Spirometra
(platyhelminth: cestode)

Overview

Platyhelminths have triploblastic acoelomate soft bodies which are markedly flattened in profile (hence their common name as flatworms). They undergo protostomial embryonic development but do not moult during growth. On the basis of molecular evidence, they are classified within the Lophotrochozoa despite the absence of lophophore mouthparts and trochophore larvae. Three classes are composed entirely of parasitic flatworms (Cestoda, Trematoda and Monogenea), which have prominent attachment organs (suckers or bothria), syncytial teguments, shell glands and vitellaria involved in ectolecithal egg development, and life-cycles involving a variety of larval stages. Cestodes (tapeworms) have elongate ribbon-like bodies ranging from a few millimetres to several metres in length. Diphyllobothriidean (formerly pseudophyllidean) tapeworms are intestinal parasites of fish-eating birds and mammals and have an anterior scolex (holdfast organ with two elongate grooved bothria) and a posterior tape (strobila) made up of segments (proglottids). Adult worms lack a gut (they absorb nutrients) and they are hermaphroditic (segments containing both male and female reproductive organs). They have indirect life-cycles involving two intermediate hosts. Eggs shed into water release motile coracidia which are ingested by copepods and develop into first-stage larvae (procercoids). When ingested by fish, they form second-stage larvae (plerocercoids or spargana) in host tissues which are transmitted to final hosts by piscivory. Aquatic animals may also act as paratenic hosts for plerocecoids. Infections by *Spirometra* spp. occur in humans and fish-eating mammals, sometimes causing enteric disorders.

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)
Phylum:	Platyhelminthes (flatworms, acoelomate, most hermaphroditic, prominent attachment organs)
Clade:	Neodermata (syncytial tegument = neodermis)
Class:	Cestoda (tapeworms, gut absent, anterior scolex, proglottid segments, heteroxenous, predator-prey cycles)
Subclass:	Eucestoda (larvae hexacanth (with six hooks))
Order:	Diphyllobothriidea (= Pseudophyllidea) (aquatic hosts, scolex with bothria, central genital pores, two IH)
Family:	Diphyllobothriidae (coracidium, procercoid in copepods, plerocercoids in frogs, often PHs)
Genus:	*Spirometra* (parasitic in small intestines of carnivores)
Species:	various species cause sparganosis in humans, dogs and cats

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. Platyhelminths (flatworms) have soft acoelomate flat bodies with three-dimensional arrays of muscles that generate a typical writhing motion (cf. longitudinal muscles in nematodes producing a thrashing motion). Flatworms do not have a single unifying characteristic (synapomorphy) but comprise diverse free-living (most Turbellaria) and parasitic (Neodermata) assemblages. Neodermata have non-ciliated syncytial (multinucleate) teguments and 3 classes are recognized, all with prominent attachment organs, namely, Cestoda with anterior bothridia/bothria (true/false suckers), Trematoda with oral and ventral suckers (acetabula), and Monogenea with posterior haptors (opisthaptors). All have shell glands surrounding the ootype, and most exhibit ectolecithal egg development (yolk not present in egg but secreted by accessory glands called vitellaria or yolk glands). Most have indirect life-cycles involving the development of adult worms in vertebrates and larval stages in intermediate hosts (usually invertebrates).

The cestodes (or tapeworms) lack digestive tracts and have elongate ribbon-like bodies (strobila); most being polyzoic (segmented) divided internally and/or externally into proglottids, although some are monozoic (unsegmented). Serial proglottids may be craspedote (overlapping) or acraspedote. Proglottids are generally hermaphroditic, possessing both male and female reproductive organs (those in which the male system matures first are protandrous, those in which the female system matures first are progynous). Terminal proglottids may detach from the strobila when they are immature (hyperapolytic), mature (euapolytic) or gravid (apolytic), or remain attached until they degenerate (anapolytic). Cestodes possess remarkable anterior attachment organs on the head (scolex): many divided into 4 membrane-bound muscular acetabula evident as suckers or bothridia (stalked, fused or bearing loculi); others bearing two weakly muscular bothria; some possessing a simple apical funnel (monobothriate); and some with a complex apical organ or rostellum that may be retractable, armed with hooks or bearing tentacles. Fertile tapeworms produce

eggs in which larval stages develop as non-ciliated oncospheres or ciliated coracidia or lycophores. These stages possess 6 or 10 hooks which they use to invade the tissues of intermediate hosts where they form encysted metacestode stages: either alacunate forms (procercoid with tail-like cercomer, plerocercus with retracted scolex, plerocercoid with an everted scolex, or merocercoid with an invaginated scolex) or lacunate forms (cysticercoid with cercomer and a retracted scolex, or cysticercus with an invaginated scolex). Two main cestode subclasses are recognized: Cestodaria with decacanth larvae (with 10 hooks) and Eucestoda with hexacanth larvae (with 6 hooks). The Eucestoda are divided into 17 orders on the basis of many morphological and biological differences, many groups being well supported by contemporary molecular characterization studies. Acetabulate orders (with bothridia) include Lecanicephalidea, Tetraphyllidea, Proteocephalidea, Cyclophyllidea, Tetrabothriidea, Phyllobothriidea and Rhinebothriidea; those bearing bothria include Bothriocephalidea, Caryophyllidea, Diphyllidea, Diphyllobothriidea, Haplobothriidea, Spathebothridea and Trypanorhyncha; while others with apical pads/suckers include Cathetocephalidea, Litobothridea and Nippotaeniidea.

