

***Polymorphus***  
(acanthocephalan)

**Overview**

Acanthocephalans have pseudocoelomate unsegmented tubular bodies and are commonly called thorny-headed worms due to the possession of a retractable anterior proboscis armed with rows of hooks for attachment. They undergo protostomial embryonic development but do not moult during growth. They are classified within the Lophotrochozoa but do not have jawed mouthparts or digestive tracts, instead they absorb nutrients through their eutelic syncytial cuticles. All species are parasites in the intestinal tracts of vertebrates and they have indirect life-cycles, involving aquatic or terrestrial arthropods as intermediate hosts. Female worms produce mature eggs that float freely in the body cavity and are passed through a unique uterine bell into the uterus to be voided with host faeces. The eggs have thick shells comprised of 4-5 membranes and contain a larval stage (acanthor) armed with hooks and spines which is infective to an invertebrate intermediate host. When ingested by arthropods, the acanthor migrates to the haemocoel and develops into an acanthella which matures into an infective cystacanth. When the arthropod is ingested by the vertebrate host, the cystacanth attaches and matures in the intestinal tract. Infections by *Polymorphus* spp. are transmitted by freshwater crustaceans to aquatic birds and have been associated with enteric disease.

**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: Lophotrochozoa (lophophore feeding structure or trochophore larva or neither)  
Clade: Syndermata (eutelic syncytial epidermis)  
Phylum: Acanthocephala (thorny-headed worms, pseudocoelomate, retractable proboscis with hooks, indirect cycles, eggs with acanthor, acanthella develops in arthropod IH (or PH))  
Class: Palaeacanthocephala (elongate eggs, sometimes with polar thickenings, body wall lacunar canals lateral)  
Order: Polymorphida (trunk may show pseudosegmentation, proboscis swollen/bulbous/cylindrical, with numerous hooks in alternating rows)  
Family: Polymorphidae (marked sexual dimorphism, spinose trunk, proboscis bulbous)  
Genus: *Polymorphus* (parasitic in small intestines of birds and mammals)  
Species: various species cause enteritis in ducks

**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 do not moult during their life-cycles are grouped together in the enigmatic clade Lophotrochozoa, including the platyhelminths, rotifers, lophophorates, annelids and molluscs. In addition to the parasitic flatworms (platyhelminths), other metazoan worm-like groups live as endoparasites in vertebrate hosts. Acanthocephalans have pseudocoelomate unsegmented round-flattened bodies and are commonly called thorny-headed or spiny-headed worms due to the possession of an anterior spherical-cylindrical invaginable proboscis bearing rows of recurved hooks used for attachment. They undergo protostomial embryonic development but do not moult during growth, thus belonging to the Lophotrochozoa (embryos with spiral mosaic cleavage) rather than the Ecdysozoa. On the basis of molecular evidence, they are classified within the clade Gnathifera even though they do not have complex cuticular jaws. They lack digestive tracts and absorb nutrients across their eutelic (constant number of nuclei) syncytial (multinucleate) epidermis, and have been grouped together with the Rotifera into the clade Syndermata.

Over 1,400 species of acanthocephalans have been described worldwide as endoparasites with adult stages living in the intestinal tracts of a wide range of fish, amphibians, reptiles, birds and mammals. They have indirect life-cycles with arthropods always acting as intermediate hosts for larval stages. Female worms pass thick-shelled eggs containing an acanthor armed with hooks and spines. When ingested by aquatic crustaceans or terrestrial insects, the acanthor migrates to the haemocoel and forms an acanthella which matures into an infective cystacanth. When the arthropod is ingested by the vertebrate host, the cystacanth attaches and matures into an adult in the intestinal tract. Within the phylum Acanthocephala, four classes are recognized: Archiacanthocephala with terrestrial cycles involving mammals/birds and insects; Palaeacanthocephala with aquatic cycles in fish/birds/seals and crustaceans; Eoacanthocephala with aquatic cycles in fish/amphibia/reptiles and crustaceans; and Polyacanthocephala with aquatic cycles in fish/crocodiles and crustaceans.

