HELMINTH PARASITES

The word 'helminth' is a general term meaning 'worm', but there are many different types of worms. Prefixes are therefore used to designate types: platy-helminths for flatworms and nemat-helminths for roundworms. All helminths are multicellular eukaryotic invertebrates with tube-like or flattened bodies exhibiting bilateral symmetry. They are triploblastic (with endo-, meso- and ecto-dermal tissues) but the flatworms are acoelomate (do not have body cavities) while the roundworms are pseudocoelomate (with body cavities not enclosed by mesoderm). In contrast, segmented annelids (such as earthworms) are coelomate (with body cavities enclosed by mesoderm). Many helminths are free-living organisms in aquatic and terrestrial environments whereas others occur as parasites in most animals and some plants. Parasitic helminths are an almost universal feature of vertebrate animals; most species have worms in them somewhere.

Biodiversity

Five major assemblages of parasitic helminths are recognised: the Nemathelminthes (nematodes), the Acanthocephala (spiny-headed worms), and the Platyhelminthes (flatworms), the latter being subdivided into the Cestoda (tapeworms), the Trematoda (digenetic flukes) and the Monogenea (monogenetic flukes):

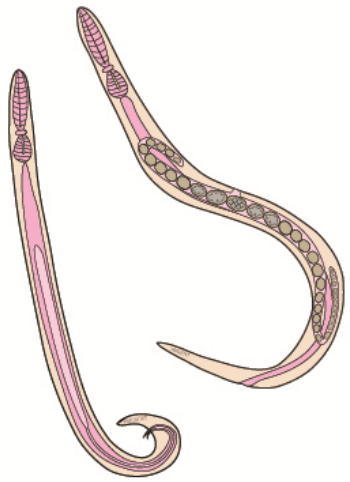
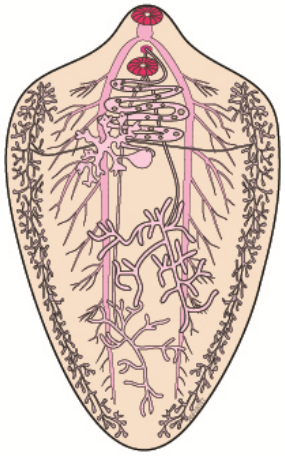
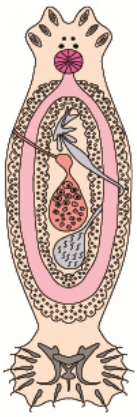
- Nematodes (roundworms) have long thin unsegmented tube-like bodies with anterior mouths and longitudinal digestive tracts. They have a fluid-filled internal body cavity (pseudocoelom) that acts as a hydrostatic skeleton providing rigidity (so-called 'tubes under pressure'). Worms use longitudinal muscles to produce a sideways thrashing motion. Adult worms form separate sexes with well-developed reproductive systems: females with 1-2 ovaries connected to the uterus via a tubular oviduct, and males with a single testis connected to the vas deferens, seminal vesicle and ejaculatory duct.

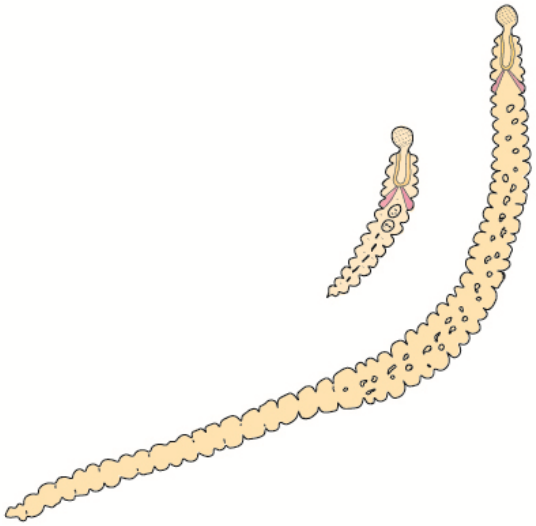
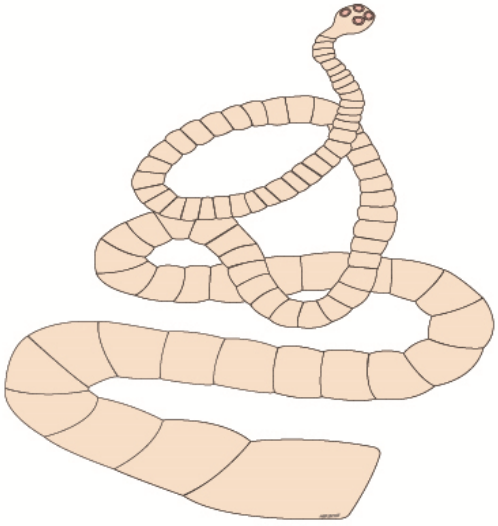
- Acanthocephalans (thorny-headed worms) have elongated flattened bodies with transverse wrinkles and a distinctive cylindrical invaginable proboscis bearing rows of recurved spines. They lack digestive tracts and absorb nutrients through their tegument. Adults form separate sexes: males having 2 testes; and females producing ovarian balls that float free in the pseudocoelom with developing eggs 'sorted' by a unique funnel-shaped uterine bell.

- Cestodes (tapeworms) have long flat ribbon-like bodies with a single anterior holdfast organ (scolex) and numerous segments. They do not have a gut and all nutrients are taken up through the tegument. They do not have a body cavity (acoelomate) and are flattened to facilitate perfusion to all tissues. Segments exhibit slow body flexion produced by longitudinal and transverse muscles. Most tapeworms are hermaphroditic and each segment contains both male and female organs.

- Trematodes (digenetic flukes) have small flat leaf-like bodies with oral and ventral suckers and a blind sac-like gut. They are acoelomate and dorsoventrally flattened with bilateral symmetry. They exhibit elaborate gliding or creeping motion over substrates using compact 3-D arrays of muscles. Most species are hermaphroditic (individuals with male and female reproductive systems) although some blood flukes form separate male and female adults. They have indirect life-cycles involving asexual reproduction in molluscs.

- Monogeneans (monogenetic flukes) have leaf-like to cylindrical acoelomate bodies with a prominent posterior attachment organ armed with hooks, suckers and/or clamps. They are hermaphroditic and have direct life-cycles involving free-swimming ciliated larvae (oncomiracidia).

nematode	digenean	monogenean
		

acanthocephalan	cestode
	

Taxonomic classification

Traditionally, most helminths (worms) were classified together with different groups recognised on the basis of body plan, development and habitats. The nematodes (roundworms) were considered a sister group to the platyhelminths (flatworms), the latter comprising cestodes (flat ribbon-like tapeworms) and trematodes (flat leaf-like flukes). The trematodes were further divided into the Monogenea and Digenea on the basis of their monogenetic (1-host) and digenetic (2 or more host) life-cycles. Many textbooks have retained this simplistic classification, which is convenient if not accurate. Modern phylogenetic studies have demonstrated considerable differences between roundworms and flatworms as well as between many flatworm groups. The extent of those differences has facilitated a complete reorganization of extant metazoan groups, with many groups reassigned to new composite taxa.