Order (+ no. families)	**No. spp.**	**DH[a]**	**Scolex**	**IH1[b]**	**Stage[d]**	**IH2[c]**	**Stage[d]**
Class: **Cestoda** (tapeworms, without gut, monoecious, endoparasites, heteroxenous, predator-prey cycles)							
monozoic (unsegmented)							
Subclass: Cestodaria (adult lacking scolex, larvae decacanth (with 10 hooks))							
Gyrocotylidea (1)	10	F,S,L	muscular sucker-like organ	-	-	-	-
Amphilinidea (1)	8	F,P	muscular proboscis, or absent	C	pro	-	-
Subclass: Eucestoda (‘true’ tapeworms, adult with variable scolex; larvae hexacanth (with six hooks))							
Caryophyllidea (4)	122	F	acetabula, loculi, bothria, apical disc or polymorphic	W	pro		
polyzoic (segmented)							
Cathetocephalidea (1)	6	S	apical pad, papillary band				
Diphyllidea (2)	59	S,R	2 bothria; armed rostellum	C,L	ple		
Trypanorhyncha (16)	315	S,R	2 or 4 bothria, 4 tentacles	C	pro	F,C,L	ple, plc
Litobothridea (1)	9	S	apical sucker, 3-5 segments				
Lecanicephalidea (3)	90	S,R	4 suckers or bothridia, and apical structure or tentacles	C,L,F	pro		
Rhinebothriidea (4)	136	R	4 stalked loculate bothridia	C	pro	F	ple
“Tetraphyllidea’ relics (6)	104	S,R,M	4 stalked bothridia	C	pro	F,L,C, M	ple, mer
Spathebothridea (4)	6	F	undifferentiated or 1-2 bothria	C	ple		
Haplobothriidea (1)	2	F	club-shaped, tentacles, bothria	C	pro	F	ple
Bothriocephalidea (7)	132	F,A	2 bothria	C	pro	F	ple
Nippotaeniidea (1)	6	F	single sucker	C			
Tetrabothriidea (1)	70	B,M	4 muscular bothridia	C,F			
Phyllobothriidea (1)	69	S,R	unarmed bothridia, apical suckers	C,F	ple		
Oncoproteocephalidea (2)	562	F,A,P,S,R	4 loculate bothridia,rostellum	C	pro	F	ple
Diphyllobothridea (6) (= Pseudophyllidea)	70	M,B,P,A	2 shallow bothria, unarmed	C	pro	F,A,P, M	ple
Cyclophyllidea (16) (incl. Mesocestoididae)	3,034	M,B,P	4 suckers, rostellum, often armed	M,A,B, L,T,I	ccc, ccs	-	-

LEGEND
[a] DH = definitive host; [b] IH1 = first intermediate host; [c] IH2 = second intermediate host;
[A = amphibian; B = bird; C = crustacean; F = teleost; I = insect; L = mollusc; M = mammal, P = reptile; R = ray; S = shark; T = acarine; W = annelid];
[d] Metacestode: pro = procercoid, plc = plerocercus; ple = plerocercoid, mer = merocercoid; ccc = cysticercoid; ccs = cysticercus, coenurus, strobilocercus or hydatid cyst

Diphyllobothriidean (= Pseudophyllidean) cestodes are polyzoic with complete or incomplete segmentation. They possess an anterior scolex with 2 shallow grooves (bothria) which are unarmed and their genital organs and pores are centrally located on the ventral surface. Adult worms are found in vertebrate definitive hosts, usually aquatic mammals such as seals and cetaceans, but infections have also been recorded in piscivorous mammals and birds (canids, felids, rodents, occasionally humans) as well as in reptiles (pythons, varanids) and amphibians (African frogs). Larval stages (metacestodes) are usually formed in two intermediate hosts: cercoids (procercoid-type) forming in first intermediate hosts (copepods); then metacercoids (plerocercoid-type) developing in second intermediate hosts (fish, amphibians, reptiles, mammals, occasionally humans). Over 240 species have been described in 19 genera in 3 families: Cephalochlamydidae, Diphyllobothriidae, and Solenophoridae (earlier works also recognized another 3 families (Ligulidae, Schistocephalidae, and Scyphocephalidae) but they are no longer considered valid).