Order	Environment	Definitive hosts	Intermediate hosts	Characters
Class: Archiacanthocephala (proboscis hooks in concentric circular rows, trunk lacking spines)				
Oligacanthorhynchida	terrestrial	birds, mammals	insects	subspherical proboscis
Gigantorhynchida	terrestrial	birds, mammals	insects, millipedes, crustaceans	conical proboscis, truncated, bipartite
Moniliformida	terrestrial	birds, mammals	insects	cylindrical proboscis
Apororhynchida	terrestrial	birds	unknown	globular proboscis
Class: Palaeacanthocephala (proboscis hooks in alternating longitudinal rows, trunk with or without spines)				
Echinorhynchida	aquatic	fish, amphibians, reptiles	crustaceans	variable proboscis (globular, cylindrical, claviform)
Polymorphida	aquatic, terrestrial	birds, mammals, amphibians, reptiles	crustaceans	variable proboscis (bulbous, spherical, oval, cylindrical)
Heteramorphida	aquatic, terrestrial	shore birds	unknown	spindle-shaped proboscis
Class: Eoacanthocephala (proboscis hooks in radial rows, trunk with or without spines)				
Gyracanthocephala	aquatic	fish	crustaceans	small spheroid proboscis
Neoechinorhynchida	aquatic	fish, amphibians, reptiles	crustaceans	variable proboscis (globular-cylindrical)
Class: Polyacanthocephala (proboscis hooks in longitudinal rows, trunk with spines)				
Polactorhynchida	aquatic	fish, crocodiles	crustaceans	long claviform proboscis

The largest and most diversified class Palaeacanthocephala contains 2 orders of aquatic acanthocephalans whose body walls contain lateral lacunar canals, 2-8 multinucleate cement glands, numerous tegumental nuclei, the ligament sacs break down in reproductive females and they lack protonephridia. Worms in the order Polymorphida have a wrinkled trunk and a bulbous-cylindrical proboscis with numerous hooks in alternating rows. The order contains 3 families (Centrorhynchidae, Plagiorhynchidae, Polymorphidae) which infect all classes of vertebrates. The family Polymorphidae contains worms with a spinose trunk and usually a bulbous proboscis bulbous and a distinct neck. The family contains 15 genera (*Andracantha*, *Ardeirhynchus*, *Arhythmorhynchus*, *Bolbosoma*, *Corynosoma*, *Diplospinifer*, *Filicollis*, *Hexaglandula*, *Ibirhynchus*, *Neoandracantha*, *Polymorphus*, *Profilicollis* (syn. *Falsifilicollis*, *Parafilicollis*), *Pseudocorynosoma*, *Southwellina*, *Tenuisoma*). The genus *Polymorphus* contains around 30 species parasitizing domestic and wild birds and mammals which become infected by consuming larval stages in intermediate hosts (aquatic crustaceans, especially amphipods). Another 10 species formerly classified within the genus have recently been transferred to the genus *Profilicollis* based on morphological and molecular differences and the use of decapod crustaceans as intermediate hosts. The genera are cosmopolitan in distribution, and several species cause significant problems in farmed waterfowl (ducks and geese).