While Protozoa (Protista) are unicellular eukaryotic organisms, the Metazoa are multicellular eukaryotes with differentiated tissues. They form a major division in the animal kingdom, exclusive of the sponges. Metazoans are triploblastic (with three body germ layers), most have a coelom (body cavity) and they exhibit bilateral symmetry (except the cnidaria (jellyfish) which exhibit radial symmetry). Their embryonic development includes a blastula stage, and two major lineages are recognised depending on the type of cleavage at the 8-cell embryonic stage and the fate of the blastopore: the protostomes (exhibiting determinate cleavage, mostly spiral, and the blastopore becomes the mouth) and the deuterostomes (with indeterminate radial cleavage and the blastopore becomes the anus). The deuterostomes comprise the echinoderms (starfish) and the chordates (including all vertebrates) while the protostomes contain most of the invertebrate animals. Molecular studies found that two major protostome lineages were well supported: Lophotrochozoa and Ecdysozoa.

The Lophotrochozoa was established as a monophyletic group based on molecular evidence and they have few unifying characteristics. The name derives from the frequent possession of a unique feeding structure called the lophophore (ring of ciliated tentacles) or the presence of a planktonic free-swimming stage called a trochophore (ovoid larva with ciliary bands). However, some groups contain neither (particularly the parasitic representatives). The Lophotrochozoa comprise the platyhelminths (flatworms), rotifers, acanthocephalans, lophophorates (bryozoa, branchiopods, phoronids) and spiralians (nemertea, annelids, molluscs). The acanthocephalans are closely related to the rotifers because members of both groups have a eutelic syncytial epidermis (with fixed numbers of nuclei). The platyhelminths are soft-bodied acoelomate flatworms that include free-living 'Turbellaria' (a taxonomically artificial group) and parasitic Trematoda, Monogenea and Cestoda. All the major parasitic groups have Mehlis' (shell) glands surrounding the ootype where the egg is constructed, and ectolecithal egg development (yolk not present in egg but secreted by accessory glands called vitellaria or yolk glands). The trematodes, monogeneans and cestodes are bound by syncytial (multiple nuclei enclosed within a single cell membrane) teguments (neodermis) and have recently been collectively classified together as the Neodermata which is considered a lineage comprised exclusively of parasites. The endoparasitic trematodes (Aspidogastrea and Digenea) have flattened leaf-like bodies with anterior adhesive organs; of these, the dominant Digenea undergo asexual sporocyst development within molluscan intermediate hosts. The ectoparasitic Monogenea have a posterior adhesive organ and have free-swimming oncomiracidial larval stages in their one-host life-cycles. The endoparasitic cestodes have flattened ribbon-like bodies with an anterior scolex and segmented proglottids that lack digestive tracts. Their life-cycles involve at least 2 hosts.

The Ecdysozoa are organisms which have hard cuticles and can only grow by periodic moulting (ecdysis). They comprise the nematodes (roundworms), onychophorans (velvet worms), tardigrades (water bears) and arthropods (myriapods, chelicerates, crustaceans and hexapods, all with jointed limbs). The nematodes are unsegmented tubular worms covered by a collagenous elastic cuticle without microvilli. They have a fluid-filled body cavity (pseudocoelom) that acts as a hydrostatic skeleton. They have prominent longitudinal muscles which are used to produce a conspicuous thrashing motion. The worms have complex sensory papillae; namely, amphids near the head particularly in free-living species but reduced in parasitic species, and supplemented by phasmids near the tail. Their differential presence has led to the recognition of two major classes: the Secernentea (secretors) with phasmids (= Phasmidea), and the Adenophorea (gland-bearers) without phasmids (= Aphasmidea). However, molecular phylogenetic studies have only partially supported morphotypic classifications and have revealed many unexpected groupings. Studies on ribosomal DNA sequences suggested the existence of five major clades while more comprehensive studies on mitochondrial DNA indicated as many as 12 clades. A revised classification based on both genotypic and phenotypic characters identified three major nematode lineages: Dorylaimia, Enoplia and Chromadoria. The Dorylaimia contains both free-living and parasitic assemblages; many being omnivores or predators and some parasitizing plants and animals (invertebrates and vertebrates). Most possess an odontostyle, a tooth for puncturing food items. The Enoplia are bactivorous or predatory nematodes in moist aquatic or terrestrial habitats or parasitic on plants. They display great osmotic tolerance and many have large hooks or teeth and complex sensory structures such as eyespots and unique stretch receptors (metanemes). The Chromadoria includes several diverse free-living and parasitic lineages whose bodies usually have annules, spiral amphids and three oesophageal glands. The previously-recognised Secernentea (Phasmidea) was found to be deeply nested within the Chromadoria, and has now been relegated to the order Rhabditida. Chromadorian nematodes are common in marine sediments and moist soils (incl. mosses and lichen). They are often small and rapidly reproducing bacterial feeders, although some are predators with sophisticated 'can-opener' teeth. Many species have chemically impermeable cuticles which probably contributed to their success as parasites, colonizers and

extremophiles. Many rhabditids are parasitic in fungi, plants or animals and have been associated with severe diseases and production losses. They possess well-developed pharynxes with one or more rounded muscular bulbs, and their life cycles often involve modified larval ('dauer') stages adapted to long-term survival. Although the phylogenetic relationships between all the disparate nematode groups are slowly being unravelled, most parasitological texts still retain conventional taxonomic classification schemes which provides good group coverage for important human and animal parasites.

