Macracanthorhynchus
(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 *Macracanthorhynchus hirudineus* are transmitted by coprophagous beetles to pigs and have been associated with mild 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:	Archiacanthocephala (oval thick-shelled eggs, body wall lacunar canals dorsal & ventral (or just dorsal))
Order:	Oligacanthorhynchida (proboscis subspherical, short rows of several hooks, protonephridial organs present)
Family:	Oligacanthorhynchidae (single family)
Genus:	*Macracanthorhynchus* (parasitic in small intestines of pigs)
Species:	*M. hirudineus* (causes enteritis in pigs)

Parasite biodiversity and host range: Most Metazoa are multicellular triploblastic animals with differentiated tissues, many being bilaterally symmetrical with a body cavity. Most invertebrate animals are protostomes as their embryonic development involves spiral determinate cleavage. Those that 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 class Archiacanthocephala contains 4 orders of terrestrial acanthocephalans whose body walls contain dorsal (and sometimes ventral) lacunar canals, usually 8 uninucleate cement glands, few elongated or branched subcuticular (tegumental) nuclei, and ligament sacs inside the pseudocoel. Worms in the order Oligacanthorhynchida possess a subspherical proboscis with short rows of several hooks and they have protonephridial organs. The order contains a single family Oligacanthorhynchidae with 13 genera (*Macracanthorhynchus, Cucullanorhynchus, Echinopardalis, Heptamegacanthus, Multisentis, Neoncicola, Nephridiacanthus, Oligacanthorhynchus, Oncicola, Pachysentis, Paraprosthenorchis, Prosthenorchis, Tchadorhynchus*). The genus *Macracanthorhynchus* contains 5 species parasitizing domestic and wild animals which become infected by consuming larval stages in intermediate hosts (insects, particularly beetles) or sometimes small vertebrate paratenic hosts (amphibians, lizards).

***Macracanthorhynchus* species**	**Definitive hosts, DH (adults in intestines)**	**Intermediate hosts, IH (larval acanthellae then cystacanths in tissues) [plus paratenic hosts, PH]**	**Distribution**
M. aegypticus	Eulipotyphla: erinaceid (hedgehog)		Africa
M. catulinus	Carnivora: canid (dog, red fox), mustelid (weasel, stoat); Rodentia: murid (spiny mouse, gerbil)	Coleoptera: tenebrionid (soil beetles, *Adesmia*, *Dissonomus, Pachyscelis, Stalagmoptera, Tentyria, Trigonoscelis*) [plus PHs, Sauria: anguid (European legless lizard), agamid (Caucasian agama, spiny-tailed lizard), gekkonid (Mediterranean house gecko), scincid (Berber skink), lacertid (trans-Caucasian racerunner, Caspian green lizard); Serpentes: colubrid (black whipsnake), elapid (Caspian cobra), viperid (blunt-nosed viper); Anura: ranid (marsh frog); Rodentia: sciurid (Tarbagan marmot); Carnivora: mustelid (badger, least weasel, steppe polecat)]	Eurasia
M. erinacei	Eulipotyphla: erinaceid (hedgehog)		Africa
M. hirudinaceus (syn. *M. gigas, Echinorhynchus gigas, E. hirudinaceus, Gigantorhynchus gigas, G. hirudinaceus, Hormorhynchus gigas,*	Artiodactyla: suid (pig); Carnivora: canid (dog); Primates: hominid (human)	Coleoptera (mainly larval grubs but also adult beetles): scarabaeid (cockchafers, rose chafer, vine chafer, shining leaf chafer, flower chafer, May bugs, June beetle, dung beetles, scarab beetles, Japanese beetle, rhinoceros beetle), carabid (ground beetles), hydrophilid	worldwide

H. hirudinaceus, Taenia haeruca, T. hirudinaceus) (giant thorny-headed worm)		(water beetles); Diptera: empidid (dance fly); Blattodea: ectobiid (wood cockroach), blattid (cockroach)	
M. ingens (syn. *Echinorhynchus, Prosthenorchis*)	Carnivora: procyonid (raccoon, ring-tailed cat), canid (dog, grey fox), mephitid (striped skunk), mustelid (American mink), ursid (American black bear); Eulipotyphla: talpid (hairy-tailed mole); Primates: hominid (human); Artiodactyla: suid (pig); Strigiformes: strigid (barred owl); Charadriiformes: larid (western gull)	Coleoptera (mainly larval grubs but also adult beetles): scarabaeid (May bugs, scarab beetles, rhinoceros beetle); Blattodea: ectobiid (wood cockroach); Diplopoda: spirobolid (large millipedes) [plus PHs, Serpentes: colubrid (eastern kingsnake, green water snake, banded water snake, eastern racer, common garter snake), viperid (cottonmouth); Anura: ranid (northern leopard frog); Cingulata: dasypodid (nine-banded armadillo)]	North America, Eurasia

