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## Diphyllobothriidea Kuchta et al., 2008 (Order):

## The Broad Tapeworms

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Phylum Platyhelminthes

Class Cestoda

Subclass Eucestoda

Order Diphyllobothriidea

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## Chapter 22

# Diphyllobothriidea Kuchta et al., 2008 (Order): The Broad Tapeworms

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### Introduction

The cestode order Diphyllobothriidea Kuchta, Scholz, Brabec & Bray, 2008 includes parasites of frogs in Africa, monitor lizards and snakes in the tropics, and fish-eating birds and mammals (including humans) worldwide (Kuchta and Scholz, 2017). The number of species that infect humans are relatively few and infections are usually asymptomatic or without serious effects on human health in the case of adult cestodes (diphyllobothriosis, and exceptionally spiro-metrosis). In contrast, larvae (plerocercoids) of species of *Spirometra* may cause a serious disease called sparganosis and plerocercoids of *Ligula intestinalis* can castrate fish intermediate hosts and larvae of another species maturing in birds, *Schistocephalus solidus*, and change the behavior of sticklebacks (Williams and Jones, 1994; Barber et al., 2000; Kuchta et al., 2015). The greatest number of species of diphyllobothriideans occurs in marine mammals, mainly in pinnipeds and cetaceans (Scholz et al., 2019). These parasites, commonly known as broad tapeworms (because they have wide segments), are among the largest helminths on the Earth and species from whales can reach more than 30 m in total length (Yurakhno, 1992). The number of nominal species exceeds 150, but only 60 species in 18 genera are considered to be valid (Kuchta and Scholz, 2017; Scholz et al., 2019).

Similar to bothriocephalideans, broad tapeworms possess paired attachment grooves, bothria (singular = bothrium), and were originally placed together in the order Pseudophyllidea

Carus, 1863. However, they differ from each other in several morphological characteristics, such as the position of the gonopores, presence/absence of an external seminal vesicle, and enlarged distal part of the uterus (Kuchta et al., 2008). Broad tapeworms usually possess a robust body with well-developed longitudinal musculature and numerous vitelline follicles scattered in the cortex of the proglottids. Their eggs are shelled and operculate (having an operculum), their outer envelope, usually called the capsule, is tanned (hardened by a polyphenol/quinone tanning process), and the eggs are poly-lecithal having a large number of vitellocytes per oocyte, and they are usually operculate (Conn and Świdorski, 2008).

### Taxonomic History

The current order Diphyllobothriidea was established by Kuchta and colleagues (2008) who split the non-monophyletic order Pseudophyllidea into the Bothriocephalidea and the Diphyllobothriidea. This taxonomic proposal has been widely accepted (Waeschenbach et al., 2012; Caira et al., 2014; Caira and Jensen, 2017).

The first described diphyllobothriideans were broad fish tapeworms recognized initially as *Taenia lata* Linnaeus, 1758 (now called *Dibothriocephalus latus*, or sometimes referred to as *Dibothriocephalus latum*) from humans, and larvae (plerocercoids) named *Taenia intestinalis* (= *Ligula intestinalis*) from cyprinid fish (adults occur in birds that eat fishes).

When cestodes (tapeworms) were first studied, early scientists did not know that they, in fact, represented different species, the techniques had not yet been developed to discern much of the morphological characters. They were therefore lumped together as ribbon worms (*Taenia*). Thereafter, a number of diphyllobothriideans were described in the 19th and 20th centuries, with the most intensive research on human-infecting taxa occurring from approximately 1930 to 2000 in the United States, Canada, Scandinavia, and the former Soviet Union (see Wardle and McLeod, 1952; Delyamure et al., 1985). In North America, Justus F. Mueller and Robert L. Rausch were notable for their numerous contributions to knowledge of diphyllobothriideans (see Scholz et al., 2019) and Delyamure and colleagues (1985) provided a synopsis of the Diphyllobothriidae. Kamo (1999) deals with all members of the Diphyllobothriidae, with a focus on human-infecting taxa.