Supergroup: Amorphea	(unikonts, with single flagellum, or nonflagellated amoebae)
Opisthokonta	(stages with single posterior flagellum)
Holozoa	(metazoans, filasterans, ichthyosporeans, choanomonads)
Metazoa	(multicellular eukaryotes, heterotrophic)
Protostomia	(triplobastic, spiral cleavage)
▪ Group: Lophotrochozoa	(lophophore feeding structure or trochophore larva or neither)
Phylum: Platyhelminthes	(acoelomate flatworms)
Neodermata	(syncytial tegument = neodermis)
• Class: Trematoda	(leaf-like flukes, anterior sucker, sac-like gut, monoecious)
•• Subclass: Aspidogastrea	(endoparasites with 2-host cycles, no asexual reproduction)
•• Subclass: Digenea	(digenetic endoparasites, asexual reproduction in first int. host)
••• Order: Diplostomatida	(blood and intestinal flukes of all vertebrate classes, cercariae usually penetrate next host)
••• Order: Plagiorchiida	('echinostomatids', plagiorchiids', all vertebrate classes, cercarial behaviour diverse)
• Class: Monogenea	(posterior opisthaptor, oncomiracidia, monoecious, monoxenous)
••• Order: Monopisthocotylea	(opisthaptor with hooks and hooklets)
••• Order: Polyopisthocotylea	(opisthaptor with clamps)
• Class: Cestoda	(tapeworms, without gut, monoecious, heteroxenous, endoparasites)
•• Subclass: Eucestoda	(larvae hexacanth (with six hooks))
••• Order: Caryophyllidea	(aquatic hosts, fish-annelids, simple scolex, one proglottid)
••• Order: Cathetocephalidea	(elasmobranchs, apical pad, papillary band)
••• Order: Diphyllidea	(elasmobranchs, 2 bothria, armed rostellum, cephalic peduncle)
••• Order: Trypanorhyncha	(elasmobranchs, 2-4 bothria, 4 spiny retractile tentacles)
••• Order: Litobothriidea	(elasmobranchs, apical sucker, 3-5 muscular pseudosegments)
••• Order: Lecanicephalidea	(elasmobranchs, 4 small suckers surmounted by globular structure)
••• Order: Rhinobothriidea	(elasmobranchs, 4 stalked loculate bothridia)
••• Order: 'Tetraphyllidea' relics	(elasmobranchs, mammals, 4 stalked bothridia)
••• Order: Spathebothriidea	(marine fish, without bothria or suckers)
••• Order: Haplobothriidea	(marine fish, club-shaped tentacles, bothria)
••• Order: Bothriocephalidea	(fish, amphibians, 2 bothria)
••• Order: Nippotaeniidea	(freshwater fish, scolex with one apical sucker)
••• Order: Tetrabothriidea	(birds, mammals, 4 muscular bothridia)
••• Order: Phyllobothriidea	(elasmobranchs, unarmed bothridia, apical suckers)
••• Order: Oncoproteocephalidea	(cold-blooded vertebrates, 4 loculate bothridia, rostellum)
••• Order: Diphyllobothriidea	(Pseudophyllidea) (aquatic hosts, unarmed scolex, 2 shallow bothria)
••• Order: Cyclophyllidea	(terrestrial hosts, scolex with four suckers, often bearing hooks)
•• Subclass: Cestodaria	(larvae decacanth (with ten hooks))
••• Order: Amphilinidea	(fish hosts, uterus N-shaped, posterior genital pores)
••• Order: Gyrocotylidea	(fish hosts, anterior testes, anterior genital pores)
Phylum: Mesozoa	('middle-animals', parasites of marine invertebrates)
Phylum: Nemertea	(ribbon worms, marine)
Clade: Gnathifera	(small cuticular jaws, except Acanthocephala)
Phylum: Gnathostomulida	(jaw worms, marine sediments)
Phylum: Micrognathozoa	(interstitial sands)

Group: Syndermata (eutelic syncytial epidermis)

Phylum: Rotifera (rotifers, ciliated corona, aquatic, epizoic or parasitic)

Phylum: Acanthocephala (thorny-headed worms, parasitic, arthropod-vertebrate cycles)
- Class: Archiacanthocephala (terrestrial cycles, myriapod/insect intermediate hosts)
  - •• Order: Apororhynchida (intestines, birds, bulbous proboscis)
  - •• Order: Gigantorhynchida (intestines, birds, long proboscis armed with two rows of 6 hooks)
  - •• Order: Moniliformida (intestines, mammals, cylindrical proboscis)
  - •• Order: Oligacanthorhynchida (proboscis subspherical, short rows of hooks, protonephridial organs)
- Class: Palaeacanthocephala (aquatic cycles, malacostracan intermediate hosts)
  - •• Order: Echinorhynchida (fish, long proboscis with 14-22 rows of 10-16 hooks)
  - •• Order: Polymorphida (proboscis bulbous/cylindrical, numerous hooks in rows)
- Class: Eoacanthocephala (aquatic cycles, maxillipod intermediate hosts)
  - •• Order: Gyracanthocephala (freshwater fish, large proboscis with 4 circles of recurved hooks)
  - •• Order: Neoechinorhynchida (freshwater fish, short proboscis with three rows of 6 hooks)

Phylum: Cycliophora (live in mouthparts of marine decapods)

Phylum: Gastrotricha (gastrotrichs, aquatic)

Phylum: Entoprocta (entoprocts, aquatic, some commensals on annelids)

Group: Lophophorates (lophophore mouths, radial cleavage)

Phylum: Ectoprocta (bryozoa, moss animals)

Phylum: Brachiopoda (lamp shells, marine sediments)

Phylum: Phoronida (phoronids, coastal waters)

Phylum: Mollusca ('soft-bodied', chitons, tusk shells, snails, slugs, nudibranchs, sea butterflies, clams, mussels, oysters, squid, octopuses, nautiluses)

Phylum: Annelida (segmented worms, oligochaetes, polychaetes, leeches)

Phylum: Echiura (spoon worms, marine sediments)

Phylum: Sipuncula (peanut worms, marine sediments)

- Group: Ecdysozoa (cuticle moulted = ecdysis)

Group: Nematoidea (collagenous cuticle without microvilli)

Phylum: Nematoda (= Nemata) (pseudocoelomate roundworms, tubular digestive tract, dioecious)

- Class: Enoplea (lacking phasmids, free-living and parasitic)
  - Subclass: Enoplia (free-living, amphids shaped like stirrups, smooth bodies)
    - •• Order: Enoplida (bactivores, algivores, omnivores, predators)
    - •• Order: Triplonchida (aquatic, some phytoparasites)
  - Subclass: Dorylaimia (free-living and parasitic, odontostyle)
    - •• Order: Dorylaimida (phytoparasites, algivores, omnivores, predators)
    - •• Order: Monochida (bactivores, algivores, omnivores, predators)
    - •• Order: Isolaimida (free-living in soils)
    - •• Order: Dioctophymatida (animal parasites)
    - •• Order: Muspiceida (vertebrate parasites)
    - •• Order: Marimermithida (invertebrate parasites)
    - •• Order: Mermithida (invertebrate parasites)
    - •• Order: Trichinellida (vertebrate parasites)

- Class: Chromadorea (free-living and parasitic, spiral amphids, three oesophageal glands)
  - Subclass: Chromadoria (soils, marine and terrestrial)
    - •• Order: Desmoscolecida (marine)
    - •• Order: Chromadorida (bactivores, algivores, omnivores, predators)
    - •• Order: Desmodorida (bactivores, algivores, omnivores, predators)
    - •• Order: Monhysterida (bactivores, algivores, omnivores, predators)
    - •• Order: Araeolaimida (bactivores, algivores, omnivores, predators)
    - •• Order: Plectida (bactivores, algivores, omnivores, predators)
    - •• Order: Rhabditida (= Secernentea, Phasmidea) (with phasmids)
      - ••• Suborder: Spirurina (animal parasites)
        - ••• Infraorder: Gnathostomatomorpha (vertebrate parasites)
        - ••• Infraorder: Oxyuridomorpha (vertebrate and invertebrate parasites)
        - ••• Infraorder: Rhigonematomorpha (invertebrate parasites)
        - ••• Infraorder: Spiruromorpha (vertebrate parasites)
        - ••• Infraorder: Ascaridomorpha (vertebrate parasites)
      - ••• Suborder Myolaimina (bactivores, phytoparasites)
      - ••• Suborder Tylenchina (fungal, plant, animal parasites)
        - ••• Infraorder: Panagrolaimomorpha (bactivores)
        - ••• Infraorder: Cephalobomorpha (bactivores)
        - ••• Infraorder: Tylenchomorpha (fungivores, phytoparasites, invertebrate parasites)
        - ••• Infraorder: Drilonematomorpha (invertebrate parasites)
      - ••• Suborder Rhabditina (often with larval ‘dauer’ stage)
        - ••• Infraorder: Bunonematomorpha (invertebrate parasites)
        - ••• Infraorder: Diplogasteromorpha (omnivores, predators, invertebrate parasites)
        - ••• Infraorder: Rhabditomorpha (entomopathogens, vertebrate/invertebrate parasites)