Members of the family Diphyllobothriidae are characterized by adult tapeworms possessing a spatulate scolex with 2 shallow elongated grooves (bothria) located dorsally and ventrally, craspedote proglottids with a small common genital atrium on the midventral surface and reproductive organs comprising a bilobed ovary, numerous testes and a cirrus sac, and eggs containing a coracidium (hexacanth embryo sheathed in a ciliated embryophore). Some 13 diphyllobothriid genera have been described: including *Adenocephalus*, *Baylisia*, *Baylisiella*, *Dibothriocephalus*, *Diphyllobothrium*, *Flexobothrium*, *Glandicephalus*, *Ligula*, *Plicobothrium*, *Pyramicocephalus*, *Schistocephalus*, *Spirometra* and *Tetragonoporus*. The genus *Spirometra* is characterized by diphyllobothrids with a spiral-shaped uterus (as opposed to the rosette-shaped uterus in *Diphyllobothrium*). Around 40 *Spirometra* species have been described as intestinal parasites of mammalian definitive hosts (wild and domestic carnivores) with larval stages developing as procercoids in first intermediate hosts (copepods, crustaceans) and then as plerocercoids (spargana) in a range of second intermediate hosts (frogs, reptiles, mammals, some birds, but not fish). Humans usually act as intermediate or paratenic hosts for tissue infections with spargana (becoming infected after drinking water contaminated with copepods, or applying animal flesh to open wounds as poultices), but occasionally humans may act as definitive hosts for intestinal infections with adult tapeworms (becoming infected after eating animal flesh containing pleroceroids). It is estimated that more than 20 million people harbour infections; most reported throughout Asia, with sporadic cases recorded in the Americas, Africa, Europe and Australia.

***Spirometra* species**	**Definitive host [adults in intestines]**	**First intermediate hosts [procercoids in tissues]**	**Second intermediate hosts, incl. paratenic hosts [plerocercoids in tissues]**	**Distribution**
Hosts for adult stages known				
S. bresslaui (syn. *Diphyllobothrium*)	Didelphimorphia: didelphid (common opossum)			South America
S. decipiens (syn. *S. longicolle, longicollis, Dibothrium, Diphyllobothrium, Dibothriocephalus*)	Carnivora: felid (jaguar, jaguarundi, cat, clouded leopard, kodkod, margay, cougar), canid (dog, crab-eating fox, South American gray fox), mephitid (Molina's hog-nosed skunk), mustelid (lesser grison, southern river otter); Didelphimorphia: didelphid (white-eared opossum, lutrine opossum); Rodentia: cricetid (olive grass mouse), murid (black rat, brown rat); Primates: hominid (human)		Anura: leptodactylid (butter frog), microhylid (painted chorus frog), ranid (dark-spotted frog)	India, China, South America
S. didelphidis (syn. *Bothriocephalus, Diphyllobothrium*)	Didelphimorphia: didelphid (big-eared opossum)			South America
S. erinaceieuropaei (syn. *Dubium, Diphyllobothrium, S. erinacei, felis, Bothriocephalus felis, maculatus, Dibothriocephalus felis, Sparganum lanceolatum, proliferum, Plerocercoides prolifer*) (zipper worm)	Carnivora: felid (cat, wildcat, leopard cat, jungle cat, leopard, clouded leopard, fishing cat, lion, tiger), canid (red fox, Japanese red fox, Pampas fox, dog, wolf, golden jackal, raccoon dog), mephitid (Molina's hog-nosed skunk); Primates: hominid (human)	Copepoda: cyclopid (*Mesocyclops leuckarti*, *Eucyclops serrulatus*)	Eulipotyphla: erinaceid (European hedgehog, Chinese hedgehog, southern white-breasted hedgehog, northern white-breasted hedgehog), soricid (Dsinezumi shrew, bicolored shrew, lesser white-toothed shrew, Mediterranean water shrew, common shrew), talpid (European mole, Japanese shrew mole); Peramelemorphia: peramelid (northern brown bandicoot, long-nosed bandicoot); Dasyuromorphia: dasyurid (fawn antechinus, brown antechinus, dusky antechinus, northern quoll, tiger quoll, eastern quoll, brush-tailed phascogale, common planigale, sandstone false	Eurasia, Americas, Australia