Several problems still remain in the taxonomy of broad tapeworms despite the considerable effort of several generations of cestodologists. Most confusion exists in the systematics of 2 species-rich genera, *Diphyllobothrium* (containing nearly 100 nominal species) and *Spirometra* (containing almost 50 species). The validity of the latter taxon has been questioned and *Spirometra* has been considered to be a junior



Figure 1. Microphotographs of diphyllbothriidean tapeworms. A) Live adults of *Cephalochlamys namaquensis* from *Xenopus laevis*, South Africa (arrow indicates the scolex). B) Live *Bothridium pithonis* in the intestine of *Xenopeltis unicolor*, Vietnam. C) Museum specimens of adults of *Diphyllobothrium cordatum* (larger), *D. lanceolatum*, and *D. schistochilos* (smaller) from *Erignathus barbatus*, Greenland. D) Live larvae (spargana) of *Spirometra erinaceieuropaei* in the muscles (arrow) and after their removal from *Pelophylax nigromaculatus*, China. E) Live larva (plerocercoid) of *Dibothriocephalus latus* in the muscles (arrow) of *Perca fluviatilis*, Italy. F) Fixed plerocercoids of *Dibothriocephalus ditremus* (smaller) and *D. dendriticus* (larger) from the body cavity of *Oncorhynchus mykiss*, United Kingdom. Source for all: R. Kuchta and T. Scholz. License for all: CC BY-NC-SA 4.0.

synonym of *Diphyllobothrium* (for example, see Schmidt, 1986). Nevertheless, molecular data provide convincing evidence that *Spirometra* is a valid genus, which is not closely related to any of several lineages of the *Diphyllobothrium*,

which is now recognized to be a polyphyletic assemblage, meaning that species assigned to this genus are not derived from a common ancestor and the group is a mixture of unrelated species (see Waeschenbach et al., 2017).

### Current Classification

Molecular phylogenetic analyses have focused on interrelationships of the order. Waeschenbach and colleagues (2017) supported the division of the group into 3 families that differ from each other in their morphology, but also with respect to the spectrum of definitive hosts (see Kuchta and Scholz, 2017). These families are discussed below.

#### Family Cephalochlamyidae Yamaguti, 1959

Species of cestodes assigned to this family are originally parasites of frogs distributed in sub-Saharan Africa and they have been imported by people to California, United States. The type genus is *Cephalochlamys* Blanchard, 1908 (with 2 species). There is an additional (monotypic) genus, *Paracephalochlamys* Jackson and Tinsley, 2001. Species of cestodes in these genera characteristically have a vas deferens that exits directly to the genital pore without expanding into a cirrus sac and the proglottids are acraspedote, that is, their posterior margin is not wider than the anterior margin of the subsequent proglottid (meaning that they have no velum on the posterior margin). The life cycle includes only 1 intermediate host, a freshwater copepod. The copepod becomes infected when it eats a ciliated free-swimming coracidium larva that hatched from the eggs in water (Thurston, 1967).

#### Family Solenophoridae Monticelli and Crety, 1891

Animals in this family are parasites mainly of varanid and boid reptiles in the tropics and subtropics. The type genus is *Solenophorus* Creplin, 1839 (which is a synonym of *Bothridium* Blainville, 1824) (with 6 species). Additional genera include *Duthiersia* Perrier, 1873 (2 species) and *Scyphocephalus* Riggenbach, 1898 (1 species). The proglottids are craspedote and the genital atrium is large. The life cycles of these species have not yet been elucidated.

#### Family Diphylobothriidae Lühe, 1910

These are typically parasites of mammals, but are also (rarely) found in birds. The type genus is *Diphylobothrium* Cobbold, 1858 (with 27 species). Additional genera include *Adenocephalus* Nybelin, 1931 (1 species), *Baylisia* Markowski, 1952 (2 species), *Baylisiella* Markowski, 1952 (1 species), *Dibothriocephalus* Lühe, 1899 (7 species), *Flexobothrium* Yurakhno, 1979 (1 species), *Glandicephalus* Fuhrmann, 1921 (2 species), *Ligula* Bloch, 1782 (5 species), *Plicobothrium* Rausch and Margolis, 1969 (1 species), *Pyramicocephalus* Monticelli, 1890 (1 species), *Schistocephalus* Creplin, 1829 (5 species), *Spirometra* Faust, Campbell and Kellogg, 1929 (4 species), and *Tetragonoporus* Skryabin, 1961 (1 species).

