

***Diphyllbothrium*, *Dibothriocephalus***  
(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. Diphyllbothriidean (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 (proceroids). 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 plerocercoids. Infections by *Dibothriocephalus latus* 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: Diphyllbothriidea (Pseudophyllidea) (aquatic hosts, scolex with bothria, central genital pores, two IH)  
Family: Diphyllbothriidae (coracidium, proceroid in copepods, plerocercoids in frogs, often PHs)  
Genus: *Diphyllbothrium*, *Dibothriocephalus* (parasitic in small intestines in piscivorous mammals)  
Species: various species cause enteritis in humans and carnivores

**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, Diphyllbothriidea, Haplobothriidea, Spathebothriidea and Trypanorhyncha; while others with apical pads/suckers include Cathetocephalidea, Litobothriidea and Nippotaeniidea.

| Order<br>(+ no. families)                                                                                                                                                                                                                                                                                                                                                                                                                                                                 | No.<br>spp. | DH <sup>a</sup> | Scolex                                                    | IH1 <sup>b</sup> | Stage <sup>d</sup> | IH2 <sup>c</sup> | Stage <sup>d</sup> |
|-------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|-------------|-----------------|-----------------------------------------------------------|------------------|--------------------|------------------|--------------------|
| Class: <b>Cestoda</b> (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           |
| Litobothriidea (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,<br>M      | ple, mer           |
| Spathebothriidea (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                |
| Diphyllbothriidea (6)<br>(= Pseudophyllidea)                                                                                                                                                                                                                                                                                                                                                                                                                                              | 70          | M,B,P,A         | 2 shallow bothria, unarmed                                | C                | pro                | F,A,P,<br>M      | ple                |
| Cyclophyllidea (16)<br>(incl. Mesocestoididae)                                                                                                                                                                                                                                                                                                                                                                                                                                            | 3,034       | M,B,P           | 4 suckers, rostellum, often armed                         | M,A,B,<br>L,T,I  | ccc, ccs           | -                | -                  |
| LEGEND<br><sup>a</sup> DH = definitive host; <sup>b</sup> IH1 = first intermediate host; <sup>c</sup> IH2 = second intermediate host;<br>[A = amphibian; B = bird; C = crustacean; F = teleost; I = insect; L = mollusc; M = mammal, P = reptile; R = ray; S = shark; T = acarine; W = annelid];<br><sup>d</sup> Metacestode: pro = procercoid, plc = plerocercus; ple = plerocercoid, mer = merocercoid; ccc = cysticercoid; ccs = cysticercus, coenurus, strobilocercus or hydatid cyst |             |                 |                                                           |                  |                    |                  |                    |

Diphyllbothriidean (= 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: Cephalochlamyidae, Diphyllbothriidae, and Solenophoridae (earlier works also recognized another 3 families (Ligulidae, Schistocephalidae, and Scyphocephalidae) but they are no longer considered valid).

Members of the family Diphyllbothriidae 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 diphyllbothriid genera have been described: including *Adenocephalus*, *Baylisia*, *Baylisiella*, *Dibothriocephalus*, *Diphyllbothrium*, *Flexobothrium*, *Glandicephalus*, *Ligula*, *Plicobothrium*, *Pyramicocephalus*, *Schistocephalus*, *Spirometra* and *Tetragonoporus*. The genera *Diphyllbothrium* and *Dibothriocephalus* are characterized by adult worms having a rosette-shaped uterus (as opposed to a spiral-shaped uterus in *Spirometra*). *Diphyllbothrium* species are commonly known as fish or broad tapeworms and more than 50 species have been described in the intestines of piscivorous definitive hosts (predominantly mammals but also birds) with larval stages developing first as proceroids in copepodid intermediate hosts and then as plerocercoids in piscine intermediate hosts (freshwater, marine or anadromous host species). On the basis of recent molecular and biological data, several workers resurrected the genus *Dibothriocephalus* essentially for *Diphyllbothrium* spp. from terrestrial carnivores, while those species infecting cetaceans have been retained in the genus *Diphyllbothrium sensu stricto* ('in the strictest sense') and those infecting pinnipeds in the genus *Diphyllbothrium sensu lato* ('in the broadest sense'). Molecular studies also suggested that the genus *Diplogonoporus* should be considered a junior synonym of *Diphyllbothrium*. Infections have been found in various human populations, notably involving *Dib. latus* (= *Dip. latum*), *Dib. nihonkaiensis* (= *Dip. nihonkaiense*) and *Adenocephalus pacificus* (= *Dip. pacificum*) in fish-eating communities in Europe, Asia and North America. It is estimated that more than 20 million people harbour infections, with the incidence varying considerably spatially and temporally reflecting differences in sanitation, food hygiene, dietary and cultural practices and public health awareness.