Polymorphid species	Definitive hosts, DH (adults in gut)	Intermediate hosts, IH (larval acanthellae then cystacanths in tissues) [plus paratenic hosts, PH]	Distribution
<i>Polymorphus</i> (when known, IHS are amphipods)			
<i>P. actuganensis</i>	Anseriformes: anatid (puddle ducks)	Amphipoda: gammarid ( <i>Gammarus bergi</i> , <i>G. lacustris</i> )	Russia
<i>P. acutis</i>	Anseriformes: anatid (duck); Podicipediformes: podicipedid (grebe); Charadriiformes: larid (gull), scolopacid (godwit); Gruiformes: rallid (coot)		North America, Russia
<i>P. ariusis</i> (syn. <i>Hexaglandula</i> )	Suliformes: bagrid (catfish)		India
<i>P. boschadis</i> (syn. <i>P. magnus</i> , <i>P. minutus</i> , <i>Echinorhynchus minutus</i> , <i>E. anatis</i> , <i>E. collaris</i> )	Anseriformes: anatid (duck, mallard, white-winged scoter, swan, mute swan, merganser, goose); Podicipediformes: podicipedid (grebe); Galliformes: phasianid (chicken); Gruiformes: rallid (moorhen, rail, coot); Accipitriformes: accipitrid (eagle); Charadriiformes: larid (gull, tern), alcid (murre, guillemot, dovekie); Procellariiformes: procellariid (fulmar); Passeriformes: corvid (rook, crow), troglodytid (wren), turdid (thrush), sturnid (starling), motacillid (white wagtail)	Amphipoda: gammarid ( <i>Gammarus bergi</i> , <i>G. pulex</i> , <i>G. duebeni</i> , <i>G. fassarum</i> , <i>G. lacustris</i> , <i>G. limnaeus</i> , <i>G. maeoticus</i> , <i>G. pulex</i> , <i>G. wilkitzkii</i> ), carinogammarid ( <i>Carinogammarus roeselii</i> ); Decapoda: cambarid ( <i>Cambarus affinis</i> ); astacid ( <i>Potamobius astacus</i> )  [plus PH: Anguilliformes: anguillid (eel); Atheriniformes: atherinid (silverside); Gobiiformes:	worldwide

		gobiid (goby); Pleuronectiformes: pleuronectid (plaice); Scorpaeniformes: cyclopterid (lumpfish); Trachiniformes: trachinid (weever)	
<i>P. brevis</i> (syn. <i>Arhythmorhynchus</i> )	Accipitriformes: pandionid (osprey); Pelecaniformes: ardeid (bittern, great blue heron, black-crowned night heron)		North America
<i>P. cetaceum</i> (syn. <i>P. arctocephali</i> )	Artiodactyla: delphinid (short-beaked common dolphin, common bottlenose dolphin), pontoporiid (La Plata dolphin); Carnivora: otariid (brown fur seal)		Australasia, South America
<i>P. chongqingensis</i>	Anseriformes: anatid (duck)		China
<i>P. cincli</i>	Passeriformes: cinclid (dipper)		Russia
<i>P. contortus</i> (syn. <i>Echinorhynchus</i> <i>collurionis</i> )	Anseriformes: anatid (ducks); Pelecaniformes: ardeid (bittern); Passeriformes: laniid (shrike)	Amphipoda: gammarid ( <i>Gammarus lacustris</i> ), hyaellid ( <i>Hyaella azteca</i> )	Europe
<i>P. corynoides</i> (syn. <i>Subcorynosoma</i> )	Anseriformes: anatid (mallard)		Asia
<i>P. corynosoma</i> ( <i>caryosoma</i> misspelling) (syn. <i>Hexaglandula</i> )	Pelecaniformes: ardeid (heron)		South America
<i>P. crassus</i>	Ciconiiformes: ciconiid (wood ibis)		Nearctic
<i>P. cucullatus</i>	Anseriformes: anatid (hooded merganser)		North America
<i>P. diploinflatus</i>	Anseriformes: anatid (ducks)		Europe, Russia
<i>P. fatimaae</i>	Passeriformes: corvid (house crow)		India
<i>P. fulicai</i>	Gruiformes: rallid (black coot)		India
<i>P. gavii</i> (syn. <i>Subfilicollis</i> )	Gaviiformes: gaviid (black-throated loon, common loon)		Russia
<i>P. inermis</i> (syn. <i>Hexaglandula</i> )	Pelecaniformes: ardeid (heron)		South America
<i>P. karachiensis</i> (syn. <i>Hexaglandula</i> )	Suliformes: bagrid (catfish)		India
<i>P. kostylewi</i>	Anseriformes: anatid (velvet scoter)		Russia
<i>P. marchii</i> (syn. <i>Corynosoma</i> )	Anseriformes: anatid (ducks); Gruiformes: rallid (water rail)		Europe, Russia
<i>P. marilis</i>	Anseriformes: anatid (white-winged scoter, lesser scaup); Suliformes: phalacrocoracid (cormorant); Charadriiformes: scolopacid (sandpiper)	Amphipoda: gammarid ( <i>Gammarus lacustris</i> )	Nearctic
<i>P. mathevossianae</i>	Anseriformes: anatid (ducks)		Russia
<i>P. meyeri</i>	Anseriformes: anatid (tufted duck, mallard)		Europe
<i>P. miniatus</i> (syn. <i>Echinorhynchus</i> )	Anseriformes: anatid (duck)		South America
<i>P. mohiuddini</i>	Strigiformes: strigid (brown wood owl)		India
<i>P. mutabilis</i> (syn. <i>Hexaglandula</i> )	Pelecaniformes: ardeid (heron, egret), threskiornithid (roseate spoonbill); Coraciiformes: alcedinid (kingfisher); Charadriiformes: larid (tern); Suliformes: phalacrocoracid (cormorant); Gruiformes: aramid (limpkin)		North America, Europe
<i>P. nickoli</i>	Passeriformes: corvid (house crow)		Pakistan
<i>P. obtusus</i>	Suliformes: anhingid (water turkey); Pelecaniformes: ardeid (heron); Anseriformes: anatid (duck, merganser)		North America
<i>P. paradoxus</i>	Rodentia: castorid (beaver), cricetid (muskrat)	Amphipoda: gammarid ( <i>Gammarus lacustris</i> )	North America
<i>P. pauchihamata</i> (syn. <i>Hexaglandula</i> )	Charadriiformes: larid (Iceland gull)		Iceland
<i>P. phippii</i>	Anseriformes: anatid (ducks, eider);		Russia