Phylum: Nematomorpha (horsehair worms, aquatic)

Phylum: Kinorhyncha (spine-necked worms, marine sediments)

Phylum: Priapulida (priapulids, marine sediments)

Phylum: Loricifera (loriciferans, marine sediments)

Group: Panarthropda (haemocoel)

Phylum: Onychophora (velvet worms, litter)

Phylum: Tardigrada (water bears, mosses, lichen, moist soil)

Phylum: Arthropoda (joint-footed, insects, arachnids and allies)

Life-cycles

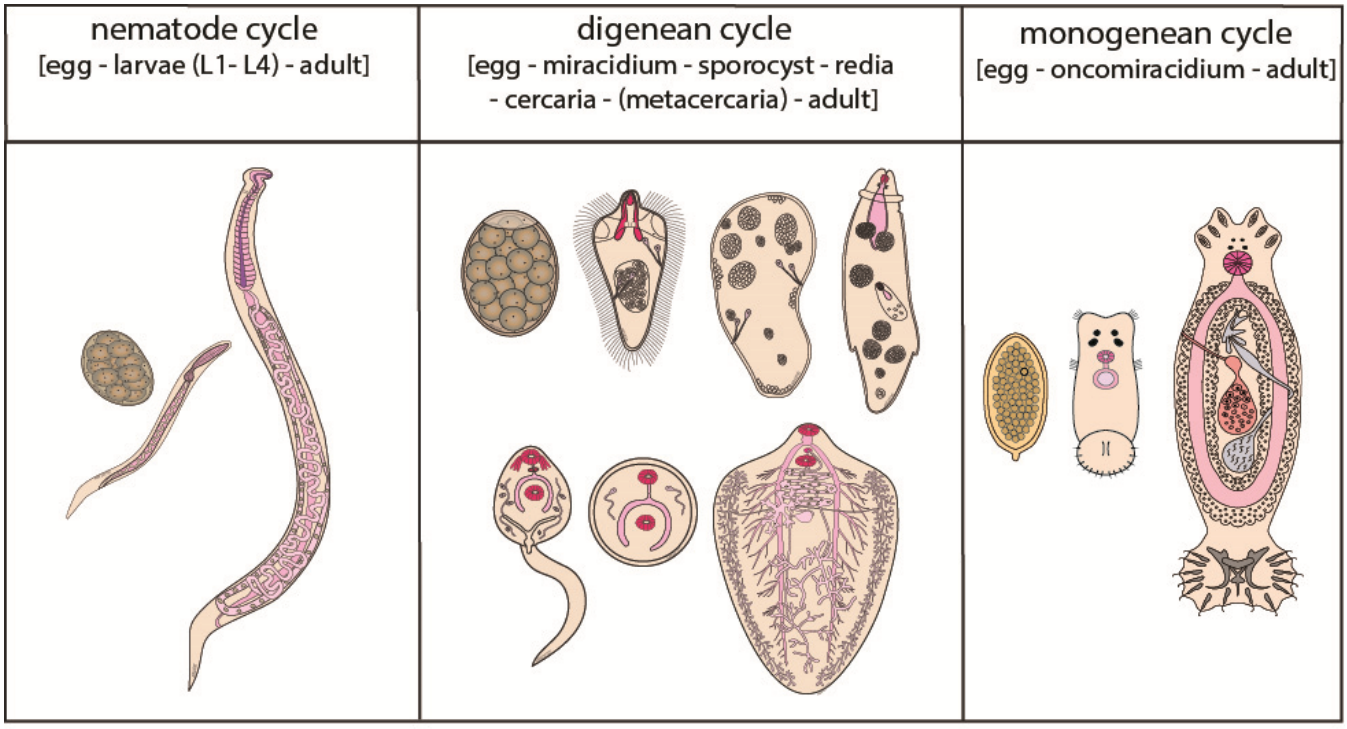
Unlike other pathogens (viruses, bacteria, protozoa and fungi), helminths typically do not proliferate within their hosts. Worms grow, mature and then produce offspring which are voided from the host to infect new hosts. Worm burdens in individual hosts (and often the severity of infection) are therefore dependent on the number of infective stages taken up. Worms also develop slowly compared to other infectious pathogens so any resultant diseases are often slow in onset and chronic in nature. Although most helminth infections are well tolerated by their hosts and are often asymptomatic, subclinical infections may be associated with significant loss of condition in infected hosts. Some helminths cause serious clinical diseases characterized by high morbidity and mortality. Clinical signs of infection vary considerably depending on the site and duration of infection. Larval and adult nematodes lodge, migrate or encyst within tissues resulting in obstruction, inflammation, oedema, anaemia, lesions and granuloma formation. Infections by adult cestodes are generally benign as they are not invasive, but the larval stages penetrate and encyst within tissues leading to inflammation, space-occupying lesions and organ malfunction. Adult flukes usually cause obstruction, inflammation and fibrosis in tubular organs, and the eggs of blood flukes can lodge in tissues causing extensive granulomatous reactions and hypertension.

Helminths form three main life-cycle stages: eggs, larvae and adults. Adult worms infect definitive hosts (those in which sexual development occurs) whereas larval stages may be free-living or parasitize invertebrate vectors, intermediate or paratenic hosts.

- Nematodes produce eggs that embryonate *in utero* or outside the host. The emergent larvae undergo 4 moults before they mature as adult male or female worms.