			antechinus, fat-tailed false antechinus, Tasmanian devil); Rodentia: murid (mouse, small Japanese field mouse, large Japanese field mouse, striped field mouse, yellow-necked mouse, rakali, brown rat), sciurid (red squirrel), cricetid (red-backed vole, golden hamster, Japanese grass vole); Carnivora: felid (cat), mustelid (Eurasian otter, beech marten, European pine marten, European badger, stoat, least weasel, ferret, American mink, Japanese marten, European polecat); Artiodactyla: suid (pig); Monotremata: ornithorhynchid (platypus), tachyglossid (short-beaked echidna); Primates: hominid (human), cercopithecid (vervet monkey, Sykes monkey, baboon); Anura: bufonid (cane toad, Argentine common toad), ranid (dark-spotted frog, poor frog, marsh frog, edible frog, rice field frog, Otton frog), hylid (desert tree frog); Serpentes: colubrid (Chinese ratsnake, Japanese striped snake, grass snake, dice snake, tiger keelback, large whip snake), pythonid (Asian rock python, Indian rock python), elapid (death adder), viperid (common European viper, painted carpet viper); Sauria: agamid (Okinawa tree lizard), anguid (European glass lizard)	
S. folium (syn. *Dibothrium*)	Carnivora: herpestid (white-tailed mongoose)			Africa
S. gracile (syn. *Diphyllobothrium*)	Carnivora: felid (long-tailed tiger cat, jaguarundi, Geoffroy's cat, margay)			South America
S. houghtoni (syn. *Diphyllobothrium*)	Carnivora: canid (golden jackal, dog), felid (cat); Primates: hominid (human)			Europe, Asia
S. janickii	Carnivora: felid (Eurasian lynx), canid (wolf)			Europe
S. mansoni (syn. *Sparganum mansoni, Bothriocephalus, Diphyllobothrium, Ligula*)	Carnivora: canid (golden jackal, dog), felid (cat, clouded leopard, lion, fishing cat), viverrid (masked palm civet); Artiodactyla: suid (pig); Primates: hominid (human)	Copepoda: cyclopid (*Cyclops*)	Anura: bufonid (cane toad), dicroglossid (Chinese edible frog, Asian grass frog), ranid (American bullfrog, darkspotted frog, common water frog); Serpentes: colubrid (Chinese garter snake, Amur rat snake, slender racer, Steppe ratsnake, tiger keelback, red-banded snake), viperid (Siberian pit viper), pythonid (Indian rock python); Artiodactyla: suid (pig);	Eurasia, South America, Australia

			Carnivora: mustelid (Siberian weasel, yellow-throated marten), canid (raccoon dog, red fox); Eulipotyphla: erinaceid (Amur hedgehog); Rodentia: murid (mouse); Primates: hominid (human); Galliformes: phasianid (chicken); Passeriformes: passerid (sparrow)	
S. mansonoides (syn. *Diphyllobothrium*)	Carnivora: felid (bobcat, cat, jungle cat, clouded leopard, fishing cat, Geoffroy's cat, ocelot, jaguar, jaguarundi, cougar, lion), canid (dog, crab-eating fox, Pampas fox), procyonid (raccoon); Didelphimorphia: didelphid (Virginia opossum); Artiodactyla: suid (pig); Primates: callitrichid (moustached tamarin), hominid (human); Pelecaniformes: pelecanid (American white pelican)	Copepoda: cyclopid (*Cyclops bicuspidatus, C. leuckarti, C. vernalis, C. viridis*)	Serpentes: colubrid (military ground snake, false coral snake, goldbauch-buntnatter), pythonid (Indian rock python); Anura: ranid (American bullfrog, leopard frog): Rodentia: murid (rats, field mouse, house mouse), cricetid (hamster, cotton mouse), caviid (guinea pig); Didelphimorphia: didelphid (opossum); Lagomorpha: leporid (cottontail rabbit); Carnivora: procyonid (raccoon), canid (grey fox), felid (cat), ursid (black bear); Primates: cercopithecid (rhesus macaque), cebid (ringtail monkey), hominid (human)	Americas
S. marginatus nom. nud. (syn. *Bothriocephalus*)	Diprotodontia: macropodid (pademelon)			Australia
S. okumurai (syn. *Diphyllobothrium*)	Carnivora: canid (dog), felid (lion)			Africa, China
S. pretoriensis (syn. *Lueheella, Diphyllobothrium*)	Carnivora: canid (bat-eared fox, African wild dig, hyena)			Africa
S. raillieti (syn. *Sparganum*)	Artiodactyla: suid (pig)			Europe
S. ranarum (syn. *Ligula*)	Carnivora: felid (cat, fishing cat, clouded leopard, lion), canid (dog, raccoon dog); Artiodactyla: suid (pig); Primates: hominid (human); Serpentes: pythonid (python)		Anura: ranid (edible frog), dicroglossid (Chinese edible frog, Indian bullfrog), leptodactylid (butter frog); Serpentes: colubrid (grass snake)	Eurasia
S. ratticola (syn. *Bothriocephalus*)	Rodentia: murid (black rat)			Asia
S. reptans (syn. *Ligula*)	Primates: cebid (common squirrel monkey), callitrichid (black-tailed marmoset); Chiroptera: noctilionid (greater bulldog bat); Carnivora: canid (dog, crab-eating fox), felid (ocelot, oncilla, leopard), mustelid (tayra, neotropical otter, giant otter, wolverine, marmoset), procyonid (South American coati, coatimundi); Rodentia: cricetid (Brazilian marsh rat); Didelphimorphia: didelphid (yellow-sided opossum, southeastern four-eyed opossum, northern red-		Anura: leptodactylid (butter frog); Sauria: amphisbaenid (red worm lizard); Serpentes: colubrid (two-headed sipo, mussurana, false coral snakes, parrot snake, Rio tropical racer, green snake, chicken snake, Wagler' snake), elapid (Caatinga coral snake), viperid (jacaraca, Neuweid's lancehead, yara, fer-de-lance); Carnivora: canid (dog); Didelphimorphia: didelphid (white-eared opossum, lutrine opossum)	South America

