***Bothriocephalus* (incl. *Schyzocotyle*)**
(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 larval development in invertebrate intermediate hosts. Eggs shed into water release motile coracidia that are ingested by copepods and develop into procercoids and/or plerocercoids which are transmitted to final hosts by piscivory. Infections by *Bothriocephalus* and *Schyzocotyle* spp. occur in freshwater fishes and transmission involves plerocercoid stages in copepods.

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:	Bothriocephalidea (aquatic hosts, scolex with 2 bothria)
Family:	Bothriocephalidae (hexacanth coracidia, procercoid larvae in copepods)
Genus:	*Bothriocephalus/Schyzocotyle* (parasitic in intestines of fish)
Species:	various species cause mortality or stunting in fish

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

Molecular studies confirmed the order Pseudophyllidea to be paraphyletic so it was recently split into two monophyletic clades: Bothriocephalidea and Diphyllobothridea. Adult bothriocephalidean worms are polyzoic with proglottids wider than long surmounted on a distinctive heart-shaped scolex with 2 prominent bothria. They are endoparasitic in the intestines of vertebrate definitive hosts, usually aquatic animals (fish or amphibians). Over 130 species have been described in 48 genera in 7 families: Ancistrocephalidae, Amphicotylidae, Bothriocephalidae, Echinophallidae, Parabothriocephalidae, Ptychobothriidae and Triaenophoridae. Members of the family Bothriocephalidae are characterized by proglottids possessing a median genital pore, bilobed ovary, testes in 2 lateral fields and eggs containing a coracidium (hexacanth embryo sheathed in a ciliated embryophore). Some 17 genera bothriocephalid genera have been described: *Anantrum, Andycestus, Bothriocephalus, Clestobothrium, Ichthybothrium, Kirstenella, Oncodiscus, Penetrocephalus, Plicatobothrium, Plicocestus, Polyonchobothrium, Ptychobothrium, Regobothrium, Schyzocotyle, Senga, Taphrobothrium* and *Tetracampos*. Most genera are relatively uniform in strobilar morphology and they were often differentiated on the basis of minor differences in scolex morphology. Some of these parasites are also unusual in that their life-cycles involve one (not two) intermediate hosts. They use invertebrates (copepods) as the only intermediate hosts,

whereas diphyllobothridean species use invertebrates as first intermediate hosts and then small vertebrates as second intermediate hosts. This has led to some confusion concerning the terminology applicable to the larval stages, which are metacestode or cercoid stages now considered to be plerocercoids, but were formerly referred to as procercoids. Recent molecular studies have indicated that the family Bothriocephalidae is polyphyletic and in need of revision. Over 20 *Bothriocephalus* species have been described in 2 major clades: one infecting freshwater fish and the other marine fish. The Asian fish tapeworm *B. acheilognathi*, now widespread in ornamental and wild freshwater fish populations, has over 20 synonyms, and recent molecular characterization studies have led to its transfer to the resurrected genus *Schyzocotyle*.