(syn. <i>Echinorhynchus borealis</i> , <i>E. mollissima</i> , <i>Subfilicollis phippsi</i> )	Podicipediformes: podicipedid (grebe)		
<i>P. piriformis</i> (syn. <i>Echinorhynchus</i> )	Passeriformes: turdid (common blackbird)		Europe
<i>P. pupa sp. inq.</i>	Anseriformes: anatid (eider)		Russia
<i>P. sichuanensis</i>	Anseriformes: anatid (duck)		China
<i>P. sindensis</i>	Passeriformes: corvid (house crow)		Pakistan
<i>P. spindulatus</i>	Pelecaniformes: ardeid (black-crowned night heron)		Peru
<i>P. striatus</i> (syn. <i>Echinorhynchus striatus</i> , <i>E. ardeae</i> )	Anseriformes: anatid (duck, merganser, swan); Pelecaniformes: ardeid (heron, egret, bittern); Accipitriformes: accipitrid (eagle)		Eurasia
<i>P. strumosoides</i> (syn. <i>Subcorynosoma</i> )	Anseriformes: anatid (goldeneye)	Amphipoda: gammarid ( <i>Gammarus pulex</i> )	Russia
<i>P. swartzi</i>	Anseriformes: anatid (Barrow's goldeneye)		Alaska
<i>P. trochus</i>	Gruiformes: rallid (American coot), Anseriformes: anatid (mallard)	Amphipoda: hyalellid ( <i>Hyalella azteca</i> )	Nearctic
<b><i>Proflicollis</i> (IHs are decapod crustaceans)</b>			
<i>Pr. altmani</i> (syn. <i>Pr. bullocki</i> , <i>kenti</i> , <i>texensis</i> )	Anseriformes: anatid (eider, scoters, surf scoter, lesser scaup); Charadriiformes: larid (European herring gull, brown-hooded gull, Franklin's gull, grey gull, kelp gull), scolopacid (sanderling, dunlin, whimbrel, willet), alcid (rhinoceros auklet); Rodentia: murid (rats)	Decapoda: hippid (Pacific sand crab, mole crab) [plus PH: Carnivora: mustelid (southern sea otter)]	Americas
<i>Pr. antarcticus</i>	Charadriiformes: chionid (sheathbill), larid (kelp gull)	Decapoda: varunid (hairy-handed crab)	South America, Shetlands, New Zealand
<i>Pr. arcticus</i>	Anseriformes: anatid (eider)		Canada, Russia
<i>Pr. biziurae</i>	Anseriformes: anatid (musk duck)	Decapoda: parastacid (yabby)	Australia
<i>Pr. botulus</i>	Anseriformes: anatid (eider, common goldeneye, Barrow's goldeneye, greater scaup, oldsquaw, seaduck, long-tailed duck)	Decapoda: nephropid (American lobster), portunid (green crab), oregoniid (great spider crab), pagurid (Northern Atlantic hairy hermit crab), varunid (green shore crab)	North America, Eurasia
<i>Pr. chasmagnathi</i> (syn. <i>Falsifilicollis</i> )	Gruiformes: rallid (coot); Podicipediformes: podicipedid (grebe); Pelecaniformes: threskiornithid (ibis); Charadriiformes: larid (Olrog's gull), recurvirostrid (white-backed stilt); Rodentia: caviid (guinea pig)	Decapoda: varunid (estuarine crabs)	South America
<i>Pr. formosus</i>	Anseriformes: anatid (duck)	Decapoda: palaemonid (freshwater shrimp)	Taiwan
<i>Pr. major</i>	Anseriformes: anatid (sea ducks, bay ducks)	Decapoda: cancrid (Atlantic rock crab) [plus PH: Carnivora: mustelid (southern sea otter)]	North America
<i>Pr. novaezelandensis</i>	Charadriiformes: haematopodid (South Island pied oystercatcher), scolopacid (bar-tailed godwit)	Decapoda: varunid (hairy-handed crab, tunnelling mud crab), macrophthalmid (stalk-eyed mud crab)	New Zealand
<i>Pr. sphaerocephalus</i>	Charadriiformes: larid (kelp gull, silver gull), haematopodid (oystercatcher); Pelecaniformes: ardeid (yellow-crowned night heron), threskiornithid (scarlet ibis); Gruiformes: rallid (wood rails)	Decapoda: grapsid (little shore crab, purple mottled shore crab, red-spotted shore crab, mottled shore crab, four-toothed shore crab), portunid (red swimmer crab)	Australia, South America