	sided opossum); Coraciiformes: alcedinid (green kingfisher, ringed kingfisher); Anseriformes: anatid (Brazilian merganser); Pelecaniformes: ardeid (cocoi heron, rufescent tiger heron, great white heron, wood stork), threskiornithid (white-necked ibis); Piciformes: bucconid (rusty-breasted nunlet), ramphastid (channel-billed toucan, toco toucan); Ciconiiformes: ciconiid (wood stork); Passeriformes: corvid (curl-crested jay, purplish jay, plush-crested jay), furnariid (anabates), icterid (brown-headed cowbird, crested oropendola), turdid (pale-breasted thrush, rufous-bellied thrush), tyrannid (strange-tailed tyrant); Accipitriformes: pandionid (osprey); Strigiformes: strigid (burrowing owl); Tinamiformes: tinamid (red-winged tinamou); Galliformes: cracid (nocturnal curassow)			
S. serpentis sp. inq. (syn. *Diphyllobothrium*)	Serpentes: elapid (Taiwan cobra)			Asia
S. serratum (syn. *Dibothrium*)	Carnivora: canid (crab-eating fox, dog)			South America
S. sulcatum (syn. *Dibothrium*)	Carnivora: felid (leopard)			Europe
S. tangalongi (syn. *Dibothrium*)	Carnivora: viverrid (Malayan civet)			Asia
S. theileri (syn. *Diphyllobothrium*)	Carnivora: felid (serval, southern African wildcat, lion), canid (dog); Primates: hominid (human)	Copepoda: cyclopid (*Cyclops*)	Rodentia: murid (mice, rats), cricetid (hamster); Artiodactyla: suid (warthog); Primates: cercopithecid (rhesus macaque)	Africa
S. trinitatis (syn. *Diphyllobothrium*)	Carnivora: procyonid (crab-eating raccoon, South American coati)			Americas
S. urichi (syn. *Diphyllobothrium*)	Carnivora: felid (ocelot)			Americas
Hosts for adult stages unknown				
S. affine (syn. *Sparganum*)			Urodela: salamandrid (newt)	Europe
S. ameiva (syn. *Sparganum*)			Sauria: teiid (South American ground lizard)	South America
S. ardeae (syn. *Sparganum*)			Pelecaniformes: ardeid (little blue heron)	South America
S. baxteri (syn. *Sparganum*)			Primates: hominid (human)	Africa
S. canis (syn. *Sparganum*)			Carnivora: canid (dog)	South America
S. cuniculi (syn. *Sparganum*)			Lagomorpha: leporid (European rabbit)	Europe
S. ellipticum (syn. *Sparganum*)			Carnivora: mustelid (beech marten)	Europe

S. falconis (syn. *Sparganum*)			Falconiformes: falconid (unspecified falcon sp.)	ns
S. fausti (syn. *Diphyllobothrium*)			Eulipotyphla: erinaceid (Amur hedgehog)	Asia
S. fernandezi (syn. *Sparganum*)			Artiodactyla: bovid (goat)	South America
S. lanii (syn. *Sparganum*)			Passeriformes: vangid (rufous vanga)	Africa
S. leptodactyli (syn. *Sparganum*)			Anura: leptodactylid (butter frog)	South America
S. liguloides (syn. *Bothriocephalus*)			Primates: hominid (human)	Asia
S. mygales (syn. *Sparganum*)			Carnivora: mustelid (Chinese ferret-badger)	Asia
S. okapiae (syn. *Sparganum*)			Artiodactyla: giraffid (okapi)	Africa
S. pancerii (syn. *Ligula*)			Serpentes: colubrid (grass snake)	Europe
S. philippinensis (syn. *Sparganum*)			Carnivora: viverrid (Asian palm civet)	Asia
S. strigis (syn. *Sparganum*)			Strigiformes: strigid (short-eared owl)	ns