Parasite species	**Definitive hosts [adults in intestines]**	**Intermediate hosts [plerocercoids in tissues]**	**Distribution**
Schyzocotyle (wide heart-shaped scolex, narrow deep bothria)			
S. acheilognathi (Asian fish tapeworm) (syn. *Bothriocephalus acheilognathi, aegypticus*, *barbus, barilii, chelai, clupeoidesii, discusae, elongata, fluviatilis*, *gambusiense, gowkongensis*, *khami, kivuensis*, *maesae, monodi, mystacoleucysi, oitense, opsariichthydis*, *phoxini, phuloi, rectangulum, rojanapaibuli, sinensis, spiraliceps, teleostei*)	Cypriniformes: cyprinid (Amur false gudgeon, bitterling, common bream, common carp, gila longfin dace, grass carp, silver carp, common bleak, Caucasian bleak, Danube bleak, Sellal bleak, Patzcuaro chub, mountain chub, spottail chub, Kura chub, Kura barbel, Balkan barbel, Hamilton's barila, white bream, Aztec chub, white-eye bream, kalabans, bangana, common barbel, Niger barb, Algerian barb, striped bystranka, shabout, pike asp, Mexican stone roller, sevan khramulya, Levantine scraper, longspine scraper, Tigris scraper, sharpray, Mesopotamian himri, goldfish, crucian carp, Prussian carp, dace, ornate shiner, largemouth bronze gudgeon, topmouth culter, blue sucker, gibbous shiner, red shiner, Proserpine shiner, spotfin shiner, blacktail shiner, Cuatro Cienegas shiner, kangal fish,, Amur carp, Manantial roundnose minnow, Devils River fish, roundnose minnow, kanyu, broadstriped barb, rosefin barb, hyphen barb, shortfin barb, papermouth, Neumayer's barb, straightfin barb, threespot barb, suckerhead, Jalisco chub, pale chub, Nazas chub, humpback chub, bonytail chub, headwater chub, arroyo chub, conchos chub, roundtail chub, field gudgeon, goby, gudgeon, naked osman, ussuri sharpbelly, sharpbelly, bighead carp, lake stargazer, predatory carp, common nase, Mesopotamian nase, rohu, smallmouth yellowfish, ripon barbel, Niger barb, largemouth yellowfish, largescale yellowfish, Ethiopian yellowfish, Virgin River spinedace, kissing loach, asp, ide, zeravshan dace, Tigris asp, Aral barbel, Bulatmai barbel, Ankara barbel, mangar, Maghreb barb, mursa, Rebot barbel, Rifian barbel, yellowfin barbel, Yahyaoui barbel, long spikyhead carp, Wuchang bream, black Amur bream, binni, spotted sucker, redmouth sucker, black carp, yellowtail barb, golden shiner, emerald shiner, Balsas shiner, Tamaulipas shiner, yellow shiner, spottail shiner, Chihuahua shiner, Papaloapan chub, Nazas shiner, sand shiner, Topeka shiner, pygmy shiner, mimic shiner, Chinese hooksnout carp, three-lips, white Amur bream, sabre carp, rosy barb, sonnenflek barb, common minnow, bluntnose minnow, fathead minnow, woundfin, fat spring minnow, stone moroko, Colorado pikeminnow, northern pikeminnow, spotted barb, speckled dace, European bitterling, white-finned gudgeon, kutum, common roach, Bloch razorbelly minnow, finescale razorbelly minnow, common rudd, creek chub, Alghad snowtrout, false osman, tui chub, barbel chub, chub, marmara chub, Aegean chub, Mesopotamian pike chub, Sakarya chub, Javean barb, olive barb, bicolor minnow, lantern minnow, tench, Javan mahseer, tor mahseer, bigscaled redfin, vimba, Yangtze gudgeon), cobitid (golden-spined loach), nemacheilid (mottled zipper loach, western crested loach, stone loach,	Copepoda: cyclopid (*Acanthocyclops robustus, A. americanus, Cyclops strenus, C. vicinus, Diacyclops thomasi, Eucyclops agilis, Mesocyclops edax, Paracyclops fimbriatus, Tropocyclops prasinus*)	worldwide

	Tibetan stone loach), catostomid (river carpsucker, white sucker, bluehead sucker, Modoc sucker, gray redhorse), gyrinocheilid (Siamese algae-eater), balitorid (Angoran loach); Cyprinodontiformes: cyprinodontid (Kizilirmak toothcarp, Mezquital pupfish, cachorrito del aquanaval), poeciliid (western mosquitofish, eastern mosquitofish, robust gambusia, blotched gambusia, Gulf gambusia, Yucatan gambusia, twospot livebearer, barred killifish, green swordtail, southern platyfish, highland swordtail, variable platyfish, Pacific molly, shortfin molly, common molly, guppy, golden livebearer, porthole livebearer, Lerma livebearer, Yaqui topminnow), fundulid (plains killifish), profundulid (headwater killifish, Guatemalan killifish, brown spotted killifish, Oaxaca killifish, portillo killifish), goodeid (bulldog goodeid, rainbow goodeid, Picotee goodeid, green goodea, dark-edged splitfin, freckled splitfin, Balsas splitfin, chapultepec splitfin, jeweled splitfin, La Luz splitfin, Patzcuaro allotoca, zacapu allotoca, White River springfish, bold characodon, twoline skiffia, olive skiffia, spotted skiffia); Perciformes: percid (European perch, zander, schraetzer), channid (northern snakehead), cichlid (convict cichlid, sieve cichlid, redside cichlid, threespot cichlid, Madagascar cichlid, Mayan cichlid, Sam Borstein's cichlid, Texas cichlid, curve-bar cichlid, blue tilapia, Mozambique tilapia, Nile tilapia, Bay snook, blue discus, red discus firemouth cichlid, Angosturan cichlid), gobiid (scribbled goby, black goby, monkey goby, round goby, tubenose goby), eleotrid (oopu, western carp gudgeon, flathead gudgeon), centrarchid (green sunfish, pumpkinseed, bluegill, largemouth bass), moronid (white bass), nanid (Gangetic leaffish); Atheriniformes: atherinid (bigscale sand-smelt), atherinopsid (Gulf silverside, Balsas silverside, blackfin silverside, largetooth silverside, slender silverside, pike silverside, bigeye silverside, shortfin silverside, mesa silverside, sharpnose silverside, longjaw silverside, Toluca silverside, Alchichica silverside, La Preciosa silverside, Quechulac silverside); Siluriformes: ictalurid (yellow bullhead, channel catfish), clariid (African sharptooth catfish), claroteid (whitehead catfish), bagrid (Tigris catfish, giant river catfish), silurid (wels catfish, Tigris catfish); Characiformes: characid (banded astyanax, Mexican tetra, cardinal tetra, neon tetra), bryconid (macabi tetra), alestid (African triggerfish); Esociformes: esocid (northern pike); Mugiliformes: mugilid (mullet); Synbrachiformes: synbranchid (Asian swamp eel); Acipenseriformes: acipenserid (Amu Darya sturgeon); Percopsiformes: percopsid (trout-perch); Salmoniformes: salmonid (rainbow trout); Beloniformes: adrianichthyid (Japanese rice fish), belonid (maya needlefish); Osmeriformes: retropinnid (Australian smelt); Urodela: ambystomatid (Patzcuaro salamander); Anura: bufonid (European green toad), hylid (European tree frog), ranid (bigfoot leopard frog, marsh frog, long-legged wood frog); Serpentes: colubrid (blackbelly garter snake); Anseriformes: anatid (mallard); Falconiformes: falconid (sooty falcon); Charadriiformes: sternid (black tern); Pelecaniformes: ardeid (little bittern); Primates: hominid (human)		
S. nayarensis (syn. *Ptychobothrium*)	Cypriniformes: cyprinid (trout barb, common snowtrout)		India
Bothriocephalus (fleshy arrowhead-shaped scolex, weakly-developed apical disc, elongate bothria)			
B. andesi	Pleuronectiformes: citharid (spotted flounder)		Atlantic