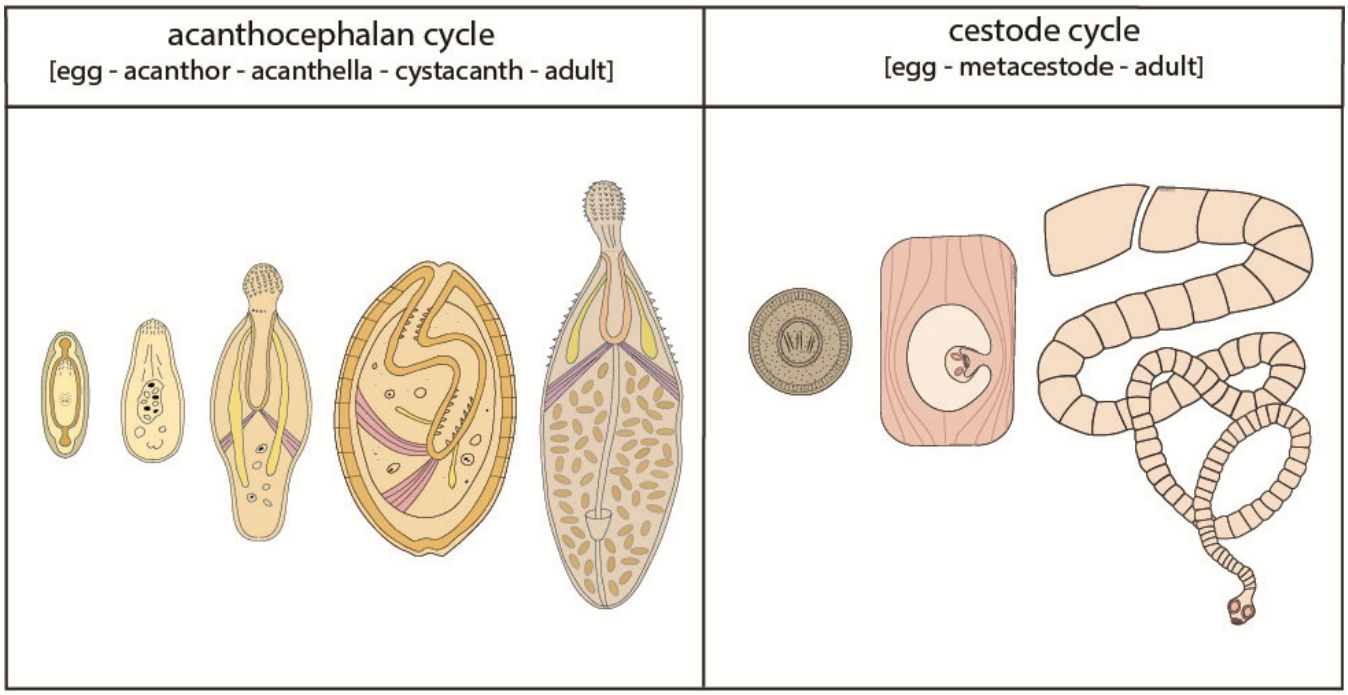
- Digenean trematodes (except for the rare Aspidogastrea) have complex life-cycles involving asexual reproduction in molluscan intermediate hosts. Eggs passed from the vertebrate definitive host hatch to release free-swimming miracidia which actively infect molluscs and develop in sac-like sporocysts to produce numerous rediae. The rediae produce cercariae which emerge from the molluscs and take one or numerous paths to infect the definitive hosts.

- Monogeneans produce eggs which hatch to release free-swimming ciliated larvae (oncomiracidia) that actively seek and attach to hosts.



- Acanthocephalans produce shelled embryos which do not hatch until eaten by an insect intermediate host. The larva (acanthor) develops into a juvenile (cystacanth) which is transmitted to the final host when it eats infected insects.

- Cestode eggs released from gravid segments embryonate to produce six-hooked embryos (hexacanth oncospheres) which are ingested by intermediate hosts. The oncospheres penetrate host tissues and become metacestodes (encysted larvae). When eaten by definitive hosts, they excyst and form adult tapeworms.



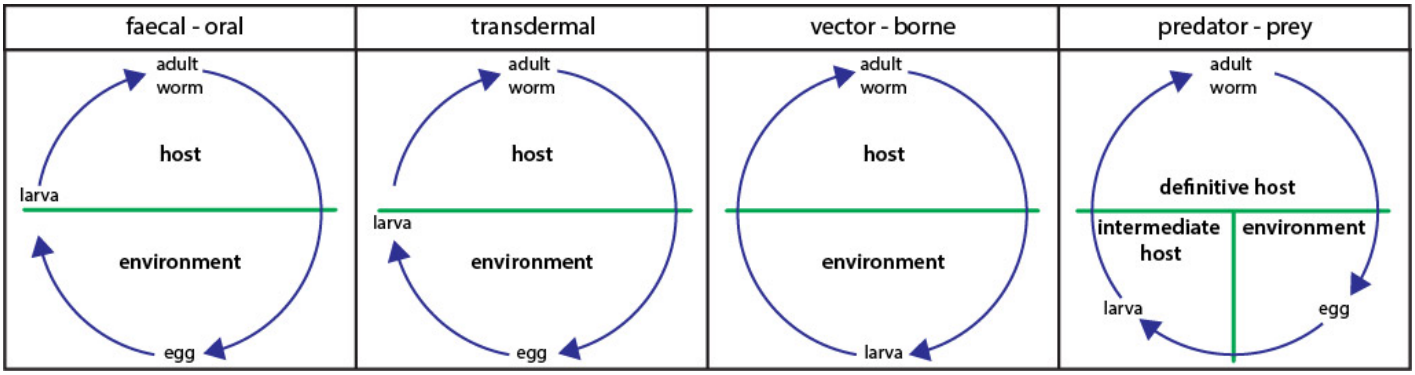
Helminth eggs have tough resistant walls to protect the embryo while it develops. Mature eggs hatch to release larvae either within a host or into the external environment. The four main modes of transmission by which the larvae infect new hosts are faecal-oral, transdermal, vector-borne and predator-prey transmission:

- faecal-oral transmission of eggs or larvae passed in the faeces of one host and ingested with food/water by another (e.g. ingestion of *Trichuris* eggs leads directly to gut infections in humans, while the ingestion of *Ascaris* eggs and *Strongyloides* larvae leads to a pulmonary migration phase before gut infection in humans).

- transdermal transmission of infective larvae in the soil (geo-helminths) actively penetrating the skin and migrating through the tissues to the gut where adults develop and produce eggs that are voided in host faeces (e.g. larval hookworms penetrating the skin, undergoing pulmonary migration and infecting the gut where they feed on blood causing iron-deficient anaemia in humans).

- vector-borne transmission of larval stages taken up by blood-sucking arthropods or undergoing amplification in aquatic molluscs (e.g. *Onchocerca* microfilariae ingested by black flies and injected into new human hosts, *Schistosoma* eggs release miracidia to infect snails where they multiply and form cercariae which are released to infect new hosts).

- predator-prey transmission of encysted larvae within prey animals (vertebrate or invertebrate) being eaten by predators where adult worms develop and produce eggs (e.g. *Dracunculus* larvae in copepods ingested by humans leading to guinea worm infection, *Taenia* cysticerci in beef and pork being eaten by humans, *Echinococcus* hydatid cysts in offal being eaten by dogs).