**Parasite morphology:** Acanthocephalan worms form three different developmental stages: eggs, larvae (acanthor, acanthella, cystacanth) and adults. The eggs are yellow-brown in colour and elongate spindle-shaped (measuring 100-120 x 12-19  $\mu\text{m}$ ) with thick polar prolongations of the middle eggshell membrane. Upon hatching in the intermediate host, the eggs release the first larval stage (acanthor) which is spindle-shaped with anterior hooks. These stages form second stage larvae (acanthellae) which are the main growing stages that increase in size before becoming encysted as resting infective stages (cystacanths). These stages slowly come to resemble small immature adult stages that have not yet developed reproductive organs. Cystacanths possess an armed proboscis that is retracted (inverted) within a proboscis receptacle while adult worms evert the proboscis anteriorly to attach to definitive host tissues. Adults are cream-orange in colour, elongate and cylindrical in shape, measuring up to 3 cm in length and 1-2 mm in width. The trunk usually has a midline constriction and the anterior body wall bears numerous spines. The cylindrical proboscis is highly conspicuous and armed with up to 20 longitudinal rows of 7-10 backward-facing hooks (the numbers of rows and hooks differing between species). They lack an alimentary system and nutrients are taken up through the syncytial tegument. Mature adult worms are dioecious and females are larger ( $> 2x$ ) than males. Males have 2 testes diagonally arranged in the center of the trunk and several long tubular glands which produce cement to plug the vagina of females after copulation. Females have ovaries which dehisce (break down) to produce ovarian balls and eggs free-floating in the body cavity, and a unique apparatus known as the uterine bell which acts as a sorting device allowing mature fertilized eggs to pass through to the uterus while immature eggs are returned for further maturation. The genera *Polymorphus* and *Profilicollis* (formerly subgenera) are distinguished primarily by the shape of the proboscis (cylindrical with bulbous expansion in *Polymorphus* cf. fully ovoid in *Profilicollis*), length of the neck (long in *Profilicollis*) and whether the fibrillar coat of the egg possesses polar swellings (present in *Polymorphus*).