| Diphyllbothriid species                                                                                                                                                                                                                                                                                                                                                                    | Definitive host (DH) [adults in intestines]                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                      | First intermediate hosts [proceroids in tissues]                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                               | Second intermediate hosts [plerocercoids in tissues]                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                            | Distribution         |
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| <b><i>Dibothriocephalus</i> (terrestrial carnivores as DH)</b>                                                                                                                                                                                                                                                                                                                             |                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                  |                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                |                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                 |                      |
| <i>Dib. alascensis</i> (syn. <i>Dip. alascense</i> , <i>alaskensi</i> )                                                                                                                                                                                                                                                                                                                    | Carnivora: canid (dog), phocid (harbor seal);<br>Primates: hominid (humans)                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                      |                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                | Gadiformes: lotid (burbot); Osmeriformes: osmerid (rainbow smelt)                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                               | North America        |
| <i>Dib. dalliae</i> (syn. <i>Dip. dalliae</i> )                                                                                                                                                                                                                                                                                                                                            | Carnivora: canid (dog, Arctic fox);<br>Charadriiformes: larid (glaucous-winged gull);<br>Primates: hominid (human)                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                               |                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                | Esociformes: esocid (Alaska blackfish);<br>Salmoniformes: salmonid (dolly varden)                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                               | North America        |
| <i>Dib. dendriticus</i> (syn. <i>Dib. sebago</i> , <i>Dip. dendriticum</i> , <i>fissiceps</i> , <i>cordiceps</i> , <i>exile</i> , <i>minor</i> , <i>canadense</i> , <i>strictus</i> , <i>obdoriense</i> , <i>nenzi</i> , <i>laruei</i> , <i>oblongatum</i> , <i>medium</i> , <i>minus</i> , <i>microcordiceps</i> , <i>norvegicum</i> , <i>sebago</i> , <i>Bothriocephalus cordiceps</i> ) | Carnivora: canid (dog, red fox, American red fox, Arctic fox), ursid (grizzly bear, Kodiak bear, black bear), mustelid (Eurasian otter), felid (cat), phocid (ringed seal, Baikal seal);<br>Rodentia: cricetid (golden hamster, golden mouse), murid (brown rat, rakali, Australian water rat);<br>Primates: hominid (human); Passeriformes: corvid (common raven)<br>Charadriiformes: larid (common gull, glaucous gull, European herring gull, great black-backed gull, Bonaparte's gull, ring-billed gull, California gull, kelp gull, black-headed gull, lesser black-headed gull, brown hooded gull, black-legged kittiwake, common tern), stercorarid (skua);<br>Pelecaniformes: pelecanid | Copepoda: diaptomid ( <i>Aglaodiaptomus</i> (D.) <i>leptopus</i> , <i>Arctodiaptomus acutilobatus</i> , <i>A. bacillifer</i> , <i>Diaptomus gracilis</i> , <i>D. graciloides</i> , <i>D. leptodus</i> , <i>Eudiaptomus gracilis</i> , <i>Leptodiaptomus</i> (D.) <i>minutus</i> ), cyclopoid ( <i>Acanthocyclops</i> (C.) <i>vernalis</i> , <i>Cyclops abyssorum</i> , <i>C. kolensis</i> , <i>C. lacustris</i> , <i>C. scutifer</i> , <i>C. serrulatus</i> , <i>C. strenuus</i> , <i>Diacyclops</i> (C.) <i>bicuspidatus</i> , <i>Mesocyclops leuckarti</i> ) | Salmoniformes: salmonid (Atlantic salmon, pink salmon, coho salmon, sockeye salmon, sharp-snouted lenok, Siberian taimen, kokanee, char, Arctic char, grayling, Arctic grayling, Mongolian grayling, white-spotted char, Arctic cisco, shortjaw cisco, blackfin cisco, chub, kiyi, lavaret, Dolly Varden trout, rainbow trout, brown trout, brook trout, cutthroat trout, lake trout, common whitefish, lake whitefish, northern whitefish, Valaan whitefish, mountain whitefish, vendace, peled, Baikal omul);<br>Osmeriformes: osmerid (rainbow smelt);<br>Gasterosteiformes: gasterosteid (threespine stickleback, fourspine | Holarctic, Australia |

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|                                                                                                                                                                          | <p>(American white pelican);<br/>Gaviiformes: gaviid<br/>(black-throated loon, red-throated loon);<br/>Anseriformes: anatid<br/>(merganser, red-breasted merganser); Suliformes: phalacrocoracid (great cormorant);<br/>Podicipediformes: podicipedid (horned grebe, great crested grebe)</p>                                                                                                                                                                                                                                                                                                                                 |                                                                                     | <p>stickleback, ninespine stickleback);<br/>Scorpaeniformes: abyssocottid (deepwater sculpin, Vitim sculpin), comephorid (Baikal oilfish, little Baikal oilfish), cottid (fourhorn sculpin), cottocomephorid (yellowfin Baikal sculpin, longfin Baikal sculpin, Kessler's sculpin);<br/>Atheriniformes: atherinopsid (silverside, cauke); Galaxiiformes: galaxiid (common galaxias); Perciformes: percid (Eurasian ruffe, European perch), percichthyid (creole perch); Gadiformes: lotid (burbot); Cypriniformes: nemacheilid (stone loach); Osmeriformes: osmerid (European smelt, rainbow smelt, grayling, puye), Siluriformes: silurid (tollo)</p>                                                                                                                                      |                                              |
| <p><i>Dib. ditremus</i><br/>(syn. <i>Dip. ditremum</i>, <i>colymbi</i>, <i>vogeli</i>, <i>hottai</i>, <i>osmeri</i>, <i>Bothriocephalus ditremus</i>, <i>osmeri</i>)</p> | <p>Anseriformes: anatid birds (merganser, greater scaup); Gaviiformes: gaviid (common loon, yellow-billed loon, red-throated loon, black-throated loon);<br/>Charadriiformes: larid (European herring gull, ring-billed gull, common tern, black-legged kittiwake), alcid (red-throated guillemot);<br/>Pelecaniformes: ardeid (grey heron);<br/>Podicipediformes: podicipedid (red-necked grebe); Suliformes: phalacrocoracid (cormorant); Carnivora: phocid (Weddell seal, common seal, harbor seal, ringed seal, Saimaa ringed seal), canid (dog, wolf), felid (cat); Rodentia: cricetid (golden hamster), murid (rat)</p> | <p>Copepoda: cyclopoid (<i>Cyclops strenuus</i>)</p>                                | <p>Salmoniformes: salmonid (brown trout, rainbow trout, cutthroat trout, lake trout, brook trout, Dolly Varden trout, grayling, Atlantic salmon, sockeye salmon, bloater, kokanee, chinook salmon, coho salmon, Arctic char, cisco, Arctic cisco, sardine cisco, tugun, vendace, lake whitefish, common whitefish, broad whitefish, northern whitefish);<br/>Osmeriformes: osmerid (Japanese surf smelt, olive rainbow smelt, pond smelt, European smelt);<br/>Gasterosteiformes: gasterosteid (threespine stickleback, fourspine stickleback, ninespine stickleback);<br/>Scorpaeniformes: cottid (Baikal oilfish), cottocomephorid (Baikal yellowfin, longfin Baikal sculpin), abyssocottid (vitim sculpin);<br/>Gadiformes: lotid (burbot); Cypriniformes: nemacheilid (stone loach)</p> | <p>Europe, Southern Ocean, Pacific Ocean</p> |
| <p><i>Dib. latus</i><br/>(broad tapeworm, broad fish tapeworm, pseudo-</p>                                                                                               | <p>Primates: hominid (human); Carnivora: canid (dog, red fox, Iberian fox,</p>                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                | <p>Copepoda: cyclopoid (<i>Cyclops insignis</i>, <i>C. lacustris</i>, <i>C.</i></p> | <p>Perciformes: percid (European perch, yellow perch, pikeperch, creole</p>                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                 | <p>Eurasia, India, Americas</p>              |