Overview of major helminth groups parasitizing animals

Nematodes

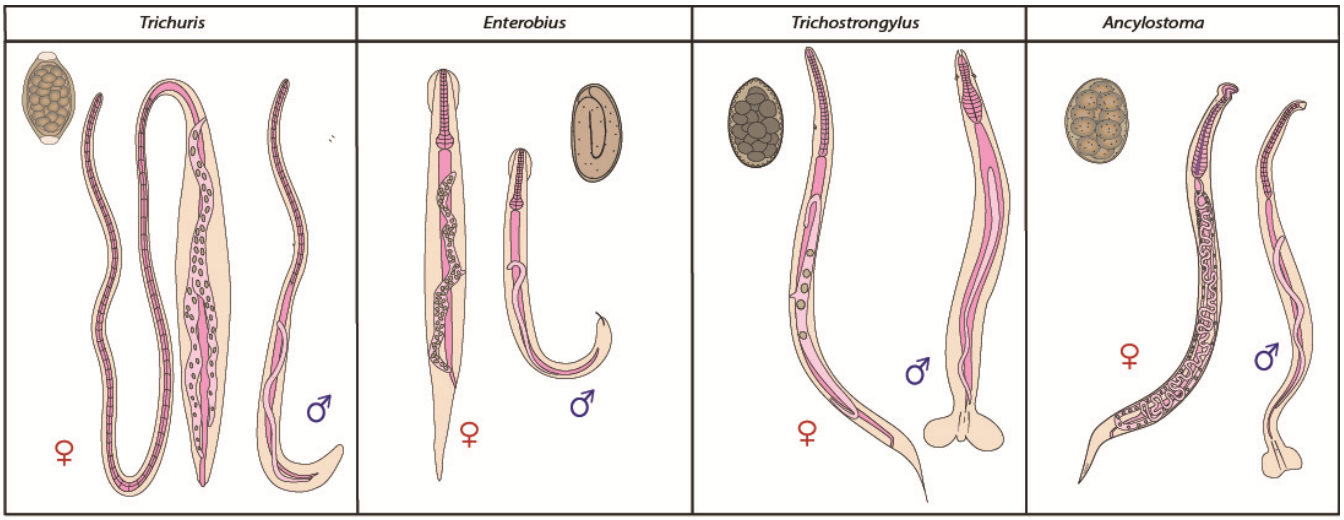
Conventionally, two classes of nematodes are recognised on the basis of the presence or absence of special chemoreceptors known as phasmids: Secernentea (= Phasmidea) and Adenophorea (= Aphasmidea). While many different orders, suborders and infraorders are now recognised in molecular phylogenies, the main parasitic assemblages infecting humans and domestic animals include one aphasmid enoplean order (Trichocephalida = Trichinellida) and three phasmid chromadorean suborders: Rhabditina (infraorder Rhabditomorpha), Spirurina (Dracunculoidea *incertae sedis* and infraorders Ascaridomorpha, Oxyuridomorpha, and Spiruromorpha) and Tylenchina (infraorder Panagrolaimomorpha).

- Trichocephalid 'whipworms' have long thin anterior ends which they embed in the intestinal mucosa of their hosts. They have simple life-cycles where infections are acquired by the ingestion of eggs and emergent larvae moult and mature to adults in the gut. *Trichuris* infections in humans may cause inflammation, tenesmus, straining and rectal prolapse.

- Oxyuridomorphid 'pinworms' have small thin bodies with blunt anterior ends. They have simple life-cycles, but with an unusual modification. Female worms emerge from the anus of their hosts at night and attach eggs to the skin. This causes peri-anal itching and eggs are transferred by hand to mouth. Infections by *Enterobius* cause irritability and sleeplessness in humans, especially children.

- Rhabditomorphid strongyloid 'trichostrongyles' have small bodies with cuticular ridges (synlophe) and males have a well-developed copulatory bursa. They have simple life-cycles where larvae develop on pastures before being ingested by grazing animals. Adult worms infect the gastrointestinal tract and heavy infections by *Trichostrongylus* spp. may cause anaemia, scours, illthrift and death in domestic livestock.

- Rhabditomorphid strongyloid 'hookworms' have dorsally curved mouths armed with ventral cutting plates or teeth which they embed in host tissues to feed on blood. They have complex life-cycles where larvae develop in the external environment (as 'geo-helminths') before infecting hosts by penetrating the skin. Once inside, they undergo pulmonary migration before settling in the gut to feed. Heavy infections by *Ancylostoma* and *Necator* cause severe iron-deficient anaemia in humans, especially children.

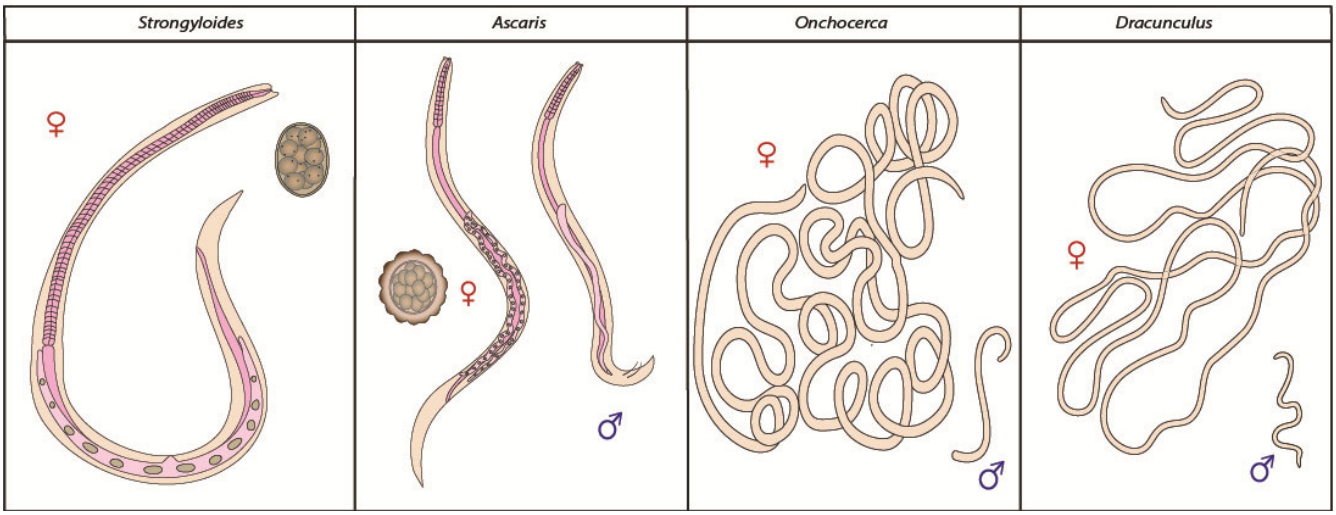


- Panagrolaimomorphid ‘threadworms’ have tiny bodies which become embedded in the host mucosa. Their life-cycle includes parasitic parthenogenetic females producing eggs which may hatch internally (leading to auto-infection) or externally (leading to transmission of infection or formation of free-living male and female adults). Super-infections by *Strongyloides* may cause severe haemorrhagic enteritis in humans.