### Morphology

Diphylobothriideans are medium-sized to large polyzoic tapeworms, that is, their body—the strobila—consists of a series of proglottids maturing consecutively from the proliferative zone (neck) situated posterior to the scolex, that is, the anterior end with the attachment function (Kuchta and Scholz, 2017). The proglottids are usually wider than long and are anapolytic. The scolex is variable in shape and is always unarmed (with no hooks or other sclerotized structures present), with dorsal and ventral longitudinal grooves (termed bothria; singular: bothrium). There are single reproductive organs in the proglottid in most taxa, and so are rarely double or multiple per proglottid. The testes are numerous and medullary, and usually in a single field. The sperm ducts are convoluted, forming a thick-walled, muscular external seminal vesicle attached to the proximal part of the cirrus sac. The cirrus sac is usually thick-walled and the cirrus is unarmed, that is, it is not covered with spinitriches (see Chervy, 2009 for terminology of microtriches in cestodes). The genital pore is ventral, median, or submedian. The ovary is medullary, usually bi-lobed, and is situated posterior to the proglottids. The vitelline follicles are numerous and are usually cortical and circum-medullary. The uterus is tubular and variable in shape, opening to the exterior through a uterine pore situated posterior to the genital pore. The eggs are operculate and unembryonated in the uterus in most taxa, and a freely swimming ciliated coracidium is present.

### Species Diversity

Opinions as to the species diversity of broad tapeworms and their classification have changed considerably and constantly over more than 250 years since description of the first 2 broad tapeworms, including *Dibothriocephalus latus*. Taxonomic and nomenclatural problems still remain in this group due to factors such as their general morphological uniformity coupled with high intraspecific variability, the difficulties in observing the internal anatomy in large-sized worms, the poor quality of specimens obtained from dead or frozen hosts, and the absence of type and voucher specimens of numerous species, among other reasons.

In the 20th century, research on broad tapeworms was quite intensive, especially in North America (for example, pivotal papers by Justus F. Mueller on *Spirometra* and Robert L. Rausch's accounts on species of *Diphylobothrium* from Alaska) and from the former Soviet Union (Delyamure et al., 1985). Numerous studies from Scandinavia and Japan are also noteworthy. However, attention paid to broad tapeworms including their taxonomy sharply declined in the last decades of the 20th century. Kuchta and Scholz (2017) provided a

