, respiratory distress)

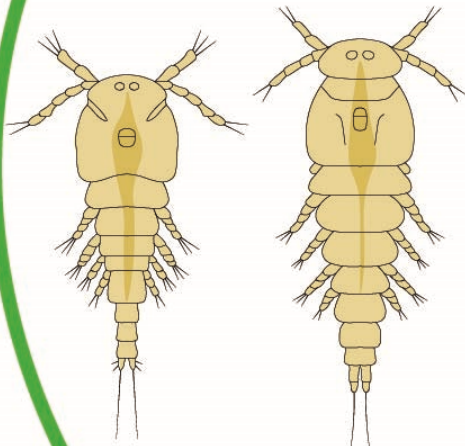


Definitive Hosts
(freshwater fish,
esp. cyprinids)

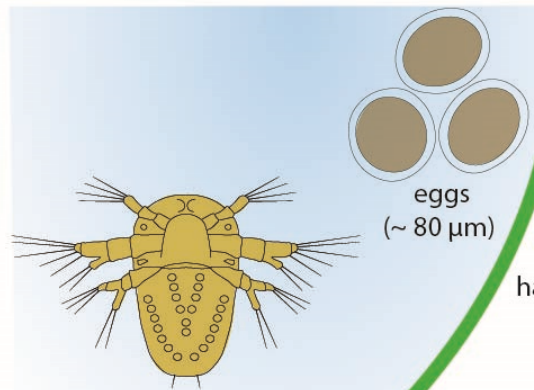


female ectoparasitic
attach using anterior
anchor-like holdfast
(feeds on host tissues)

adult female
(~ 15 mm)



male female
copepodid (dorsal)
(~ 5 mm)
[5 instars]



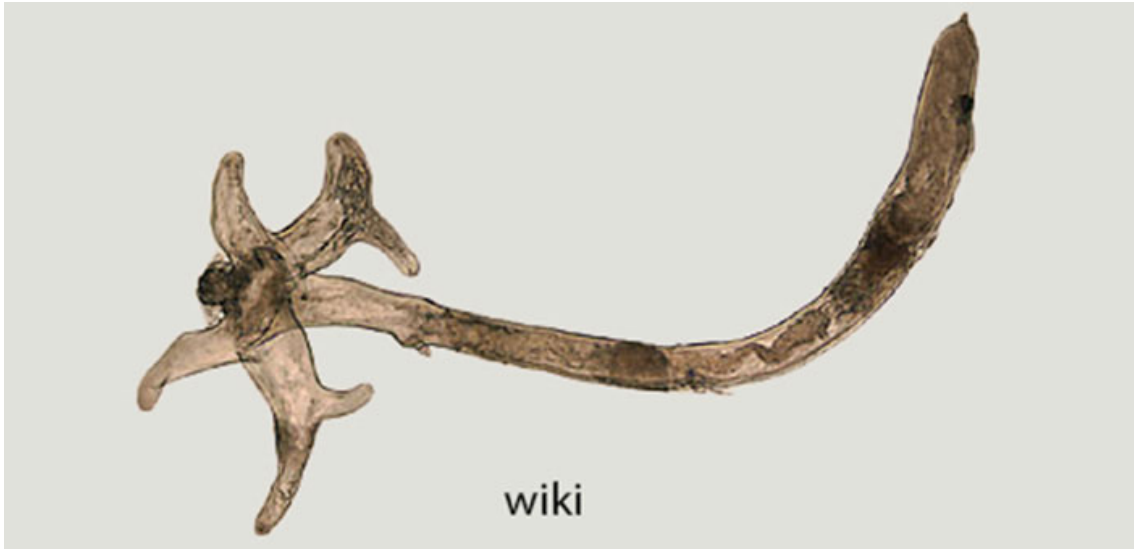
nauplius (ventral)
(~ 0.8 mm)
[3 instars]

eggs
shed
in
water

hatch

ectoparasitic stages
(copepodids attach to hosts,
detach and re-attach)

free-swimming
stage



Lernaea adult



Lernaea adult, egg sacs



Lernaea adult, egg sac junction