Parasite morphology: *Spirometra* spp. form 4 sequential stages in their developmental cycles: eggs, procercoid larvae, plerocercoid larvae and adult tapeworms. Eggs are ovoid-ellipsoid in shape measuring from 55-70 x 31-50 µm, but are slightly asymmetrical with uneven lateral curvature. They are surrounded by a smooth transparent yellow-brown eggshell with a conical operculum at one end and a thickening at the abopercular end. The eggs are unembryonated when passed in faeces but then form an ovoid coracidium comprising a hexacanth (6 hooked) embryo (oncosphere) surrounded by ciliated embryonic membrane (embryophore). Procercoid larvae are pyriform measuring 55-145 µm long by 20-75 µm wide, alacunate (without internal cavities) and display an anterior invagination with minute spines and a knob-like tail (cercomer) containing oncospheral hooks. Plerocercoid larvae (spargana) have white ribbon-like bodies measuring 2-115 mm long by 1-6 mm wide and are surrounded by a thick tegument. The body is alacunate (without an internal cavity or bladder) and unsegmented but has a wrinkled-corrugated appearance (pseudo-segmented). Most possess an everted protoscolex (developing scolex) with 2 developing bothria (sucker-like grooves), although it is absent or inconspicuous in some species. Adult tapeworms have long dorso-ventrally flattened bodies measuring from 60-110 cm in length by 0.5-1.0 cm in width, some attaining a length of 1.5 m. They have an anterior spoon-shaped scolex measuring 1.8-2.0 x 0.2-0.5 mm which possesses 2 long shallow muscular grooves (bothria) measuring ~ 1 mm in length. The scolex is mounted on a thin unsegmented neck region which gives rise to a long robust segmented strobila formed by up to 1,000 segments (proglottids) which are wider than long (6-10 mm wide by 1.0-2.5 mm long) and sometimes with serrate margins. Adult worms are hermaphroditic with each proglottid containing a single set of male and female reproductive organs, including numerous ovoid testes connected to a common sperm duct, the seminal vesicle and cirrus sac fused together and containing a muscular cirrus (male copulatory organ), numerous vitelline follicles, a bilobed ovary connected to a centrally-located spiral-shaped uterus with 3-5 closely compressed coils (rosette-shaped in *Diphyllobothrium*) and a tubular vagina. The cirrus and vaginal pores open separately on the ventral surface anterior to the uterine (birth) pore. The central location of these pores gives the appearance of a zipper down the middle of the worm (hence the common name of 'zipper worm'). Gravid proglottids contain many eggs which are released through uterine pore into gut lumen and passed unembryonated in faeces. Egg production eventually becomes exhausted and the spent proglottids disintegrate or are shed in faeces.

Site of infection: Adult *Spirometra* worms infect the small intestines of their definitive hosts, mostly carnivorous mammals but sometimes possibly involving rodents, primates, birds and reptiles. Procercoid larvae develop in the body cavities of zooplanktonic crustaceans (notably copepods which act as first intermediate hosts), while plerocercoid larvae (spargana) form in the tissues in a range of vertebrate hosts (including amphibia, reptiles, birds, mammals (carnivores, herbivores, rodents, primates) which act as second intermediate hosts or paratenic transport hosts). Spargana may occur in a variety of tissues and organs, notably subcutaneous tissues, visceral organs, the orbit of the eye, and rarely the brain.

Pathogenesis: Infections by adult tapeworms rarely cause clinical signs in most definitive hosts, although heavy infections may cause enteritis in companion animals, resulting in diarrhoea, weight loss, emaciation, vomiting, irritability, abnormal or exaggerated appetite and occasionally stunted growth in nursing young. Adult worms and plerocercoid larvae have also been shown to deplete vitamin B_{12} from their hosts, possibly contributing to the development of anaemia (as occurs for some *Diphyllobothrium* infections). In contrast, infections by plerocercoid larvae (spargana) may cause a range of clinical conditions depending on which tissues have been infected. Infections have been recorded in a wide range of vertebrates acting as second intermediate and/or

paratenic hosts, notably mammals (carnivores, herbivores, rodents and primates, including humans) but also in birds, reptiles and amphibians. Once ingested, spargana migrate throughout the body but then settle and form nodules at various sites. The early migratory and developmental phases may be asymptomatic, but nodule formation and growth induces intense inflammatory reactions with erythema, oedema, heat, pain, pruritus, urticaria, leucocytosis, eosinophilia and fibrosis (although the larvae do not become encysted). Nodules often appear, disappear and migrate with time (the parasites apparently using a mimic of human growth factor to aid migration), persisting in the host for a long time (up to 20-30 years). The disease sparganosis may manifest in 5 different ways: subcutaneous, visceral, ocular, cerebral or proliferative. The most common form is subcutaneous sparganosis where irregular nodules (1-2 cm) develop in connective tissues in the abdomen, chest and scrotum, accompanied by inflammation, pruritus, urticaria and oedema (sometimes elephantitis). Visceral sparganosis occurs when nodules develop in the intestines, mesenteries, kidneys, pleural cavity, lungs, pericardium or heart resulting in organ malfunction, including gut obstruction or perforation leading to peritonitis or pericardial effusion. Infections in the inner ear have also been associated with vertigo or deafness. In Asia, the most common form is ocular sparganosis where larvae migrate to the conjunctiva and enter the orbit of the eye, producing intense pain, excessive watering, oedema, lacrimation, pruritus, exophthalmos (protrusion of eyeball), cellulitis, corneal ulceration and blindness. A rare form is cerebral sparganosis which occurs when nodules grow in the cerebrum or cerebellum leading to various neurological symptoms, including motor weakness, fatigue, headache, seizures, confusion, memory loss, paresthesias (tingling or numbing sensation of the skin), abscesses, paralysis and coma. A most severe form known as proliferative sparganosis occurs when larvae undergo massive asexual reproduction (by budding or branching) resulting in the spread of nodules often from subcutaneous sites to the muscles and internal organs. Such proliferation take place over years and can prove fatal. Most cases have been traced to infection by the pleomorphic species *S. proliferum* which forms irregular branches and proliferative buds, although several cases involving pleuritis and pneumothorax in dogs have characterized the species responsible as *S. erinacei.*