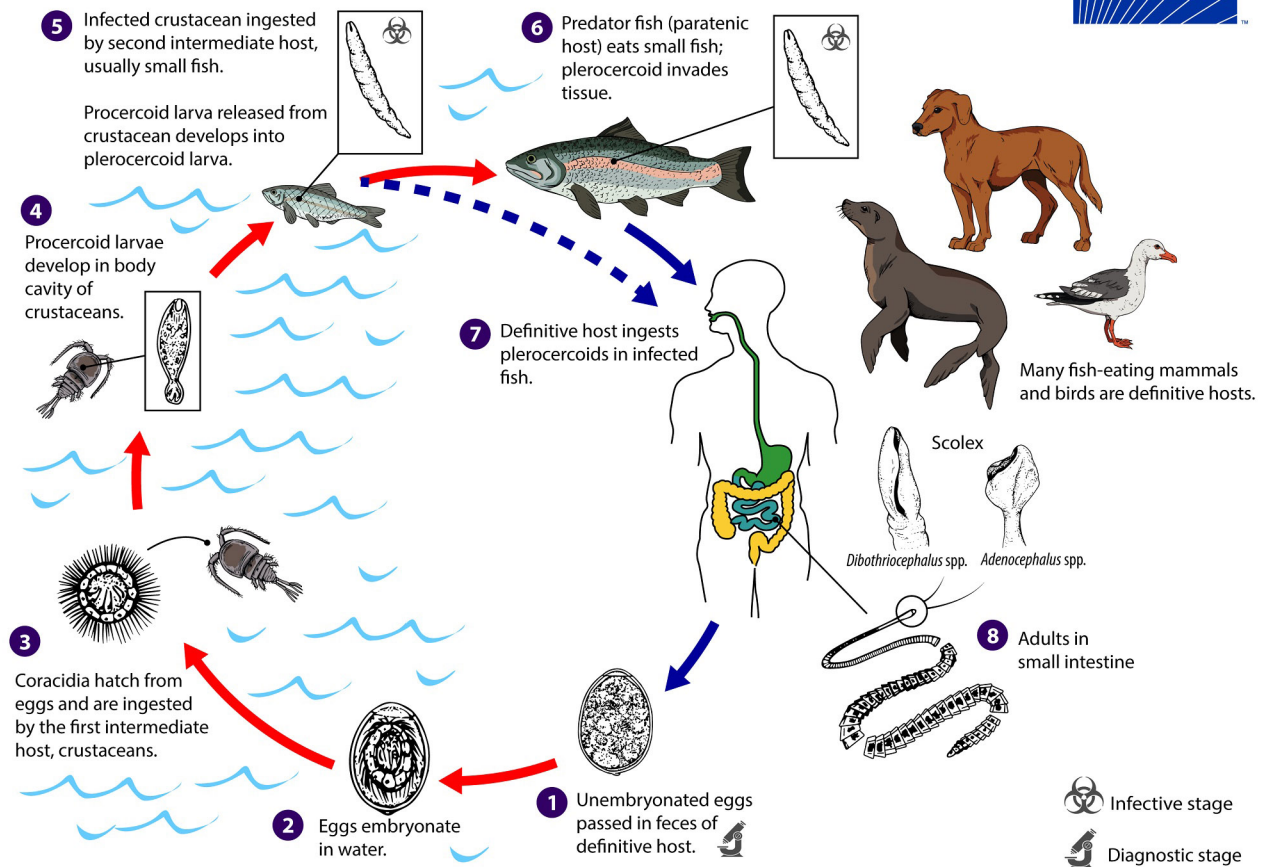


Figure 2.

survey of the whole order, with the complete list of all species recognized as valid (a total of 70 species from 18 genera) with their type hosts. Scholz and colleagues (2019) provided lists of species parasitizing marine mammals and nominal species of *Spirometra*.

### Life Cycles

Life cycles of only a limited number of species, especially those infecting humans, are known (see, for example, the life cycle depicted in Figure 2), but planktonic crustaceans (copepods) likely serve as first intermediate hosts of most, if not all broad tapeworms. They are the only intermediate hosts of cephalochlamydids from frogs (Thurston, 1967). Life cycles of species of the Solenophoridae are still unknown, but most likely involve a second intermediate host which is a vertebrate. The life cycles of the Diphyllobothriidae are always connected to an aquatic environment (freshwater or marine), because the first larva (coracidium) swims in the water and is then swallowed by the first aquatic intermediate host, which

is a copepod (subphylum Crustacea: subclass Copepoda). Second intermediate hosts are vertebrates, especially freshwater or marine teleost fishes (Dubinina, 1980; Kuchta et al., 2015). The exception is the life cycle of species of *Spirometra*, which includes a wide spectrum of amphibians, reptiles, birds, or small mammals as second intermediate hosts, but not teleosts (Kuchta and Scholz, 2017; Scholz et al. 2019).

### Host Associations

Broad tapeworms are peculiar among all but 1 (Cyclophylidae) of the cestode orders in successful colonizing of all major tetrapod groups. Molecular data reveal that the main lineages, which correspond to 3 families, generally reflect the evolutionary history of their tetrapod definitive hosts. Species of Cephalochlamydidae mature in amphibians (frogs), members of the Solenophoridae in monitors and snakes, and species of the most derived lineage of broad tapeworms, the Diphyllobothriidae, mature in mammals including humans and, to a lesser extent, birds. The earliest diverging groups of

diphyllobothriids (*Spirometra* and *Schistocephalus*) colonized terrestrial ecosystems followed by radiation in marine mammals (pinnipeds and cetaceans: *Diphyllobothrium*, *Adenocephalus*, and so on). Species of the most recently diverging groups (*Ligula* and *Dibothriocephalus*) use terrestrial mammals and fish-eating birds as their definitive hosts (Waeschenbach et al., 2017; Scholz et al., 2019).