B. antarcticus	Perciformes: channichthyid (mackerel icefish)		Indian Ocean
B. apogonis	Kurtiformes: apogonid (cardinalfish)		Pacific
B. atherinae	Atheriniformes: atherinid (bigscale sand smelt)		Atlantic
B. auriculatus (syn. *Anthobothrium*)	Torpediniformes: torpedinid (marbled electric ray)		Atlantic
B. australis	Scorpaeniformes: platycephalid (southern sand flathead)		Australia
B. bengalensis	Perciformes: carangid (barcheek trevally)		Indian Ocean
B. branchiostegi	Perciformes: malacanthid (red tilefish)		Pacific
B. brotulae	Ophidiiformes: ophidiid (goatsbeard brotula)		Pacific
B. carangis	Perciformes: carangid (blue trevally)		Pacific
B. celineae	Perciformes: serranid (golden hind)		Pacific
B. cepolae	Perciformes: cepolid (red bandfish)		Atlantic
B. clavibothrium	Pleuronectiformes: bothid (Mediterranean scaldfish)		Atlantic
B. claviceps (syn. *B. anguillae, Taenia claviceps, T. anguilla*)	Anguilliformes: anguillid (European eel, American eel, sharp-nosed eel, giant mottled eel); Percopsiformes: percopsid (trout-perch); Gasterosteiformes: gasterosteid (threespine stickleback); Perciformes: centrarchid (rock bass, largemouth bass, smallmouth bass, warmouth, green sunfish, longear sunfish, pumpkinseed, bluegill), sciaenid (freshwater drum), percid (sauger)	Copepoda: cyclopid (*Macrocyclops albidus, M. fuscus, Megacyclops viridis, Cyclops strenuus, C. vicinus, Acanthocyclops vernalis*)	Holarctic
B. cuspidatus (syn. *B. musculosus, B. texomensis*)	Perciformes: percid (walleye, Johnny darter, sauger, Iowa darter, yellow perch, common logperch, channel darter), centrarchid (green sunfish, rock bass, pumpkinseed, bluegill, smallmouth bass, largemouth bass), moronid (white bass); Hiodontiformes: hiodontid (goldeye, mooneye); Cichliformes: cichlid (Jack Dempsey); Clupeiformes: clupeid (American gizzard shad); Salmoniformes: salmonid (whitefish, Dolly Varden trout, lake trout); Esociformes: esocid (northern pike, muskellunge); Cypriniformes: cyprinid (emerald shiner); Siluriformes: ictalurid (brown bullhead); Gadiformes: lotid (burbot)		North America
B. euryciensis	Urodela: plethodontid (long-tailed salamander)		North America
B. formosus	Percopsiformes: percopsid (trout-perch); Cypriniformes: cyprinid (creek chub); Perciformes: percid (Iowa darter, Johnny darter, common logperch)		North America
B. gadellus	Gadiformes: morid (beardless codling)		Atlantic
B. japonicus (syn. *B. brachysoma*)	Anguilliformes: anguillid (Japanese eel, giant mottled eel)		Japan
B. kerguelensis	Perciformes: nototheniid (blue rockcod)		Indian Ocean
B. lateolabracis	Perciformes: lateolabracid (Japanese seabass)		Pacific
B. manubriformis (syn. *B. histiophorus*, *B. laciniatus*)	Istiophoriformes: istiophorid (white marlin, Indo-Pacific sailfish); Elopiiformes: megalopid (Atlantic tarpon)		cosmopolitan
B. monticelli	Lampriformes: trachipterid (scalloped ribbonfish)		Atlantic
B. nigropunctatus	Scorpaeniformes: sebastid (rockfish)		Atlantic
B. occidentalis	Scorpaeniformes: sebastid (rockfish)		Atlantic
B. pearsei	Cichliformes: cichlid (Mayan cichlid)		North America
B. rarus	Urodela: salamandrid (eastern newt)		North America
B. sciaenae	Perciformes: sciaenid (white croaker)		Pacific
B. scorpii (syn. *B. bipunctatus, luehei, punctatus, rhombi*)	Scorpaeniformes: cottid (shorthorn sculpin, European bullhead); Pleuronectiformes: scophthalmid (brill)		cosmopolitan
B. suecicus	Salmoniformes: salmonid (Atlantic salmon)		Atlantic
B. tetragonus	Perciformes: anarhichadid (spotted wolffish)		Atlantic
B. timii	Perciformes: bovichtid (Channel bull blenny)		South America
B. travassosi	Anguilliformes: anguillid (giant mottled eel)		Pacific
B. typhlotritonis	Urodela: plethodontid (grotto salamander)		North America