**Site of infection:** Adult worms infect the small intestines of their vertebrate definitive hosts (mainly birds) while larval stages occur in the body cavities of their crustacean intermediate hosts (amphipods, decapods).

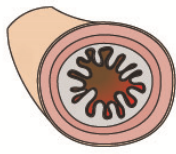
**Pathogenesis:** Acanthocephalans do not feed on host tissues but adults damage the gut when they attach by inserting their armed proboscis deeply into the intestinal wall, often reaching to the muscularis interna and sometimes perforating the wall. Sites of attachment become inflamed and fibrous connective tissue forms small nodules 2-3 mm in diameter. There are often more nodules than worms as juveniles move between sites and are often found free in the lumen. After mating, females attach permanently and begin egg laying while males pass out of the gut. Most infections are light and subclinical, but heavy infections may cause severe enteritis and even peritonitis contributing to death. Heavy infections have commonly been recorded in shorebirds and waterfowl exhibiting weakness, emaciation and stunting. Episodic clinical infections also appear to occur in sea otters as accidental or paratenic hosts, with significant intestinal inflammation and peritonitis observed in carcasses washed up on North American coasts.

**Developmental cycle and mode of transmission:** Polymorphid acanthocephalans have indirect life-cycles involving cyclic transmission between definitive hosts (birds infected with adult worms) and aquatic crustaceans as intermediate hosts (mostly amphipods for *Polymorphus* spp. and decapods for *Profilicollis* spp.). Female worms lay eggs which are voided with host faeces. When ingested by crustacean hosts, the eggs hatch releasing larval acanthors which penetrate to the body cavity and grow through an acanthella stage into infective cystacanths over a period of weeks. Some infections in amphipods have also been associated with altered host behaviour, making them more prone to predation by being attracted to light, swimming to the surface and even latching onto aquatic vegetation. When infected crustaceans are eaten by avian definitive hosts, the cystacanths evert their proboscis, attach to the gut wall and grow into sexually mature adults. Following mating, female worms produce numerous embryonated eggs over a period of months thus completing the life-cycle. The duration of the entire cycle is variable as eggs may remain viable for several months in water at 10-17°C, acanthors may take up to 2 weeks to establish, acanthellae grow over 6-8 weeks, cystacanths may remain viable for several months, and adults take up to 3-4 weeks to mature and produce eggs. Epidemiological studies suggest seasonal patterns to infection (with summer peaks), often associated with host behaviour as many waterfowl spend less time on water as they age.

**Differential diagnosis:** Infections by most polymorphid worms can be diagnosed by coprological examination of bird droppings for characteristic eggs, although egg shedding by some species (e.g. *P. minutus*) can be sporadic generating false negative results. Infections may also be detected at postmortem by finding incriminating nodules and adult worms in gut samples.

**Treatment and control:** No satisfactory treatment for polymorphid acanthocephalans of waterfowl or shorebirds has been established although some partial successes have been reported using niclosamide, carbon tetrachloride, fenbendazole and loperamide. Some success in reducing worm populations in domesticated stock has also been reported by with-holding food and starving infected birds for several days. Prevention by controlling intermediate host populations is difficult as amphipod and decapod crustaceans are ubiquitous in aquatic environments.