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| tapeworm)<br>(syn. <i>Dip. latum</i> ,<br><i>americanus</i> ,<br><i>fuscus/fuscum</i> , <i>luxi</i> ,<br><i>parvum</i> , <i>stictus</i> ,<br><i>tungussicum</i> , <i>skrjabini</i> ,<br><i>Taenia lata</i> , <i>vulgaris</i> ,<br><i>membranacea</i> , <i>tenella</i> ,<br><i>dentata</i> , <i>grisea</i> ,<br><i>Bothriocephalus fuscus</i> ,<br><i>latus</i> , <i>balticus</i> , <i>cristatus</i> ,<br><i>reticulatus</i> , <i>taenioides</i> ,<br><i>Dibothrium latum</i> ,<br><i>serratum</i> ,<br><i>Bothriocephalus</i><br><i>cristatus</i> ,<br><i>Dibothriocephalus</i><br><i>cristatus</i> ,<br><i>Diancyrobothrium</i><br><i>taenioides</i> ) | Arctic fox, crab-eating<br>fox, coyote, wolf, golden<br>jackal, raccoon dog), felid<br>(cat, jungle cat, European<br>wildcat, leopard, leopard<br>cat, clouded leopard,<br>jaguar, lynx, tiger, long-<br>tailed tiger cat, ocelot),<br>ursid (brown bear,<br>American black bear,<br>polar bear), procyonid<br>(raccoon), mustelid<br>(wolverine, Eurasian otter,<br>European pine marten,<br>sable, European badger,<br>American mink),<br>odobenid (Pacific walrus),<br>phocid (ringed seal,<br>bearded seal, hooded seal,<br>leopard seal,<br>Mediterranean monk seal,<br>common seal, harbor<br>seal); Artiodactyla:<br>phocoenid (harbor<br>porpoise), suid (pig);<br>Rodentia: cricetid (golden<br>hamster);<br>Charadriiformes: larid<br>(kelp gull, brown-headed<br>gull) | <i>strenuus</i> (= <i>C.</i><br><i>furcifer</i> ), <i>C. vicinus</i> ,<br><i>Ectocyclops</i><br><i>phaleratus</i> ,<br><i>Acanthocyclops</i><br><i>viridis</i> ,<br><i>Acanthocyclops</i><br><i>vernalis</i> , <i>Eucyclops</i><br><i>serrulatus</i> ,<br><i>Microcyclops</i><br><i>varicans</i> ,<br><i>Mesocyclops</i><br><i>leuckarti</i> , <i>M.</i><br><i>araucanus</i> ,<br><i>Thermocyclops</i> ( <i>M.</i> )<br><i>oithonoides</i> ,<br><i>Tropocyclops</i><br><i>prasinus</i> ),<br>centropagid<br>( <i>Gladioferens</i><br><i>brevicornis</i> ,<br><i>Boeckella gracilis</i> ,<br><i>B. minuta</i> ),<br>diaptomid<br>( <i>Acanthodiaptomus</i><br><i>denticornis</i> ,<br><i>Aglaodiaptomus</i><br><i>leptopus</i> (= <i>D.</i><br><i>piscinae</i> ),<br><i>Arctodiaptomus</i><br><i>ulomskyi</i> ,<br><i>Diaptomus vulgaris</i> ,<br><i>Eudiaptomus</i><br><i>zacharias</i> , <i>E.</i><br><i>transylvanicus</i> (= <i>E.</i><br><i>coeruleus</i> ), <i>E. (D.)</i><br><i>gracilis</i> , <i>E. (D.)</i><br><i>graciloides</i> ,<br><i>Hemidiaptomus</i><br><i>ignatovi</i> ,<br><i>Leptodiaptomus (D.)</i><br><i>minutus</i> L. ( <i>D.</i> )<br><i>siciloides</i> ,<br><i>Mastigodiaptomus</i><br>( <i>D.</i> )<br><i>albuquerqueensis</i> ,<br><i>Onychodiaptomus</i><br>( <i>D.</i> ) <i>sanguineus</i> ,<br><i>Skistodiaptomus</i><br>( <i>D.</i> ) <i>oregonensis</i> , <i>S.</i><br>( <i>D.</i> )<br><i>mississippiensis</i> ,<br><i>Tumeodiaptomus</i><br><i>diabolicus</i> (= <i>D.</i><br><i>diabolicus</i> ), calanoid<br>( <i>Eurytemora</i><br><i>affinis</i> ); Diptera:<br>muscid ( <i>Musca</i><br><i>domestica</i> ) | perch, ruffe, Eurasian<br>ruffe, zander, walleye,<br>sauger), centropomid<br>(common snook), zoarcid<br>(viviparous eelpout);<br>Esociformes: esocid<br>(northern pike),<br>Salmoniformes: salmonid<br>(pink salmon, chum<br>salmon, sockeye salmon,<br>masu, char, Arctic char,<br>white-spotted char,<br>Atlantic salmon, rainbow<br>trout, brown trout, brook<br>trout, Biwa trout, common<br>whitefish, grayling,<br>vendace); Atheriniformes:<br>atherinid (cauque,<br>silverside); Gadiformes:<br>lotid (burbot);<br>Mugiliformes: mugilid<br>(redlip mullet, so-iuy<br>mullet); Osmeriformes:<br>osmerid (puye, European<br>smelt); Siluriformes:<br>silurid (wels catfish),<br>heteropneustid (Asian<br>stinging catfish);<br>Gasterosteiformes:<br>gasterosteid (ninespine<br>stickleback);<br>Cypriniformes: cyprinid<br>(long-spine bream,<br>common bleak, common<br>minnow, common roach),<br>nemacheilid (stone loach);<br>Anguilliformes: anguillid<br>(European eel);<br>Scorpaeniformes: cottid<br>(European bullhead);<br>Aulopiformes: synodontid<br>(bummalo); Gobiiformes:<br>gobiid (sand goby) |                     |
| <i>Dib. nihonkaiensis</i><br>(syn. <i>Dip. nihonkaiense</i> ,<br><i>klebanovskii</i> , <i>giljadicum</i> )                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                              | Carnivora: ursid (brown<br>bear, grizzly bear),<br>American black bear,<br>Asian black bear); canid                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                               |                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                  | Salmoniformes: salmonid<br>(cherry salmon, chum<br>salmon, sockeye, pink<br>salmon, Japanese huchen,                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                  | Asia, North Pacific |