Reassigned *Bothriocephalus* species	Definitive hosts [adults in intestines]	Intermediate hosts [plerocercoids in tissues]	Distribution
B. abyssmus (now *Andycestus*)	Perciformes: zoarcid (eelpout)		Atlantic
B. belones (syn. *B. restiformis*) (now *Ptychobothrium*)	Beloniformes: belonid (Atlantic needlefish)		Europe
B. bicolor (now *Tentacularia coryphaenae*)	Scombriformes: scombrid (skipjack tuna)		
B. cestus (syn. *Dibothrium*) (now *Eubothrium*)	Salmoniformes: salmonid (char)		North America
B. claviger (now *Hepatoxylon trichuri*)	Carangiformes: coryphaenid (mahi-mahi)		North America
B. coniceps (now *Diphyllobothrium schistochilus*)	Carnivora: phocid (bearded seal)		Arctic Ocean
B. cordatus (now *Diphyllobothrium*)	Carnivora: canid (dog)		Europe
B. cordiceps (now *Dibothriocephalus dendriticus*)	Salmoniformes: salmonid (brook trout)		North America
B. corollatus (now *Nybelinia lingualis*)	Rajiformes: rajid (common skate)		Atlantic
B. coronatus (now *Acanthobothrium*)	Torpediniformes: torpedinid (marbled electric ray)		Europe
B. crassiceps (now *Clestobothrium*)	Gadiformes: merlucciid (European hake)		Europe
B. cristatus (now *Dibothriocephalus latus*)	Primates: hominid (human)		
B. dalmatinus (now *Fistulicola plicata*)	Zeiformes: zeid (John Dory)		Europe
B. dendriticus (now *Dibothriocephalus*)	Charadriiformes: larid (black-legged kittiwake)		North America
B. didelphidis (syn. *Diphyllobothrium*) (now *Spirometra*)	Didelphimorphia: didelphid (big-eared opossum)		South America
B. ditremus (now *Dibothriocephalus*)	Gaviiformes: gaviid (common loon); Anseriformes: anatid (red-breasted merganser)		Europe
B. dubius (now *Diphyllobothrium tetrapterum*)	Carnivora: canid (dog)		Iceland
B. elegans (now *Diphyllobothrium*)	Carnivora: phocid (hooded seal)		Europe
B. ellipticus (now *Abothrium gadi*)	Gadiformes: gadid (Atlantic cod)		Atlantic
B. eriocis (now *Eubothrium crassum*)	Salmoniformes: salmonid (brown trout)		North America
B. fasciatus (now *Diphyllobothrium tetrapterum*)	Carnivora: phocid (ringed seal)		Europe
B. felis (now *Spirometra erinaceieuropaei*)	Carnivora: felid (cat)		Europe
B. fuscus (now *Dibothriocephalus latus*)	Carnivora: canid (dog)		Iceland
B. ganapatti (syn. *B. penetratus*) (now *Penetrocephalus*)	Aulopiformes: synodontid (greater lizardfish)		Indian Ocean
B. heteropleurus (now *Amphicotyle*)	Scombriformes: centrolophid (black ruff)		Pacific
B. indicus (now *Oncodiscus sauridae*)	Aulopiformes: synodontid (greater lizardfish)		Indian Ocean