Marine mammals are definitive hosts of nearly two-thirds of diphyllobothriids (37 of 58 known species). They infect mainly pinnipeds (reported from 17 and 15 species of the Phocidae and Otariidae families, respectively), but also cetaceans (reported from 8 and 21 species of the Mysticeti and Odonoceti suborders, respectively; see Scholz et al., 2019). The infection rate in seals can be extraordinarily high, with prevalence reaching up to 100%, and extremely high intensity of infections, especially in Antarctic seals. The most heavily infected seal harbored as many as 3,600,000 individuals of *Diphyllobothrium mobile*, but the majority of specimens were juvenile (Yurakhno and Maltsev, 1997).

Broad tapeworms of terrestrial vertebrates are represented by 21 species within 4 genera, *Dibothriocephalus*, *Ligula*, *Schistocephalus*, and *Spirometra* (36% of all known diphyllobothriids). They infect a much wider spectrum of hosts and generally exhibit far lower host range compared to marine species. Members of the genera *Dibothriocephalus* and *Spirometra* are typical parasites of carnivores (several unrelated families, but not pinnipeds), and occasionally of fish-eating birds (some species of *Dibothriocephalus*). Species of *Spirometra* occur in warmer latitudes than species of *Dibothriocephalus* (see Figure 3 in Scholz et al., 2019).

Most species of *Ligula* and *Schistocephalus* are euryxenous at the level of the definitive host, with adults of these genera having been reported from almost 80 species of fish-eating birds (Dubinina, 1980). For example, *S. solidus* has been reported from as many as 42 species of birds across 8 orders (Vik, 1954). In contrast, the 3-spined stickleback, *Gasterosteus aculeatus*, serves as the only second intermediate host species of this cestode. Its plerocercoids continue to grow for an unusually long time (several months), and nearly reach sexual maturity in the fish host. In the definitive host, adults of *S. solidus* survive only few days, producing great numbers of eggs (Dubinina, 1980).

### Geographic Distribution

According to Waeschenbach and colleagues (2017), terrestrial and freshwater species of broad tapeworms (Diphyllobothriidea) represent 46% of the total species richness (33 species); they occur in the Palaearctic (17 species; 22%), Nearctic (10 species; 14%), and Ethiopian (8 species; 10%) regions. Most species, especially those of the family

Diphyllobothriidae, occur predominately in colder climates between 50–60 °N and 40–70 °S, including 14 species belonging to 4 genera (*Baylisia* Markowski, 1952, *Baylisiella* Markowski, 1952, *Flexobothrium* Yurakhno, 1989, and *Glandicephalus* Fuhrmann, 1921) endemic to Antarctic seals (Delyamure et al., 1985; Scholz et al., 2019). In contrast, species of the early diverging groups, that is, Cephalochlamydidae, Solenophoridae, and *Spirometra* spp., are well adapted to warmer climate zones; and members of the 2 former families occur exclusively in tropical and subtropical latitudes.

### Phylogenetic Relationships

Waeschenbach and colleagues (2017) provide the most robust hypothesis to date of interrelations of diphyllobothriidean cestodes, using a phylogenetic framework of 30 species of 11 genera based on large and small nuclear ribosomal RNA subunits (*ssrDNA* and *lsrDNA*), a large subunit of mitochondrial ribosomal RNA (*rrnL*) and cytochrome c oxidase subunit I (*cox1*) sequences. This first multigene family-wide phylogeny of the order provides support for the current classification of the order, recognizing 3 families specific to amphibians (Cephalochlamydidae), reptiles (Solenophoridae), and mammals and birds (Diphyllobothriidae) proposed by Kuchta and colleagues (2008) and Kuchta and Scholz (2017).

Molecular data also reveal the polyphyly of *Diphyllobothrium* and invalidity of *Diplogonoporus*. As a result, a new, more natural classification of broad tapeworms is proposed, including new generic assignment of the most important causative agents of human diphyllobothriosis, namely, *Dibothriocephalus latus* and *D. nihonkaiensis* (see Waeschenbach et al., 2017). Synonymy of *Spirometra* with *Diphyllobothrium* (including the currently resurrected *Dibothriocephalus*) previously proposed by a number of authors is not supported because both genera are not closely related. The former genus is 1 of 2 earliest diverging diphyllobothriid lineages, whereas *Dibothriocephalus* belongs among the most recently diverging clades of broad tapeworms (Waeschenbach et al., 2017).