- Ascaridomorphid ‘roundworms’ have large bodies with 3 prominent anterior lips. Their life-cycles involve a stage of pulmonary migration where larvae released from ingested eggs invade the tissues and migrate through the lungs before returning to the gut to mature as adults. *Ascaris* infections in humans cause gastroenteritis, protein depletion and malnutrition and heavy infections can cause gut obstruction.

- Spiruromorphid filarioid ‘filarial worms’ occur as long thread-like adults in blood vessels or connective tissues of their hosts. The large female worms release live larvae (microfilariae) into the blood or tissues which are taken up by blood-sucking mosquitoes or tissue-feeding flies and transmitted to new hosts. *Onchocerca* infections cause nodules, skin lesions and blindness in humans, while those of *Wuchereria* cause elephantiasis.

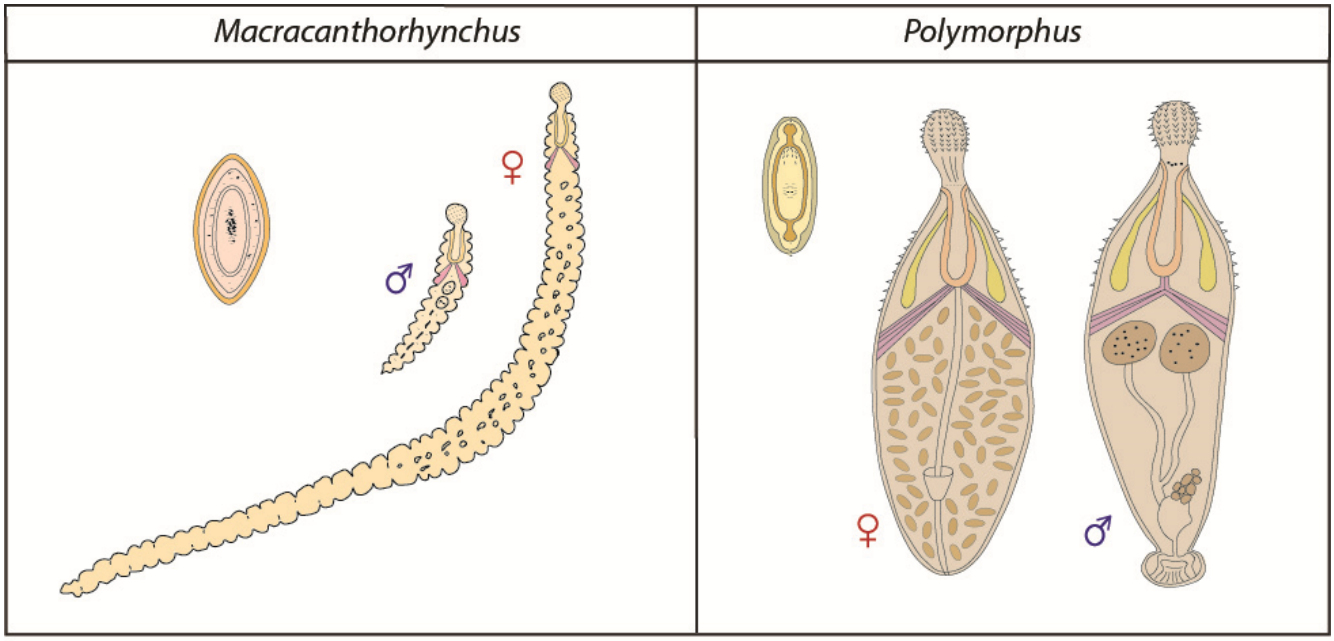
- Dracunculoid ‘guinea worms’ infect host tissues where the large females cause painful blisters on the feet and legs. When hosts seek relief by immersion in water, the blisters rupture releasing live larvae which infect copepods that are subsequently ingested with contaminated drinking water. The ‘fiery serpents’ mentioned in historical texts are thought to refer to *Dracunculus* infections.



Acanthocephalans

Thorny-headed worms have heteroxenous (2-host) life-cycles where adult worms live in the intestines of vertebrate hosts (fish, amphibians, reptiles, birds and mammals) and larval stages develop in arthropod intermediate hosts (insects, crustaceans). Four classes of Acanthocephala are recognised:

- Archiacanthocephala with terrestrial cycles involving mammals/birds and insects (e.g. *Macracanthorhynchus* in pigs and beetles);
- Palaeacanthocephala with aquatic cycles in fish/birds/seals and crustaceans (e.g. *Polymorphus* in ducks and amphipod crustaceans);
- Eoacanthocephala with aquatic cycles in fish/amphibia/reptiles and crustaceans; and
- Polyacanthocephala with aquatic cycles in fish/crocodiles and crustaceans.