B. janickii (now *Plicocestus*)	Perciformes: coryphaenid (dolphinfish)		Indian Ocean
B. lanceolatus (now *Diphyllobothrium lanceolatum*)	Carnivora: phocid (bearded seal)		Greenland
B. liguloides (now *Spirometra erinaceieuropaei*)	Primates: hominid (human)		Japan
B. lonchinobothrium (now *Echinophallus*)	Perciformes: coryphaenid (dolphinfish)		Indian Ocean
B. maculatus (now *Spirometra erinaceieuropaei*)	Carnivora: felid (leopard)		Africa
B. mansoni (now *Spirometra*)	Primates: hominid (human)		China
B. microcephalus (syn. *B. monorchis*) (now *Anchistocephalus*)	Tetraodontiformes: molid (ocean sunfish)		Europe
B. neglectus (now *Clestobothrium*)	Gadiformes: gadid (tadpole fish)		Atlantic
B. osmeri (now *Dibothriocephalus ditremus*)	Osmeriformes: osmerid (European smelt)		Europe
B. peltocephalus (now *Echinobothrium*)	Scombriformes: centrolophid (Imperial blackfish)		Atlantic
B. pilula (now *Clestobothrium crassiceps*)	Gadiformes: merlucciid (European hake)		Europe
B. platycephalus (now *Australicola*)	Beryciformes: berycid (alfansino)		Pacific
B. plicatus (now *Fistulicola*)	Istiophoriformes: xiphiid (swordfish)		Pacific
B. polycalceolus (now *Diphyllobothrium hians*)	Carnivora: phocid (harbour seal)		Atlantic
B. polypteri (now *Polyoncobothrium*)	Anabantiformes: channid (striped snakehead); Cypriniformes: cyprinid (rohu)		India
B. proboscideus (now *Eubothrium crassum*)	Salmoniformes: salmonid (Atlantic salmon)		Atlantic
B. prudhoei (now *Kirstenella gordoni*)	Siluriformes: clariid (mudfish)		Africa
B. pycnomerus (now *Senga*)	Anabantiformes: channid (bullseye snakehead)		India
B. quadratus (now *Diphyllobothrium quadratum*)	Carnivora: phocid (leopard seal)		Southern Ocean
B. ratticola (now *Spirometra*)	Rodentia: murid (black rat)		Asia
B. reticulatus (now *Dibothriocephalus latus*)	Carnivora: canid (dog)		Europe
B. sagittatus (now *Anchistrocephalus microcephalus*)	Tetraodontiformes: molid (ocean sunfish)		Europe
B. schistochilos (now *Diphyllobothrium*)	Carnivora: phocid (bearded seal)		Europe
B. solinosomum (syn. *B. centrolophipompilii*) (now *Bothriocotyle*)	Scombriformes: centrolophid (black ruff)		Pacific, Atlantic
B. taenioides (now *Dibothriocephalus latus*)	Primates: hominid (human)		Europe
B. tectus (syn. *Baylisiella tecta*) (now *Diphyllobothrium lashleyi*)	Carnivora: phocid (southern elephant seal)		Southern Ocean
B. tetrapterus (now *Diphyllobothrium tetrapterum*)	Carnivora: phocid (harbour seal)		Europe
B. variabilis (now *Diphyllobothrium tetrapterum*)	Carnivora: phocid (harp seal)		Europe
B. wagneri (now *Echinophallus*)	Scombriformes: centrolophid (black ruff)		Pacific
B. zschokkei (now *Schistocephalus pungitii*)	Gasterosteiformes: gasterosteid (ninespine stickleback)		Eurasia

A number of other species have been named but subsequent revisions have disputed their identity: either as *species inquirena* (species of doubtful identity requiring further investigation): *B. alessandrinii* (from river trout), *B. affinis* (from red scorpionfish), *B. angustatus* (from red scorpionfish), *B. angusticeps* (from rose fish), *B. bramae* (from Atlantic pomfret), *B. breviceps* (from cutthroat eel), *B. capillicollis* (from Ballan wrasse, ide), *B. columbae* (from pigeon), *B. granularis* (from carp), *B. hirondellei* (from sargassum pipefish), *B. labiatus* (from Atlantic pomfret), *B.labracis* (from European bass), *B. levinseni* (from lumpfish), *B. longispiculus* (from crake), *B. lophii* (from angler monkfish), *B. macrobothrium* (from scalloped ribbonfish), *B. marietani* (from water rail), *B. minutus* (from greater pipefish), *B. motellae* (from fourbeard rockling), *B. palumbi* (from piper gunard), *B. parvus* (from lesser sand eel), *B. pusillus* (from rock partridge), *B. salvelini* (from Arctic char), *B. sauridae* (from clouded lizardfish), *B. schilbeodis* (from easterm madtom), *B. sciuri* (from fox squirrel), *B. similis* (from arctic fox), *B. speciosus* (from tesellated darter), *B. spinachidae* (from sea stickleback), *B. squali* (from blue shark), *B. tintinnabulus* (from dragonet), *B. trachypteri* (incl. *B. trachypteri-iris*, *B. trachypteri-liopteri*) (from Mediterranean dealfish, ribbonfish) and *B. vallei* (from red mullet); or as *nomen dubium* (doubtful name): *B. barbatulae* (from stone loach), *B. barbatus* (from brill), *B. funiculus* (from fivebeard rockling); *B. gregarius* (from turbot), *B. sinensis* (from long spiky-head carp), and *B. ursi* (from brown bear).