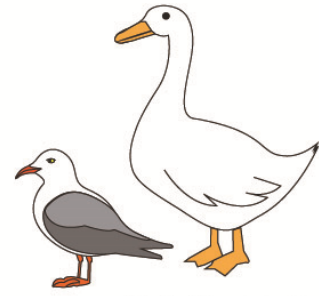
# Polymorphus



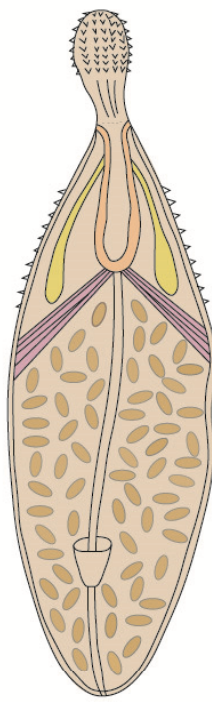
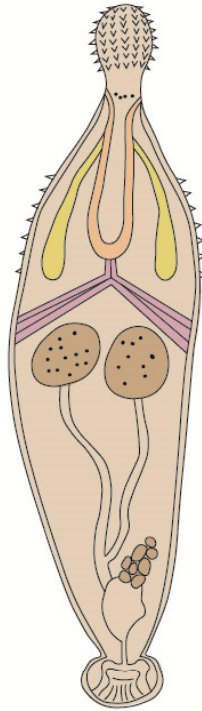
intestines  
(trauma,  
nodules)

adult male  
(~ 20 mm)

adult female  
(~ 20 mm)



Definitive Hosts  
(waterfowl, shore birds)



excretion

egg  
(~ 120  $\mu$ m)

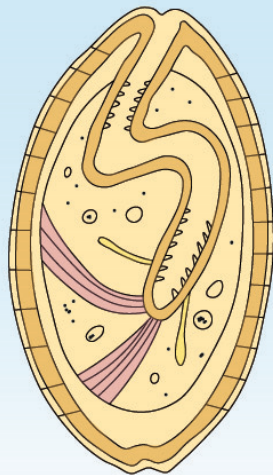


ingestion

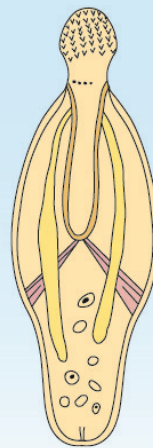
acanthor  
(~ 150  $\mu$ m)

ingestion

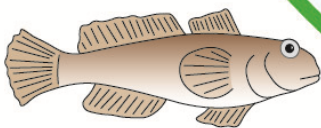
aquatic cycle



cystacanth  
(~ 10 mm)