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|                                                                                                                                              | (wolf, dog, fox), mustelid (American mink);<br>Artiodactyla: suid (pig);<br>Rodentia: cricetid (golden hamster); Primates: hominid (human)                                                     |  | whitespotted char, taimen); Mugiliformes: mugilid (so-iuy mullet)                                                |                |
| <i>Dib. ursi</i><br>(syn. <i>Diphyllbothrium</i> )                                                                                           | Carnivora: ursid (Kodiak bear, brown bear, American black bear);<br>Primates: hominid (human); Charadriiformes: larid (glaucous-winged gull)                                                   |  | Salmoniformes: salmonid (sockeye salmon)                                                                         | North America  |
| <b><i>Diphyllbothrium</i></b> (comprising 2 groups, one with cetaceans as DH, one with pinnipeds as DH)                                      |                                                                                                                                                                                                |  |                                                                                                                  |                |
| <i>Dip. archeri</i><br>(syn. <i>Dibothriocephalus</i> )                                                                                      | Carnivora: phocid (Weddell seal)                                                                                                                                                               |  |                                                                                                                  | Southern Ocean |
| <i>Dip. balaenopterae</i><br>(syn. <i>Dip. brauni</i> , <i>Krabbea grandis</i> , <i>Diplogonoporus balaenopterae</i> , <i>fukuokaensis</i> ) | Artiodactyla: balaenopterid (sei whale, common minke whale, blue whale, fin whale, humpback whale);<br>Carnivora: canid (dog), felid (cat); Primates: hominid (human)                          |  | Clupeiformes: engraulid (Japanese anchovy), clupeid (Japanese pilchard); Scombriformes: scombrid (skipjack tuna) | circumpolar    |
| <i>Dip. cameroni</i>                                                                                                                         | Carnivora: phocid (Hawaiian monk seal);<br>Primates: hominid (human)                                                                                                                           |  |                                                                                                                  | Pacific        |
| <i>Dip. cordatum</i><br>(syn. <i>Dib. cordatus</i> , <i>Bothriocephalus</i> , <i>Dibothrium</i> )                                            | Carnivora: phocid (bearded seal, harp seal, spotted seal, harbor seal, common seal, Greenland seal), otariid (Stellar sea lion), odobenid (walrus);<br>canid (dog); Primates: hominid (human); |  |                                                                                                                  | Holarctic      |
| <i>Dip. elegans</i><br>(syn. <i>Dip. pterocephalum</i> , <i>Bothriocephalus</i> , <i>Dibothriocephalus</i> )                                 | Carnivora: phocid (Mediterranean monk seal, harbour seal, hooded seal, common seal), otariid (Steller's sea lion)                                                                              |  |                                                                                                                  | Arctic Ocean   |
| <i>Dip. fasciatus</i><br>(syn. <i>Bothriocephalus</i> )                                                                                      | Carnivora: phocid (ringed seal)                                                                                                                                                                |  |                                                                                                                  | Greenland      |
| <i>Dip. fayi</i>                                                                                                                             | Carnivora: odobenid (Pacific walrus)                                                                                                                                                           |  |                                                                                                                  | Pacific        |
| <i>Dip. fuhrmanni</i>                                                                                                                        | Artiodactyla: delphinid (Pacific white-sided dolphin, long-snouted dolphin, spotted dolphin), phocoenid (finless porpoise)                                                                     |  |                                                                                                                  | Asia           |
| <i>Dip. gondo</i><br>(syn. <i>Dip. subtile</i> )                                                                                             | Artiodactyla: delphinid (short-finned pilot whale)                                                                                                                                             |  |                                                                                                                  | Atlantic       |
| <i>Dip. hians</i><br>(syn. <i>Dib. hians</i> , <i>polycalceolus</i> , <i>variabile</i> )                                                     | Carnivora: phocid (Hawaiian monk seal, Mediterranean monk seal, harbour seal, bearded seal, ringed seal, hooded seal, common seal); Primates: hominid (human);                                 |  |                                                                                                                  | circumpolar    |
| <i>Dip. lanceolatum</i><br>(syn. <i>Dibothriocephalus</i> , <i>Bothriocephalus</i> ,                                                         | Carnivora: phocid (bearded seal, ringed seal, harp seal, common seal,                                                                                                                          |  | Salmoniformes: salmonid (sardine cisco)                                                                          | circumpolar    |