Parasite morphology: Acanthocephalan worms form three different developmental stages: eggs; larvae (acanthor, acanthella and cystacanth); and adults. The eggs are oval (measuring 90-110 x 50-65 µm), dark brown in colour, embryonated (containing the first larval stage known as an acanthor), and thick-shelled (surrounded by 3 embryonic envelopes). Acanthors released in the intermediate host are spindle-shaped with anterior hooks and spines. They penetrate to the body cavity where they encapsulate and moult into second stage larvae (acanthella) which are the main growing stages. They increase in size from mm to cm and come to resemble miniature adult worms, albeit immature in that they do not yet possess mature reproductive organs. They form encysted infective stages (cystacanths), essentially resting juveniles containing an inverted proboscis. When ingested by a definitive host, they excyst, evert their proboscis and attach to the gut wall to develop further. Adult worms have elongated curved sac-like bodies, some species measuring up to 1 m in length by 3-9 mm wide. They have 3 main body regions (proboscis, neck and trunk) and are usually flattened bilaterally (although specimens pretreated with water before fixation may become turgid and cylindrical). Most worms are cream in colour but may occasionally be pigmented (yellow-brown to pink) depending on host gut content. Adults do not contain alimentary tracts, the body cavity being bound by syncytial body walls with prominent transverse wrinkles and minute crypts greatly increasing their surface area for the exchange of gases, nutrients and wastes by diffusion. Much of the tegument comprises radial fibers with a fluid-filled lacunar system continuous with the tubular muscles of the body wall. Worms possess an excretory system consisting of protonephridial organs and flame cells. A distinctive feature of these thorny-headed or spiny-headed worms is the possession of a retractable (invertible) cylindrical proboscis or rostellum armed with several rows of recurved spiny hooks. The bulk of the trunk contains the proboscis receptacle, retractor muscles and associated lemnisci (elongate hydraulic sacs thought to act a reservoirs for lacunar fluid). Mature worms are dioecious, with females being larger than males (10-65 cm long compared to 2-15 cm). Males possess two testes, each with a vas deferens, cement glands and a common ejaculatory duct and Safftigen's pouch terminating in a small eversible copulatory bursa. During copulation, sperm ejected into the vagina escape into the body cavity via the genital duct and the male then plugs the vagina using the cement glands to prevent further copulation. Females contain a unique funnel-shaped uterine bell that receives and delivers developing shelled embryos to the uterus (only mature eggs are delivered, while immature eggs are returned to the pseudocoelom for further maturation).

Site of infection: Adult worms infect the small intestines of their definitive hosts (suids, rodents and carnivores) while larval stages (acanthella and cystacanths) form in the haemocoel (body cavity) of their intermediate hosts (insects) or encyst within the internal tissues of paratenic hosts (amphibians, reptiles and carnivores).

Pathogenesis: Adult acanthocephalans do not feed on host tissues but absorb nutrients across their body walls. However, adult worms insert their armed proboscis deeply into the wall of the intestine and they also move occasionally to attach to new sites. Intestinal bacteria usually infect attachment sites forming inflammatory granulomatous nodules (sometimes called blackberry spots). These lesions may become haemorrhagic with blood and protein loss. Recently vacated sites appeared as deep infected ulcers while old healed sites appear as firm fibrous nodules. Nonetheless, light infections by only a few parasites often remain subclinical, while heavy infections by many parasites may result in significant unthriftiness due to blood loss, impaired nutrition and escalating inflammation (cumulative effects of many localized lesions leading to enteritis and gastritis). Clinical signs of diarrhoea, emaciation, abdominal pain and poor weight gain have been described in pigs infected with *M. hirudinaceus*. On occasion, the long parasite proboscis may perforate the thin intestinal wall and if not sealed off by host inflammatory reactions, such perforations may lead to peritonitis and death. Infected pigs become listless, unthrifty and may experience severe pain if the gut wall is perforated. Most human cases have involved mild infections of the gastrointestinal tract, although one case reported an ectopic infection of a patient's eye.