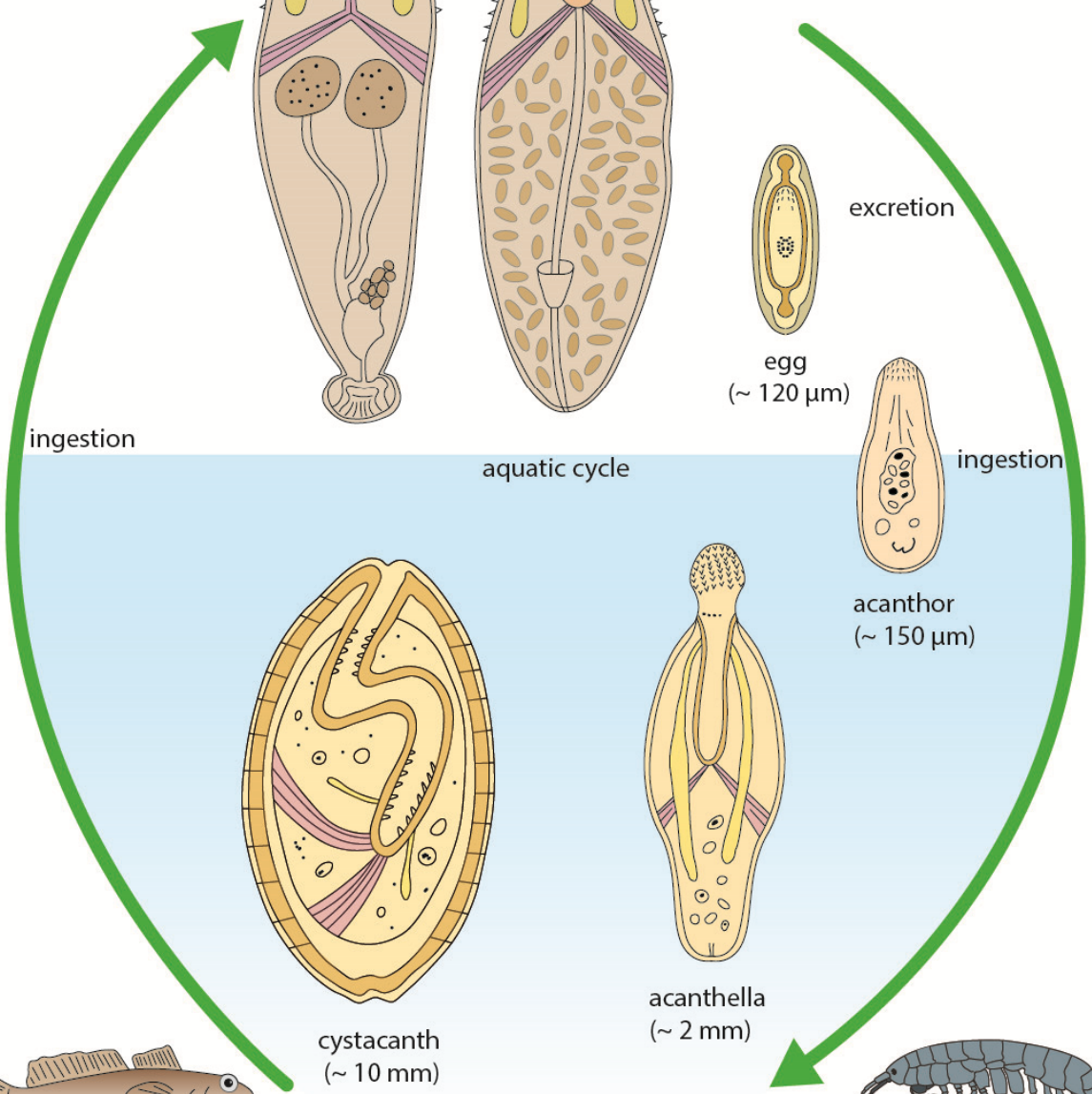
acanthella  
(~ 2 mm)

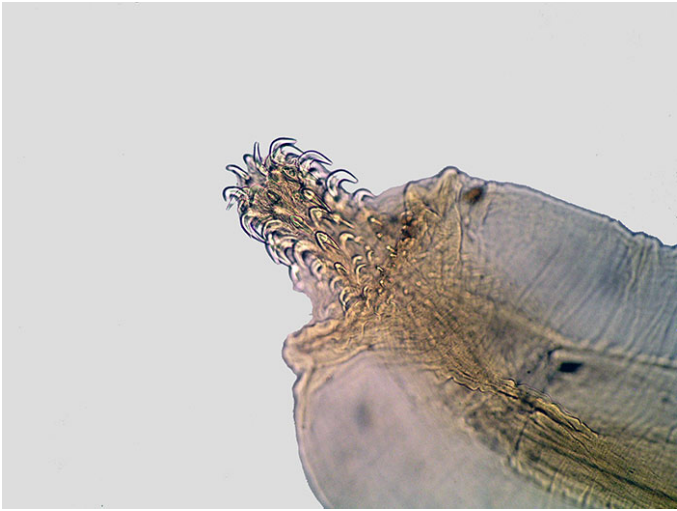


Occasional Paratenic Hosts  
(small fish e.g. gobies)  
(tissue cysts, lesions)



Intermediate Hosts  
(amphipods, decapods)  
(body cavity)





*Polymorphus proboscis*