Parasite morphology: Bothriocephalid parasites form 3 developmental stages: eggs, larvae (cercoids) and adult tapeworms. The eggs are ovoid in shape measuring from 32-63 µm in length by 21-41 µm in width. They are thick-walled with an operculum (10-11 µm wide) at the narrower pole and are unembryonated when laid. Embryonated eggs contain a coracidium consisting of a hexacanth (6-hooked) embryo (oncosphere) surrounded by a ciliated envelope (embryophore). Cercoid larvae are alacunate (without internal cavities) and vary considerably in size growing from small ovoid stages some 30 µm in diameter to larger elongate stages measuring up to 380 µm long by 140 µm wide. Early stages sometimes possessed knob-like tails (cercomers) containing remnants of embryonic hooks (thus resembling procercoids), but the cercomers were soon lost as the larvae matured and developed anterior indentations and an everted scolex (thus better conforming to descriptions of plerocercoids). Adult tapeworms have long ribbon-like bodies ranging in size depending not only on parasite species but also host species, host size, host age, intensity of infection and possibly prevailing ecological conditions. Most species grow to a length of 3.5-8.0 cm, but some species may reach 60-100 cm. They have an elongate anterior scolex (0.4-1.4 mm long) immediately giving rise to flattened segments (proglottids). The scolex has a distinctive arrowhead shape and is fleshy being wider than the first body segments. The scolex is unarmed but possesses a weakly-developed apical disc measuring 100-200 µm wide and 2 elongate anterolaterally-directed attachment grooves (bothria) with non-crenulate margins. The genus *Schyzocotyle* has been resurrected mostly on the basis of molecular evidence, although its 2 cognate species are considered to be morphologically characterised by the occurrence of a wide heart-shaped scolex with narrow deep bothria. The strobila of both genera is comprised firstly of immature segments (lacking fully developed genitalia) that are wider than long, then mature segments (with developed genitalia) and gravid segments (containing eggs) that are rectangular and longer than wide. Adult worms are hermaphroditic with proglottids containing one set of male and female reproductive organs. Proglottids contain numerous spherical testes in 2 lateral medullary fields, and a muscular cirrus sac that opens into a common genital atrium. They also contain numerous corticular vitelline follicles, a bilobed ovary, a short sinuous vagina that opens into the common genital atrium, and a saccular uterus that opens to a dorso-median uterine (birth) pore from which eggs are released.

Site of infection: Infections by adult tapeworms occur in the small intestines of their piscine definitive hosts, while procercoid larvae develop in the body cavities of their copepodid intermediate hosts.

Pathogenesis: Tapeworms attach to the wall of the anterior small intestines, just posterior to the bile duct. Adult worms lack digestive tracts and do not feed on host tissues but absorb nutrients from the gut lumen. Nonetheless, infections can cause significant pathology, not only at their sites of attachment, but also posteriad where their presence may perturb gut function. Attachment of the worm produces an inflammatory response, leading to desquamative catarrhal enteritis, necrosis, haemorrhage, ulceration, fibrosis, increased mucus production, and degeneration of the intestinal wall with extensive destruction of villi. Heavy tapeworm burdens (or the presence of large tapeworms) may block the intestinal tract causing severe distention, congestion, compression, pressure necrosis, mucosal atrophy, perforation and death. Occluded organs often become grossly enlarged, very thin-walled and stretched to the point of transparency, revealing the presence of squirming white worms. Clinical signs in affected fish vary greatly depending on the site and extent of infection, most often including inappetence, weight loss, slow growth, loss of condition, emaciation, anaemia, and mortality (especially in juveniles). Other internal organs may also be affected, particularly the gall bladder becoming swollen and turgid, and the liver exhibiting signs of hepatocyte atrophy contributing to nutritional deficiencies, in some cases consistent with starvation. Infected fish may also become more susceptible to secondary bacterial infections. The Asian fish tapeworm (*S. acheilognathi*) presents significant problems to cyprinid aquaculture by causing severe damage to the intestinal tracts of young fish, physiological disturbances (protein depletion, altered digestive enzyme activity, elevated muscle fatigue), reduced growth, loss of condition and mortality (sometimes as high as 100% in hatchery ponds).