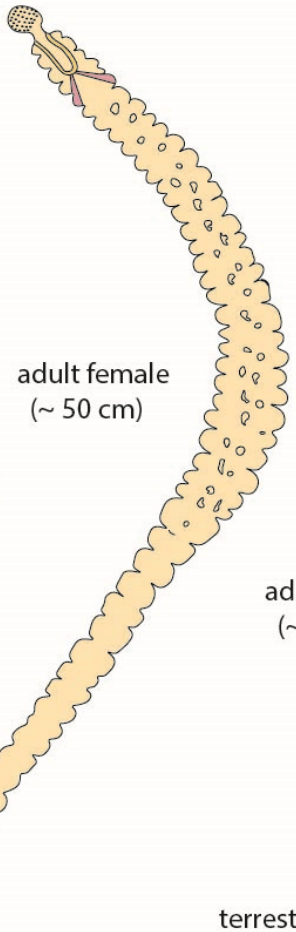
Developmental cycle and mode of transmission: Acanthocephalans have indirect life cycles involving cyclic transmission between definitive hosts (vertebrates infected with adult stages), intermediate hosts (invertebrates infected with larval stages) and sometimes paratenic hosts (vertebrates infected with larval stages) or post-cyclic hosts (vertebrates infected with adult stages). Mature female worms lay embryonated eggs which are voided into the environment with host faeces. The eggs do not hatch until they are ingested by an appropriate arthropod intermediate host (including beetles, esp. larval grubs, cockroaches, flies and millipedes). They then release the enclosed acanthor which burrows into the host body cavity (haemocoel) where they encapsulate and grow through an acanthella stage to a resting infective cystacanth in 6-12 weeks. These stages do not develop further until infected intermediate hosts are ingested by suitable definitive hosts, whereupon they excyst, evert their armed proboscis and attach to the gut wall to feed, grow and develop into sexually mature adult worms over 8-12 weeks. If the cystacanths of some species are ingested by inappropriate hosts (non-definitive hosts), they may bore through the gut wall into the body cavity and then re-encyst (thus utilizing these hosts as paratenic hosts). *M. ingens* and *M. catulinus* have been found to use amphibians, snakes, lizards, rodents and armadillos as paratenic hosts, but *M. hirudinaceus* does not. Post-cyclic transmission may also occur when adults in definitive hosts are ingested by predators in which they may survive. In definitive hosts, adult worms mature, mate and females begin egg production (individual females may lay up to 250,000 eggs per day for several months). The prepatent period (time from infection until egg production) is around 2-3 months and worms may live for up to 1 year. Infections in pigs are most prevalent in areas where animals are kept under poor hygienic conditions and beetles have access to pig faeces. Infections in humans generally occur in areas where insects are eaten for dietary or medicinal reasons.

Differential diagnosis: Infections can be difficult to detect by ante-mortem coprological examination because the parasite eggs are heavy and do not float reliably in most conventional salt solutions. Sedimentation techniques should therefore be used. Adult worms can be detected on post-mortem examination of gut samples, and darkened nodular lesions are often visible through the serosal surface.

Treatment and control: Anthelmintic chemotherapy with levamisole, ivermectin or doramectin has proven effective against clinical infections in pigs, dogs and humans. The drugs fenbendazole, niclosamide and loperamide have also been used with some success against infections in pigs, but earlier treatments with carbon tetrachloride, tetrachlorethylene and nicotine sulphate were only partly effective. Many infections in livestock, however, appear to be self-limiting and do not persist so chemoprophylaxis is not widely used except in high-risk situations. Parasite control in piggeries is best afforded by improving housing hygiene, regular removal of faeces, proper effluent treatment and disposal, limiting exposure to contaminated lots or pastures, insect-proofing feed storage areas and restricting access of beetles (the usual intermediate hosts) to pigs and pig faeces.

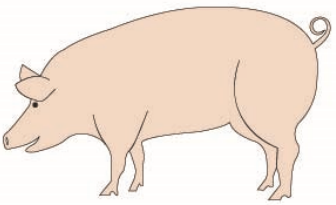
Macracanthorhynchus

intestines
(trauma, nodules)



adult female
(~ 50 cm)

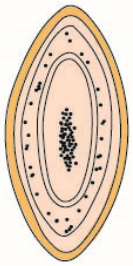
proboscis
(thorny-headed)



Definitive Hosts
(pigs, some carnivores)

adult male
(~ 5 cm)

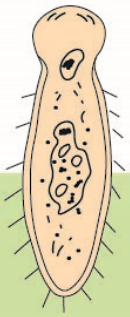
excretion



egg
(~ 100 µm)

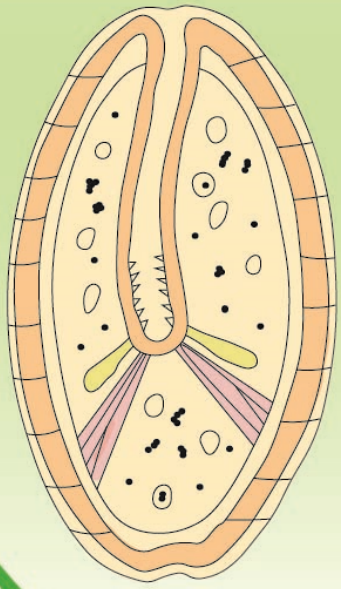
ingestion

terrestrial cycle

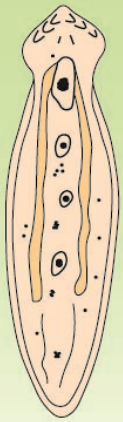


ingestion

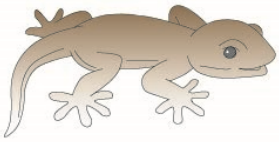
acanthor
(~ 120 µm)



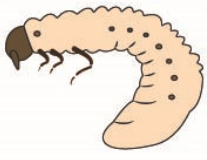
cystacanth
(~ 5 cm)



acanthella
(~ 5 mm)



Occasional Paratenic Hosts
(lizards, snakes, frogs, rodents)
(tissue cysts, lesions)



Intermediate Hosts
(beetle larvae)
(haemocoel)

Macracanthorhynchus adult worms

Macracanthorhynchus anterior proboscis