|                                                                                                                                              |                                                                                                                                                                                                                |                                                                                                                          |                                       |                         |
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| <i>Cordiocephalus</i> )                                                                                                                      | ribbon seal, harbor seal, Mediterranean monk seal), otariid (Stellar sea lion); Artiodactyla: phocoenid (harbour porpoise), monodontid (beluga whale); Carnivora: canid (dog); Primates: hominid (human)       |                                                                                                                          |                                       |                         |
| <i>Dip. lashleyi</i><br>(syn. <i>Dibothriocephalus tectus</i> )                                                                              | Carnivora: phocid (Weddell seal, Ross seal, leopard seal, southern elephant seal)                                                                                                                              |                                                                                                                          |                                       | Southern Ocean          |
| <i>Dip. lobodoni</i>                                                                                                                         | Carnivora: phocid (crabeater seal)                                                                                                                                                                             |                                                                                                                          |                                       | Southern Ocean          |
| <i>Dip. macroovatum</i>                                                                                                                      | Artiodactyla: balaenopterid (minke whale), eschrichtiid (gray whale)                                                                                                                                           | Copepoda: acartiid ( <i>Acartia clausi</i> ), oithinid ( <i>Oithina nana</i> ), pontellid ( <i>Labidocera japonica</i> ) |                                       | Asia                    |
| <i>Dip. minutus</i>                                                                                                                          | Carnivora: phocid (Hawaiian monk seal)                                                                                                                                                                         |                                                                                                                          |                                       | Pacific Ocean           |
| <i>Dip. mobile</i><br>(syn. <i>Dibothriocephalus</i> )                                                                                       | Carnivora: phocid (Ross seal, Weddell seal)                                                                                                                                                                    |                                                                                                                          |                                       | Southern Ocean          |
| <i>Dip. orcini</i>                                                                                                                           | Artiodactyla: delphinid (killer whale); Primates: hominid (human)                                                                                                                                              |                                                                                                                          |                                       | Pacific                 |
| <i>Dip. polyrugosum</i>                                                                                                                      | Artiodactyla: delphinid (long-finned pilot whale)                                                                                                                                                              |                                                                                                                          |                                       | Atlantic                |
| <i>Dip. pseudowilsoni</i>                                                                                                                    | Carnivora: phocid (leopard seal)                                                                                                                                                                               |                                                                                                                          |                                       | Southern Ocean          |
| <i>Dip. quadratum</i><br>(syn. <i>Dip. resimum</i> , <i>Dib. coatsi</i> , <i>Bothriocephalus</i> )                                           | Carnivora: phocid (leopard seal, Weddell seal, crabeater seal)                                                                                                                                                 |                                                                                                                          |                                       | Indian, Southern Oceans |
| <i>Dip. rauschi</i>                                                                                                                          | Carnivora: phocid (Hawaiian monk seal)                                                                                                                                                                         |                                                                                                                          |                                       | Pacific Ocean           |
| <i>Dip. romeri</i><br>(syn. <i>Dibothriocephalus</i> )                                                                                       | Carnivora: odobenid (walrus), phocid (bearded seal, harp seal)                                                                                                                                                 |                                                                                                                          |                                       | Atlantic                |
| <i>Dip. schistochilos</i><br>(syn. <i>Dib. schistochilus</i> , <i>coniceps</i> , <i>macrohallus p.p.</i> , <i>Bothriocephalus coniceps</i> ) | Carnivora: phocid (bearded seal, harbor seal, harp seal, common seal, Greenland seal, Mediterranean monk seal)                                                                                                 |                                                                                                                          |                                       | Arctic Ocean            |
| <i>Dip. scoticum</i><br>(syn. <i>Dibothriocephalus scoticus</i> , <i>pygoscelis</i> )                                                        | Carnivora: phocid (leopard seal, Weddell seal, southern elephant seal), otariid (southern sea lion); Primates: hominid (human)                                                                                 |                                                                                                                          |                                       | circumpolar             |
| <i>Dip. stemmacephalum</i><br>(syn. <i>Dip. yonagoensis</i> , <i>ponticum</i> )                                                              | Artiodactyla: phocoenid (harbor porpoise), delphinid (common dolphin, bottle-nosed dolphin, spinner dolphin, Risso's dolphin, Pacific white-sided dolphin, long-finned pilot whale); Primates: hominid (human) |                                                                                                                          |                                       | circumpolar             |
| <i>Dip. tetrapterum</i><br>(syn. <i>Bothriocephalus</i> )                                                                                    | Carnivora: phocid (common seal, harbor                                                                                                                                                                         |                                                                                                                          | Salmoniformes: salmonid (pink salmon) | Holarctic               |

|                                                                                                                                                                                                            |                                                                                                                                                                                                                                                                                                                                                                                        |  |                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                    |                                            |
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| <i>tetrapterus, dubius, fasciatus, variabilis, Diplogonoporus, Dip. septrionalis, violettiae, mutabilis, Dib. variabilis)</i>                                                                              | seal, bearded seal, hooded seal, ribbon seal, harp seal, spotted seal, ringed seal, monk seal), otariid (northern fur seal, Steller sea lion), mustelid (sea otter, American mink), canid (dog); Rodentia: murid (brown rat)                                                                                                                                                           |  |                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                    |                                            |
| <i>Dip. ventropapillatum</i>                                                                                                                                                                               | Carnivora: phocid (leopard seal)                                                                                                                                                                                                                                                                                                                                                       |  |                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                    | Russia (zoo)                               |
| <i>Dip. wilsoni</i> (syn. <i>Dip. scotti, Dib. mobilis, Dibothrocephalus</i> )                                                                                                                             | Carnivora: phocid (Ross seal, Weddell seal, crabeater seal, leopard seal)                                                                                                                                                                                                                                                                                                              |  |                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                    | Southern Ocean                             |
| <b><i>Adenocephalus</i> (pinnipeds and terrestrial carnivores as DH)</b>                                                                                                                                   |                                                                                                                                                                                                                                                                                                                                                                                        |  |                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                    |                                            |
| <i>A. pacificus</i> (syn. <i>Dip. pacificum, glaciale, giljadicum, arctocephali, arctocephalinum, krotovi, atlanticum, A. septentrionalis Bothriocephalus macrophallus p.p.</i> ) (Pacific broad tapeworm) | Carnivora: otariid (South American fur seal, Antarctic fur seal, Kurile fur seal, Alaskan fur seal, Juan Fernandez fur seal, brown fur seal, Subantarctic fur seal, northern fur seal, Steller sea lion, Afro-Australian fur seal, Australian sea lion, South American sea lion, California sea lion, Galapagos sea lion), canid (dog, black-backed jackal); Primates: hominid (human) |  | Perciformes: sciaenid (Lorna drum, Callao drum, Peruvian banded croaker, snakehead king croaker, Peruvian weakfish, kingfish), carangid (Paloma pompano, Chilean jack mackerel), haemulid (Peruvian grunt), coryphaenid (dolphinfish), serranid (Peruvian rock seabass); Scombriformes: centrolophid (palm ruff), scombrid (eastern Pacific bonito, chub mackerel, Atlantic Spanish mackerel); Siluriformes: ariid (Tete sea catfish, Peruvian sea catfish); Pleuronectiformes: paralichthyid (fine flounder); Gadiformes: merlucciid (Peruvian hake); Ophidiiformes: ophidiid (pink cusk-eel); Mugiliformes: mugilid (flathead grey mullet); Carcharhiniformes: triakid (sickle fin smooth-hound) | Pacific, Indian, Atlantic, Southern Oceans |
| <b>Reassigned species</b>                                                                                                                                                                                  |                                                                                                                                                                                                                                                                                                                                                                                        |  |                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                    |                                            |
| <i>Dip. antarcticus</i> (syn. <i>Bothriocephalus, Dibothrium, Diplogonoporus, Dibothrocephalus</i> ) (now <i>Glandicephalus</i> )                                                                          | Carnivora: phocid (Ross seal)                                                                                                                                                                                                                                                                                                                                                          |  |                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                    | Antarctic                                  |
| <i>Dip. perfoliatum</i> (syn. <i>Dip. rufum, clavatum</i> ) (now <i>Glandicephalus</i> )                                                                                                                   | Carnivora: phocid (Weddell seal)                                                                                                                                                                                                                                                                                                                                                       |  |                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                    | Antarctic                                  |
| <i>Dip. phocarum</i> (now <i>Pyramicocephalus</i> )                                                                                                                                                        | Carnivora: phocid (hooded seal, bearded seal, spotted seal, common seal, ringed seal, Caspian seal), otariid (Stellar sea lion, northern fur seal)                                                                                                                                                                                                                                     |  |                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                    | circumpolar, Caspian Sea                   |