Developmental cycle and mode of transmission: *Spirometra* spp. have indirect life-cycles involving predator-prey transmission between at least 3 different hosts, with adult tapeworms infecting vertebrate definitive hosts, larval procercoids infecting invertebrate intermediate hosts, and larval plerocercoids developing in vertebrate intermediate and paratenic hosts. Unembryonated eggs released by adult tapeworms are passed in host faeces into the external environment. The eggs embryonate in water over several days depending on temperature (taking longer in cold water) and then hatch releasing a ciliated coracidium. The free-swimming coracidia are ingested by zooplanktonic crustaceans (invariably cyclopid copepods) which act as first intermediate hosts. After ingestion, the coracidia shed their cilia and the oncospheres penetrate the gut wall and form procercoid larvae in the body cavity over several weeks. Infected copepods are then consumed (often in contaminated drinking water) by a wide range of terrestrial and amphibious vertebrates (mammals, birds, reptiles, frogs), which act as second intermediate hosts. The larvae penetrate host tissues and develop over several weeks into worm-like plerocercoid larvae (also called spargana) which may persist for many years. Should animals infected with spargana be eaten by predators that are unsuitable as definitive hosts, the spargana may be transferred to their tissues, thus making them paratenic (transport) hosts. Spargana may ascend the food-chain by passing through several paratenic hosts before infection of the definitive host. Eventually, spargana are ingested by suitable definitive hosts, particularly hunters and scavengers preying on smaller rodents, reptiles and frogs (incl. tadpoles). The larval plerocercoids attach to the gut wall of the definitive host and develop into adult tapeworms. The prepatent period (time from infection to first egg release) ranges from 2-4 weeks and adult worms can live for 0.5-4.0 years. Humans can become infected with several *Spirometra* spp., usually by larval stages in the tissues and rarely by adult tapeworms in the gut. Infections are acquired by eating raw or poorly-cooked meat containing spargana (often from feral pigs, game animals, chickens, reptiles and frogs) resulting usually in the retention of larval spargana in the tissues (humans acting as paratenic hosts) and rarely the development of adult tapeworms in the gut (humans acting as definitive hosts). In Asia, sparagana have also developed in humans after the flesh of infected animals (usually frogs or snakes) has been applied to open wounds, ulcers or sore eyes as medicinal or ritualistic poultices (humans acting as paratenic hosts). Lastly, humans may develop spargana after drinking water containing copepods infected with procercoid larvae (humans acting as second intermediate hosts).

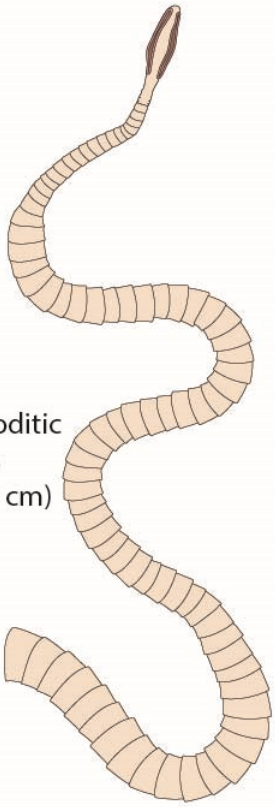
Differential diagnosis: Intestinal infections by adult tapeworms are usually diagnosed by the microscopic detection of eggs in faecal samples following concentration by sedimentation and/or floatation techniques. It is recommended that multiple consecutive samples be examined as egg excretion by worms may be cyclic. Occasionally, strands of spent proglottids may be detected in faecal or vomitus samples. Infections by larval spargana are more difficult to diagnose because pleurocercoids may be located in superficial tissues or deeper in vital organs, thus generating a broad spectrum of clinical symptoms/signs often associated with space-occupying nodules. Like many helminthiases, infections may be accompanied by a marked eosinophilia. Various medical imaging techniques have been applied to the diagnosis of sparganosis, including computed tomography (CT) and magnetic resonance imaging (MRI) scans which reveal migratory nodular lesions characterized by multifocal hypodense regions with irregular punctuate areas of calcification (referable to larval calcareous corpuscles). Differential diagnosis should also consider inflammatory granulomas, tuberculomas, benign and malignant tumours. Where possible, nodules may be surgically removed and the presence of plerocercoid larvae confirmed by microscopic examination. Enzyme immunoassays have been developed to detect host antibodies in serum or cerebrospinal fluid samples to spargana antigens, but some cross-reactivity was noted with other tapeworm genera. Molecular techniques have also been applied to the characterization of adult tapeworms and spargana by polymerase chain reaction (PCR) amplification and sequencing of nuclear (small (18S) and large (28S) subunit rRNA, internal transcribed spacers 1 and 2) and mitochondrial (cytochrome c oxidase subunits 1 and 3 (cox1, cox3), NADH dehydrogenase subunits 1, 3 and 4 (nad1, nad3, nad4) and succinate dehydrogenase subunit 3 (sdh3)) genes.