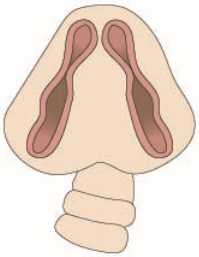
Developmental cycle and mode of transmission: Bothriocephalid tapeworms have indirect heteroxenous (2-host) life-cycles, alternating between adult stages in fish (definitive hosts) and larval stages in copepods (intermediate hosts). Unembryonated eggs are passed in host faeces into water where they embryonate over several days (1-28 days depending on water temperature, longer in colder water). The eggs hatch releasing a ciliated coracidium which swims sporadically in the water attracting the attention of zooplanktonic crustaceans, in this case cyclopoid copepods. Coracidia eaten by copepods shed their ciliated embryophore and the oncosphere penetrates the gut and forms plerocercoid larval stages within the body cavity over 6-12 days. When infected copepods are eaten by fish definitive hosts, the plerocercoids attach to the gut wall and develop into adult tapeworms over 20–23 days. Gravid segments produce and shed eggs which are passed in host faeces. While fishes normally become infected by eating infected copepods, there is some evidence that adult worms may be transmitted directly to piscivorous fishes (a phenomenon known as postcyclic transmission). Several experiments have implicated aquatic birds in the spread of infections, although they may simply eat infected fish and spread worm eggs with their faeces. The Asian fish tapeworm (*S. acheilognathi*) has spread widely throughout the world from East Asia due to many translocations of fish for aquaculture, ornamental and bait fish supply, aquatic weed control, and even mosquito control. Many patterns of infection have been observed, particularly intermittent and seasonal patterns with peak incidence in summer.

Differential diagnosis: Infections may be diagnosed ante-mortem by the microscopic detection of worm eggs in faecal samples, but are most often diagnosed post-mortem by the detection of adult worms in dissected gut samples. Mature worms are usually conspicuous within the intestines of infected fish, but the presence of plerocercoid larvae or juvenile immature worms is best facilitated by the microscopic examination of mucosal scrapings, washes or squash preparations. More recently, molecular techniques have been used to characterize species following polymerase chain reaction (PCR) amplification of nuclear (18S ribosomal RNA) and mitochondrial (cytochrome c oxidase subunit 1 (cox1), large subunit (16S) mitochondrial rRNA (rrnL)) genes.

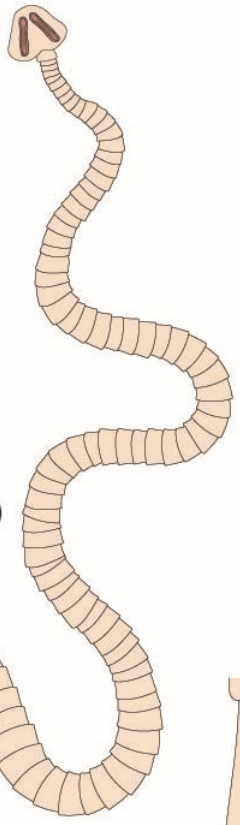
Treatment and control: Infections in fish have been treated with various anthelmintic drugs exhibiting cestodicidal activity, notably the isoquinoline (praziquantel) applied as a bath or given orally (mixed in fish food with oil), but also including the inhibitory salicylanilide (niclosamide) and the purgative halogenated hydrocarbon (butynorate). Various natural products have also shown some limited efficacy; including infusions of lupin seeds, conifer needles, tobacco dust and horse radish leaves. A wide range of preventive measures have been developed in attempts to curb the worldwide spread of infections. Many governments have introduced legislation within the aquaculture and aquarium trades for the screening, impoundment, treatment and quarantine of live fish and broodstock. Various industry recommendations have also been made to modify management practices designed to reduce the likelihood of transmission of parasites to juvenile fish, particularly with respect to providing clean holding facilities, reducing overstocking stress, and reducing copepod intermediate host populations by water treatment (filtration, disinfection) or pond management (draining, drying, liming). Several experiments were also conducted using insecticides to reduce copepod populations, but their overt use should be curtailed due to environmental and health concerns.