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| <i>Dip. tectum</i><br>(now <i>Baylisiella</i> ) | Carnivora: phocid<br>(southern elephant seal,<br>Weddell seal, leopard<br>seal) |  |  | Southern Ocean |
|-------------------------------------------------|---------------------------------------------------------------------------------|--|--|----------------|

**Parasite morphology:** These aquatic tapeworms form 4 developmental stages: eggs, larval proceroids, larval plerocercoids and adults. The eggs are ovoid in shape and variable in size depending on species, ranging from 35-85 µm in length by 25-65 µm in width (those of *Dib. latus* range from 50-85 x 40-60 µm). They have smooth tanned eggshells which are yellow-brown and have an ellipsoidal operculum at one pole (some species also having a small knob at the opposite (abopercular) pole). The eggs are laid unembryonated and are polylecithal (containing a large amount of yolk). The eggs mature in the aquatic environment to contain a hexacanth (6-hooked) embryo (oncosphere) covered with a ciliated outer envelope (embryophore), this stage being called a coracidium. In intermediate hosts, the parasites form 2 sequential larval stages, first proceroids then plerocercoids, both being alacunate (without internal cavities). Proceroids are elongate and globular growing to 500 µm in length and they are essentially undifferentiated stages filled with parenchymal tissue. They lack an anterior scolex but have a posterior knob-like tail (cercomer) with 6 embryonic hooks. Plerocercoids (or spargana) are elongate and lanceolate measuring from several mm to several cm in length (e.g. < 5 cm for *Dib. latus*, but 10-20 cm for *Dip. dendriticus*). They appear as white corrugated (pseudo-segmented) tubes with an anterior everted scolex with 2 shallow bothria and several internal cellular masses corresponding to developing organs. Adult tapeworms are large in size ranging from 3-15 m in length (some species reaching 25 m). They have a small spatulate unarmed scolex (2.5 mm long) with 2 shallow elongated (1-2 mm) sucker-like grooves (bothria) located dorsally and ventrally. The tapeworm body has a narrow proliferative zone (neck) giving rise to the elongate dorso-ventrally flattened strobila containing up to 4,000 craspedote proglottids that are wider (10-20 mm) than long (2-7 mm). Adults are hermaphroditic with each segment containing a single set of male and female reproductive organs. Mature segments have numerous ovoid testes connected to a common sperm duct which enlarges distally to form an external seminal vesicle that enters the cirrus sac containing the muscular cirrus (copulatory organ). Segments also contain numerous vitelline follicles, a bilobed ovary (germarium), a central rosette-shaped uterus (spiral uterus in the case of *Spirometra*) and a tubular vagina. The cirrus and vaginal pores are fused into a common genital atrium on the midventral surface (those of *Spirometra* spp. remain separated), yet separate from the uterine (birth) pore. Gravid proglottids release numerous dark operculate eggs but eventually become spent and degenerate (process of anapolyxis).

**Site of infection:** Adult diphyllbothriid tapeworms infect the small intestines of their piscivorous definitive hosts: one *Diphyllbothrium* group infecting cetaceans; another group infecting pinnipeds; *Dibothriocephalus* infecting terrestrial carnivores; and the monospecific *Adenocephalus* infecting pinnipeds and terrestrial carnivores. Adult worms usually attach to the ileal or jejunal wall, and on rare occasion to the bile duct. Proceroid larvae develop in the haemocoel (body cavity) of copepods (first intermediate hosts) while plerocercoid larvae develop in the tissues and organs of many fish species, particularly salmonids (second intermediate hosts).

**Pathogenesis:** Despite the large size of adult tapeworms, most infections are asymptomatic as the worms lack digestive tracts and do not feed on host tissues but absorb nutrients from the gut lumen. Many infections in humans have also been found to consist of only one worm. Chronic and/or heavy infections may cause clinical manifestations attributable to host responses to parasite metabolic wastes, degenerating proglottids, mucosal irritation and inflammation, including constipation, diarrhoea, abdominal pain, nausea, vomiting, weight loss, anorexia, asthenia (physical weakness), vertigo (dizziness), numbness of extremities, sensation of hunger, craving for salt, sometimes headache, allergic reactions, eosinophilia, psychosomatic disorders (often when the patient learns of the presence of the worm) and less commonly, intestinal obstruction, cholecystitis or cholangitis (inflammation of the bile duct or gall bladder). Some patients with protracted infections may also develop megaloblastic pernicious anaemia (hyperchromic, macrocytic, low platelet counts, low leucocyte counts) due to the worms causing vitamin B<sub>12</sub> deficiency through the dissociation of vitamin B<sub>12</sub>-intrinsic factor complex. This manifestation is particularly common in Finland, where individuals have a genetic predisposition to pernicious anaemia. Anaemic patients develop pallor, breathlessness, weakness, numbness and disturbances in coordination due to degeneration of spinal and peripheral nerves. On occasion, humans may become infected with larval stages of the parasite and develop a condition known as sparganosis, which is caused by the encystment of plerocercoids in host tissues after they have ingested infected copepods. While the cysts are often benign, physical stress may impact on organ structure and/or function, with the most severe symptoms occurring when spargana infect the brain or eye.