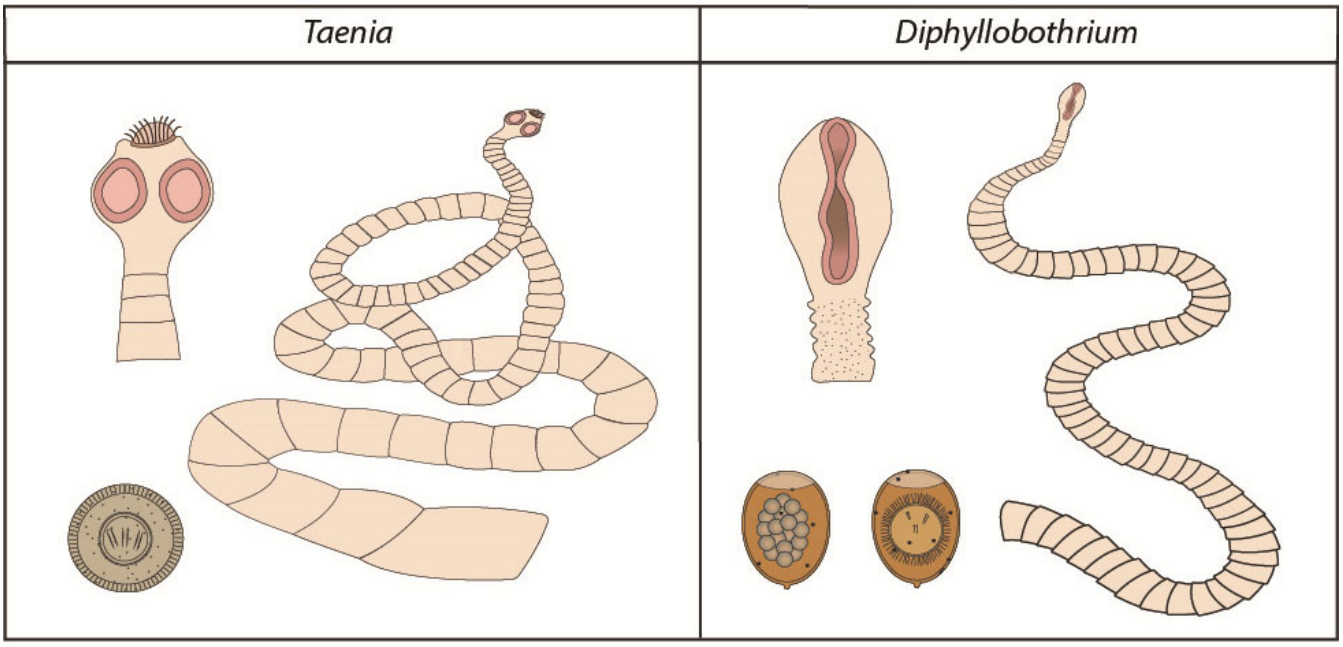


Cestodes

Two subclasses of cestodes are differentiated on the basis of the numbers of larval hooks, the Cestodaria being decacanth (10 hooks) and the Eucestoda being hexacanth (6 hooks). Collectively, 14 orders of cestodes have been identified according to differences in parasite morphology and developmental cycles. Two orders have particular significance as parasites of medical and veterinary importance.

- Cyclophyllidean cestodes have terrestrial 2-host life-cycles where adult tapeworms develop in carnivores (scolex with four suckers and sometimes hooks) while larval metacestodes form bladder-like cysts in the tissues of herbivores. The larvae of *Taenia* spp. cause cysticercosis in cattle, pigs and humans, while those of *Echinococcus* cause hydatid disease in humans, domestic and wild animals.

- Diphyllobothriidean (formerly Pseudophyllidean) cestodes have aquatic 3-host life-cycles, involving the sequential formation of adult tapeworms in fish-eating animals (scolex with two longitudinal bothria), procercoid larval stages in aquatic invertebrates (copepods) and then plerocercoid (spargana) stages in fish e.g. *Dibothriocephalus* (formerly *Diphyllobothrium*) in humans, dogs and cats being transmitted through copepods and fish.

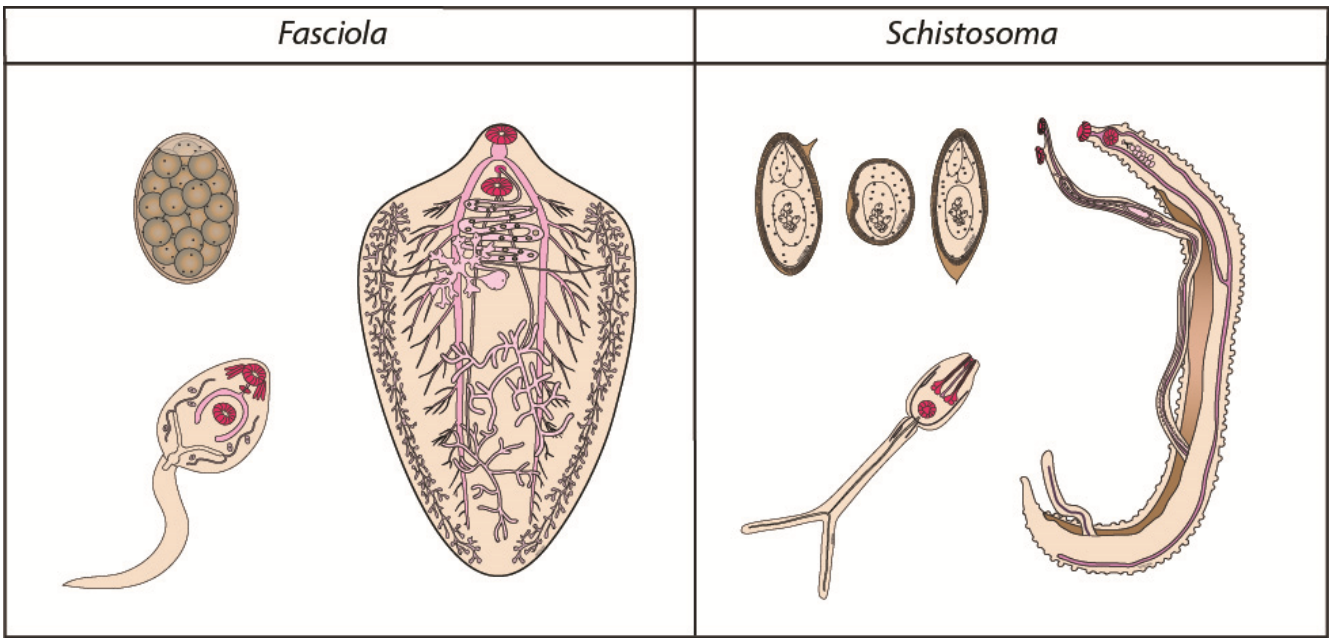


Trematodes

The Trematoda is divided into 2 subclasses: the Aspidogastrea with divided or loculated ventral suckers and the absence of asexual reproduction; and the Digenea with undivided ventral suckers and the occurrence of asexual reproduction in the first intermediate host in addition to sexual reproduction in the definitive host. The Digenea is divided into 2 orders: Diplostomida and Plagiorchiida.

- The Diplostomida contains one suborder which includes the blood flukes of fishes, reptiles, birds and mammals (including humans). The genus *Schistosoma* has multiple species that infect humans by direct penetration of the skin by fork-tailed cercariae. Infections may cause a debilitating disease known as schistosomiasis or bilharzia when fluke eggs become trapped in host tissues and organs resulting in extensive granuloma formation.

- The Plagiorchiida is a much larger and more diverse order containing 14 suborders that include many species of importance in human and animal health; e.g. *Clonorchis* and *Opisthorchis* liver flukes in humans, *Fasciolopsis* intestinal flukes in humans and pigs, *Fasciola* liver flukes in domestic livestock, *Paramphistomum* stomach flukes in ruminants, and *Paragonimus* lung flukes in carnivores and rodents.



Monogeneans

Monogeneans are almost exclusively ectoparasites of fishes although a few species infect the urinary tracts of some turtles, frogs and birds and the eyes of the hippopotamus. They have direct life-cycles where the oncomiracidium that hatches from the egg swims directly to the host, attaches and begins development to the adult worm. Two subclasses are recognised mainly in the complexity of the posterior attachment structures: the Monopisthocotylea; and the Polyopisthocotylea.

- The Monopisthocotylea have a posterior haptor comprising a single symmetrical attachment unit with hooks and hooklets (but no haptoral clamps). Adults feed on fish epithelia and most species are oviparous and lay eggs (e.g. *Dactylogyrus* gill flukes, and *Benedenia* skin flukes) although some are viviparous and produce live young (e.g. *Gyrodactylus* skin flukes). Infestations may cause morbidity and mortality in fishes, especially in hatcheries, aquaria and intensive aquaculture systems.

- The Polyopisthocotylea have complex opisthaptors with several clamps or suckers used to attach to gill filaments where most feed on blood. Infestations have been recorded on a wide range of freshwater and marine fishes, elasmobranchs, holocephalans and some frogs.