Treatment and control: Several anthelminthic drugs have been used to successfully treat *Spirometra* infections, both gut infections by adult worms and tissue infections by larval spargana. The isoquinoline, praziquantel, is effective against immature and mature worms and can be administered by many routes (oral, subcutaneous, transcutaneous, intramuscular), but higher and repeated doses may be required to avoid re-infection. The hexyloxynaphthamidine, bunamidine, has been used to treat companion animals but care should be taken to avoid unpleasant side-effects (diarrhoea, vomiting, ventricular fibrillation). The benzimidazole-methylcarbamates (albendazole, fenbendazole and mebendazole) and hydropyrazino-benzazepine (epsiprantel) have proven particularly effective in treating sparganosis, although dead and dying nodules of parasites may present significant challenges to the host. Alternatively, spargana may be surgically removed where feasible, usually by lumpectomy from subcutaneous sites. Various precautions may be taken to prevent infections in domestic and agricultural settings, while little can be done to limit sylvatic cycles in wildlife where many parasite species exhibit broad host specificities. Control strategies centre around minimizing faecal contamination of water (through proper waste/effluent disposal, sewage treatment), reducing transmission to and from copepods (by water treatment and/or filtration) and restricting transmission to vertebrates (by improved food hygiene, cooking meat, curbing hunting and scavenging behaviours, and prohibiting the use of raw meat poultices). Public health education campaigns are mandated as it is difficult to change the dietary habits and medicinal customs of human populations.

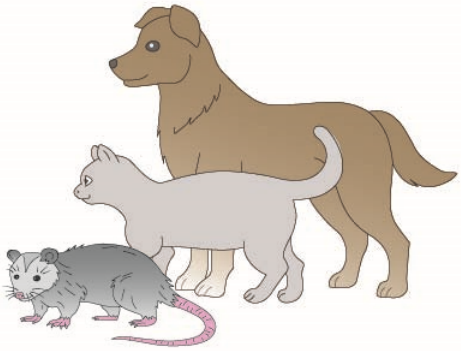
Spirometra

intestines
(sometimes, enteritis,
diarrhoea, emaciation)

scolex

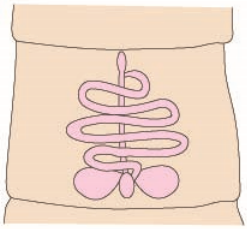


hermaphroditic
adults
(~ 60-110 cm)

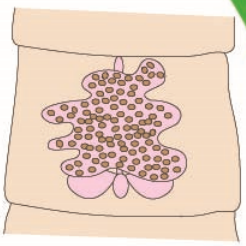


Definitive Hosts
(carnivores)

transmission
through
ingestion
of infected
tissues



mature
proglottid



gravid
proglottid

excretion
of eggs in
faeces

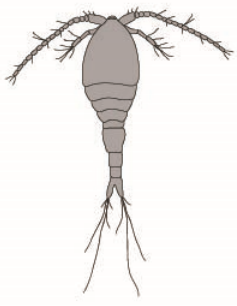
pleurocercoid
(spargana)
(2-100 µm)

eggs
(~ 65 µm)

free-swimming
coracidium
(~ 70 µm)

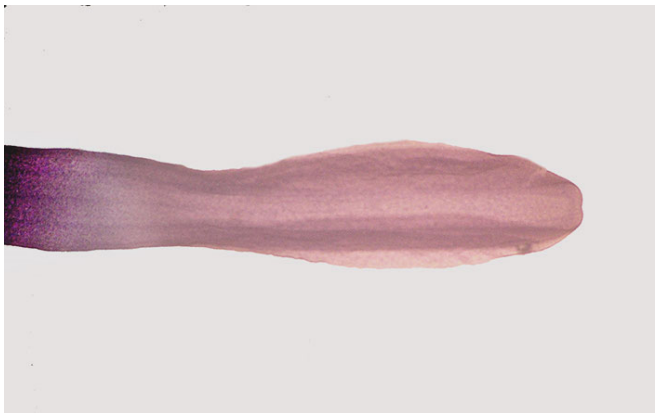
procercoid
(< 100 µm)

Second Intermediate Hosts and Paratenic Hosts
(IH-2/PH) (fish, frogs, lizards, rodents)
(tissue lesions, sparganosis)



First Intermediate Hosts
(IH-1) (copepods)
(body cavity)

Spirometra adult worms



Spirometra scolex

Spirometra segments

Spirometra egg