Bothriocephalus

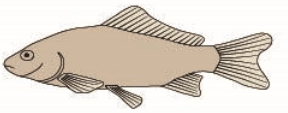
intestines
(sometimes enteritis,
obstruction, emaciation)

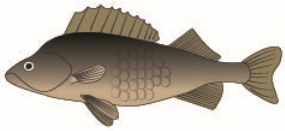


scolex



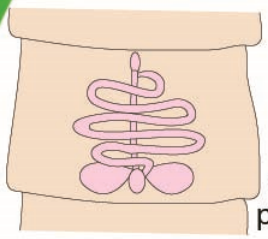
hermaphroditic
adults (3-8 cm)
(some up to 1 m)



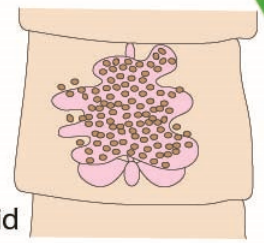


Definitive Hosts
(freshwater and
marine fish)

transmission
through
ingestion
of infected
tissues

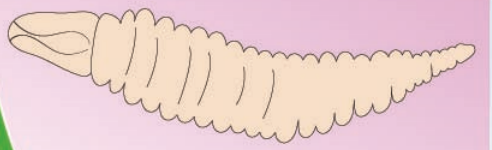


mature
proglottid



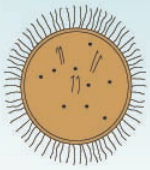
gravid
proglottid

excretion
of eggs in
faeces

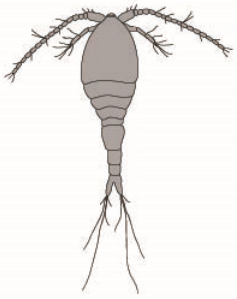


cercoid larvae
(mostly plerocercoid)
(30-380 µm)

eggs
(~ 50 µm)

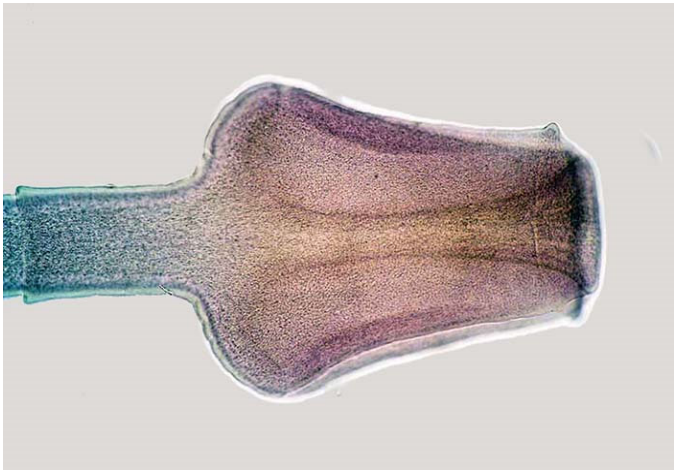


free-swimming
coracidium
(~ 60 µm)

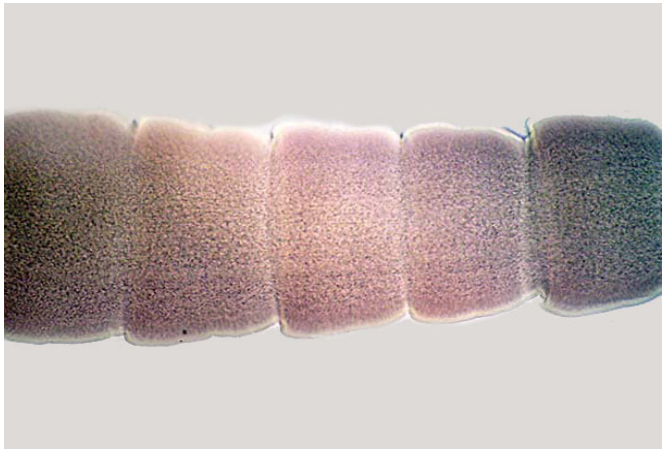


Intermediate Hosts
(copepods)
(body cavity)

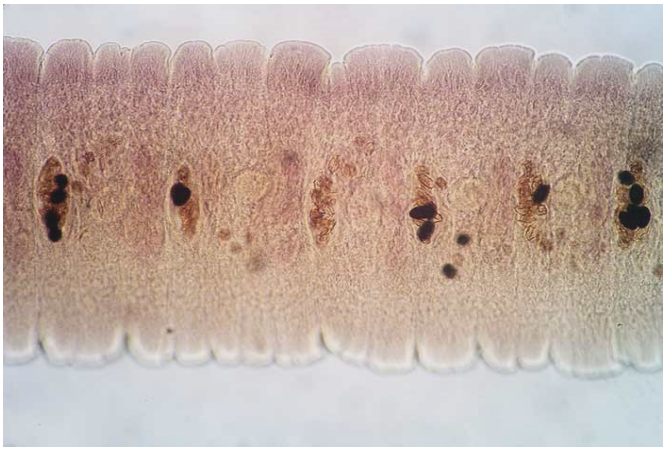
Bothriocephalus scolex



Bothriocephalus scolex



Bothriocephalus segments



Bothriocephalus segments