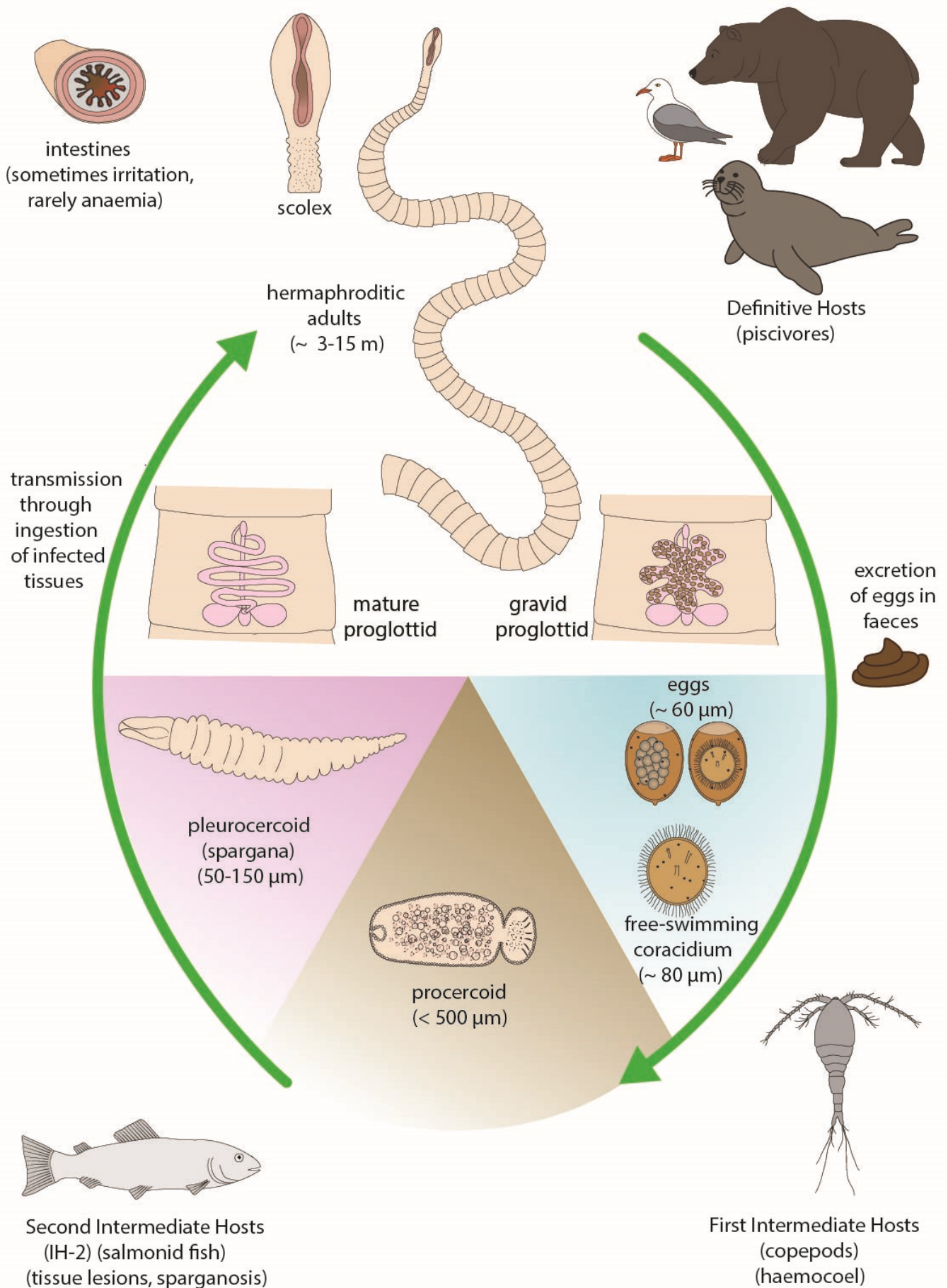
**Developmental cycle and mode of transmission:** *Diphyllbothrium*/*Dibothriocephalus* tapeworms have indirect aquatic life-cycles involving 3 hosts with predator-prey transmission occurring between first and second intermediate hosts and definitive hosts. Adult tapeworms release numerous eggs from gravid segments until their uterine contents become exhausted. Terminal segments become senile and degenerate often detaching in chains of spent segments of variable length. Eggs passed in host faeces are unembryonated and require 1-3 weeks in water (depending on temperature) for embryonic development to be completed. The eggs then hatch releasing a ciliated coracidium which swims sporadically in the water column to attract the attention of zooplanktonic crustaceans (copepods) which act as first intermediate hosts. Coracidia will perish if not ingested by copepods within 24 hours of hatching. Once consumed, the coracidium sheds its ciliated embryophore and the hexacanth larva penetrates the gut wall and develops into a

proceroid larva in the haemocoel within 14-18 days. Infections have been recorded in over 40 copepod species, mostly diaptomid, cyclopoid, centropagid and temorid genera. Proceroids deplete host copepod nutrients and impair their mobility, thus increasing their chances of predation. Infected copepods are eaten by a variety of fish species which act as second intermediate hosts, particularly anadromous salmonids, freshwater predatory fish (pike, perch, burbot) and marine foraging fish (mullet, anchovy, sardines). Many infections have been reported in fish from cold waters in circumpolar regions, but an increasing number are being detected in subtropical and even tropical regions. Digestion of the infected copepods in the fish gut releases the proceroid larvae which burrow through gut wall and develop to infective plerocercoid larvae over 1-5 weeks. Plerocercoids (or spargana) occur free (unencapsulated) in most host tissues and organ (even the abdominal cavity) or encysted (encapsulated) within connective tissues in muscles, viscera, gut or gonads. Some plerocercoids have also been observed migrating from the viscera to the muscles after death of the host. Plerocercoids often ascend piscivorous food chains as they may re-establish in the tissues of larger predatory fish which have eaten smaller infected prey fish (the larger fish thus acting as a paratenic host). Plerocercoids may remain dormant (inactive) for several years, and they can re-establish several times in successive predatory fish. Plerocercoids are ultimately infective to piscivorous definitive hosts; both aquatic (cetaceans, pinnipeds) and terrestrial (carnivores, birds). When ingested, plerocercoids attach to the intestinal wall and develop rapidly into adult tapeworms (prepatent period of 2-6 weeks). Adult tapeworms grow sometimes at the rate of several cm per day, often reaching a length of several metres. Some species may live for up to 20 years and produce up to 1 million eggs per day. Sylvatic cycles may be maintained indefinitely in many countries between a wide range of wild animals, while domestic cycles in humans and companion animals may be regionally specific depending on cultural practices regarding the consumption of uncooked, partly-cooked or pickled fish. Human infections commonly occur in communities eating sashimi (raw sliced fish), sushi (rice balls with fish, egg, vegetables wrapped in seaweed), carpaccio (thin slices of raw fish), tartare maison (raw salmon), ceviche (raw fish pieces freshly marinated in lemon and salt), gefilte fish (balls of finely chopped fish mixed with crumbs, eggs and seasoning, cooked in broth), caviar (raw or partly cooked roe), or lightly cured fish (salted, smoked or marinated). The geographic distribution of infections has changed markedly over recent years with the globalization of trade (import/export of fish products) and growing cosmopolitanism (esp. shared dietary practices). Humans may also become infected with larval plerocercoids (spargana) after accidentally ingesting copepods (harbouring proceroids) in drinking water.