### Selected Taxa from the Nearctic Region

A total of 49 species of diphyllobothriid cestodes have been reported from the Nearctic region and the Neotropical part of Mexico. Of these, the following species are selected to document diversity, host associations, life cycles, and phylogenetic affinities in this group of cestodes in North America.

#### *Dibothriocephalus latus*

*Dibothriocephalus latus* is the most important causative agent of human diphyllobothriosis (about 20 million human cases estimated annually). The species has been known as a

human parasite for long time as evidenced by archaeoparasitological data from mummies and coprolites. These data reveal the presence of eggs of diphyllobothriid cestodes at least since the early Neolithic period (Mitchell, 2013). Several foci of human infections in North America, especially in the Great Lakes region, were reported in the 20th century, but other species such as *D. nihonkaiensis* may have been misidentified as *D. latus*, especially on the Pacific coast of North America.

#### ***Dibothriocephalus nihonkaiensis***

*Dibothriocephalus nihonkaiensis* was identified as *D. latus* for long time until Yamane and colleagues (1986) distinguished broad fish tapeworms from Japan from genuine *D. latus*. The Japanese broad tapeworm utilizes different fish intermediate hosts (anadromous Pacific salmon) compared to *D. latus* (freshwater perch, pikeperch, pike, and burbot). Both species also differ from each other in their geographical distribution, with *D. nihonkaiensis* occurring originally on the northern Pacific coast of the United States, whereas the distribution of *D. latus* as a freshwater species is limited to temperate latitudes of Eurasia and North America (Scholz et al., 2019). About 1,000 human cases have been reliably documented, especially in Japan, but human cases have also been reported from northwestern North America (Kuchta et al., 2015; Scholz and Kuchta, 2016).

#### ***Spirometra* spp.**

Several species such as *Spirometra mansonoides* Mueller, 1935 have been reported from North America, but their validity, host range, and distribution are insufficiently known. Adults are reported mainly from felids and canids, whereas larvae (spargana) are known from water snakes. These larvae may also infect humans who consume uncooked infected intermediate hosts. Most of the patients in the United States are from the eastern seaboard and Gulf Coast (Kuchta et al., 2015; Scholz et al., 2019).

#### ***Schistocephalus solidus***

Plerocercoids of *Schistocephalus solidus*, which matures in fish-eating birds, are very common in the 3-spined stickleback in the Northern Hemisphere. These large larvae (metacestodes) may cause deformation of the body of heavily infected fish, but also change their behavior to facilitate parasite transmission, that is, predation of fish hosts infected with cestode larvae (Barber et al., 2000). The stickleback-*Schistocephalus* model has been successfully used in ecological, behavioral, and evolutionary studies (Heins et al., 2014; Heins, 2017).

### **Conclusions**

Broad tapeworms are among the largest tapeworms on Earth and some species have been known as human parasites for a long time. However, species diversity of these usually large-sized tapeworms is still poorly known, partly because of the existence of numerous unresolved taxonomic problems. They currently get more attention due to the appearance of several human cases in non-endemic areas as a result of importation of unfrozen fish that serves as a significant source of human infection. In contrast, broad tapeworms in wildlife such as marine mammals (pinnipeds and cetaceans) remain largely neglected, even though their actual impact on heavily infected hosts remains to be clarified. These tapeworms may serve as a suitable model group for studies on host-parasite relationships because of their relatively narrow host range, especially taxa in marine mammals. The serious problem that impedes better understanding of the biology, host associations, and epidemiology of these cestodes is a shortage of properly processed material suitable for application of methods of integrative taxonomy and molecular systematics. Molecular data are crucial for reliable diagnosis and species identification of most taxa because of their general morphological uniformity and high intraspecific variability. DNA-based identification using suitable molecular markers (*cox1* sequences) is also inevitable to detect sources of human infection.

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