**Differential diagnosis:** Infections by adult tapeworms are readily diagnosed in definitive hosts by the microscopic detection of tapeworm eggs in faecal samples. Sometimes chains or strands of spent proglottids may be detected visually in samples, while a range of egg concentration and high contrast microscopic illumination methodologies have been used to improve diagnostic sensitivity, including sedimentation and/or floatation techniques. Infections by larval stages (proceroids in copepods and plerocercoids in fish) may be detected upon post-mortem dissection, but their specific identification is difficult due to their similar morphologies. Nonetheless, the plerocercoids of several species common in Holarctic fishes have been reliably differentiated on basis of several morphological characteristics (body surface wrinkled or smooth, length and density of microtriches, retraction of scolex, number of subtegumental longitudinal muscles). More recently, molecular characterization techniques have been applied to the differentiation of species and reconciling larval and adult stages. Isoenzyme and immuno-electrophoresis were used to characterize parasite proteins and antigens, restriction fragment length polymorphism (RFLP) analyses were used as species-specific markers, and polymerase chain reaction (PCR) amplification was used to sequence both nuclear DNA (18S ribosomal RNA (rRNA), internal transcribed spacers 1 and 2 (ITS1 and ITS2), elongation factor 1- $\alpha$ ) and mitochondrial DNA (cytochrome c oxidase subunit 1 (cox1) and subunit 3 (cox3), cytochrome b (cob), tRNA pro, tRNA Ile, tRNA lys, NADH dehydrogenase subunits 1, 3 and 4 (nad1, nad3, nad4)) for diagnostic and phylogenetic purposes.

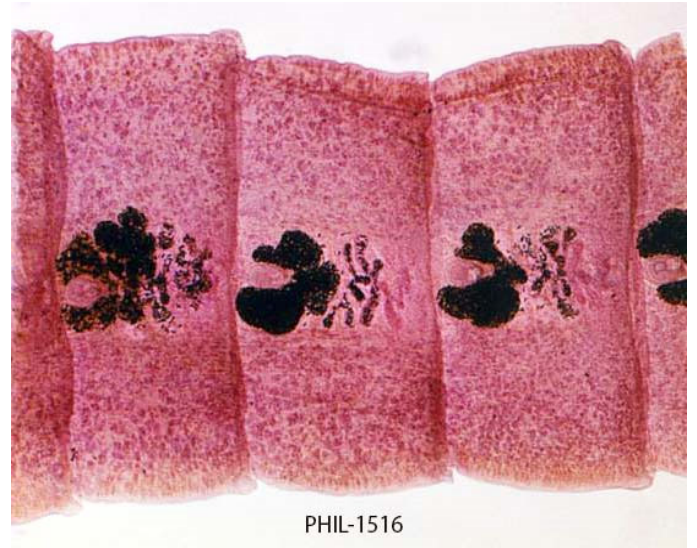
**Treatment and control:** Infections by adult tapeworms in humans and animals have been successfully treated with the anthelmintics praziquantel, niclosamide and albendazole. There may be some vague side-effects following praziquantel treatment, including abdominal discomfort with nausea, headache, dizziness, malaise/fatigue, fever, lower back pain and rarely urticaria. Niclosamide treatment has not been associated with many side-effects as it is not absorbed from the gastrointestinal tract. There is some evidence that the anti-ulcer agent gastropin and the contrast medium gastrografin may cause worms to detach and be excreted. In patients with pernicious anaemia, worms must be eliminated to allow the anaemia to resolve and vitamin B<sub>12</sub> supplementation is recommended. Patients infected with spargana often go untreated as the larvae eventually die, but chemotherapy can be used should clinical problems arise or accessible cysts may be surgically removed (lumpectomy). Various prevention and control strategies have been proposed for domestic settings and aquaculture facilities to break the parasite life-cycle by stopping water contamination by faeces (better sanitation, sewage treatment), reducing copepod populations (water filtration/treatment), and minimizing transmission to fish-eating mammals (improving food hygiene, handling and cooking). Plerocercoids in fish products have been rendered nonviable by freezing (at least 24-48 hours at -10 to -35°C), desiccation (completely dried), brining (in 12% salt) or cooking (at 55°C for 5 minutes). Translocations (import/export) of partially processed fish products should be avoided, particularly from endemic regions.

# *Diphyllobothrium*



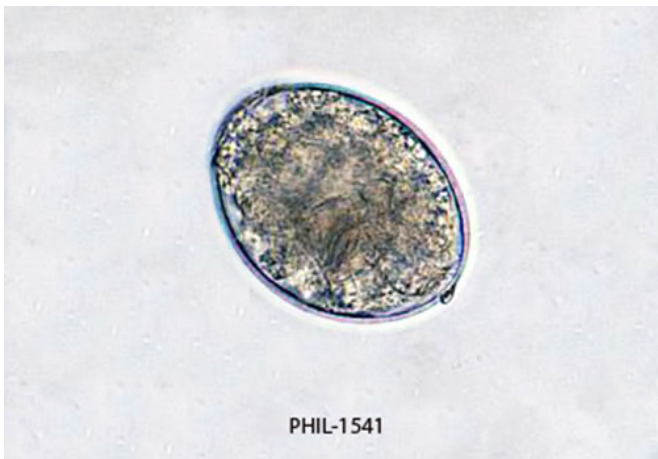


*Diphyllbothrium* scolex



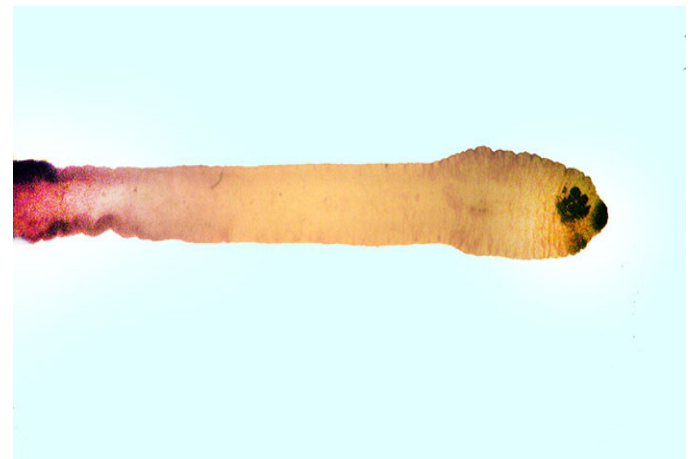
PHIL-1516

*Diphyllbothrium* segments



PHIL-1541

*Diphyllbothrium* egg



*Diphyllbothrium* pleurocercoid