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Diphyllidea van Beneden in Carus, 1863 (Order)

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Phylum Platyhelminthes

Class Cestoda

Subclass Eucestoda

Order Diphyllidea

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Chapter 25

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Introduction

This group of small and polyzoic cestodes inhabiting the spiral valve of elasmobranchs (most commonly, species of *Carcharhiniformes*, *Myliobatiformes*, *Rajiformes*, and *Rhinopristiformes*, according to Ivanov and Caira, 2013) is distributed worldwide. One of the most remarkable traits of this group is the presence of only 2 bothridia on the scolex (feature from which the name of this order derived: **di** (= 2, Latin) and from **phyllidium** (= leaf, Greek)) and a genital pore at the mid-ventral region. Despite the wide variation in the presence or absence and arrangement of the scolex structures, in general diphylleideans may bear an apical organ armed with hooks, lateral hooklets, a cephalic peduncle that may be armed with spines, and a corona of spines (Caira et al., 2013; 2017).

This order, proposed by van Beneden in Carus (1863), currently is widely accepted, although their validity has been controversial (see Caira et al., 2017). The monophyly of the order has been demonstrated by morphological data by Ivanov and Hoberg (1999) and ratified based on molecular data by Caira and colleagues (1999; 2013) and Waeschenbach and colleagues (2012).

This order contains only 1 family (**Echinobothriidae**) with 6 genera and 59 described species. *Echinobothrium* is the genus with the highest number of species (see Figure 1), with 33, followed by *Halysioncum*, with 16 species, *Coronocetus*, with 6 species, and *Ditrachybothrium*, with 2 species. The genera *Andocadoncum* and *Ahamulina* are monotypic (Caira et al., 2017).

Diphylleideans are cosmopolitan. According to Spalding and colleagues (2007), its members have been recorded in all marine realms.

Main Morphological Characteristics

Diphylleideans are polyzoic worms, relatively small in body size, ranging from 0.46 mm in *Echinobothrium weipaense* (Ivanov and Caira, 2012) to 95.3 mm-long in the largest species (*Ditrachybothridium piliformis*, see Faliex et al., 2000).

The scolex is composed of a pair of sessile bothridia (1 dorsal and 1 ventral), often bearing a corona of spines, a cephalic peduncle armed with spines, and hooks and lateral hooklets on the apical organ (Khalil, 1994; Caira et al., 2017). In contrast, the cephalic peduncle in *Ditrachybothridium* is short and unarmed and lacks apical hooks (Ivanov and Hoberg, 1999). The scolex is covered by spinitriches of different types, distributed in patterns that vary at the species level. The cephalic peduncle lacks spinitriches and filitriches are present in some species (Ivanov and Caira, 2013).

They have acraspedote and apolytic strobila (that is, those that release gravid proglottids). Their mature proglottids are longer than they are wider. A common trait among the species of this order is the arrangement of the hermaphroditic reproductive system with the genital pore placed on the mid-ventral line in the posterior part of the proglottid, a bilobed ovary in cross section located in the posterior margin, as well as an absence of uterine pores (Ivanov and Hoberg, 1999). Other reproductive characteristics shared by diphylleideans are the presence of a vaginal opening posterior to that of the unipartite cirrus sac, a cirrus with spinitriches, testes disposed in 2 columns anterior to the ovary (between 4–6 in *Halysioncum rayallemangi*, according to Tyler (2006) to 43–81 in *Ditrachybothridium piliformis*; see Faliex et al. (2000)), vitellaria in 2 lateral bands or circumcortical in cross section, and a saccular uterus (Caira et al., 2017). Eggs in most species are without filaments, and some have a polar

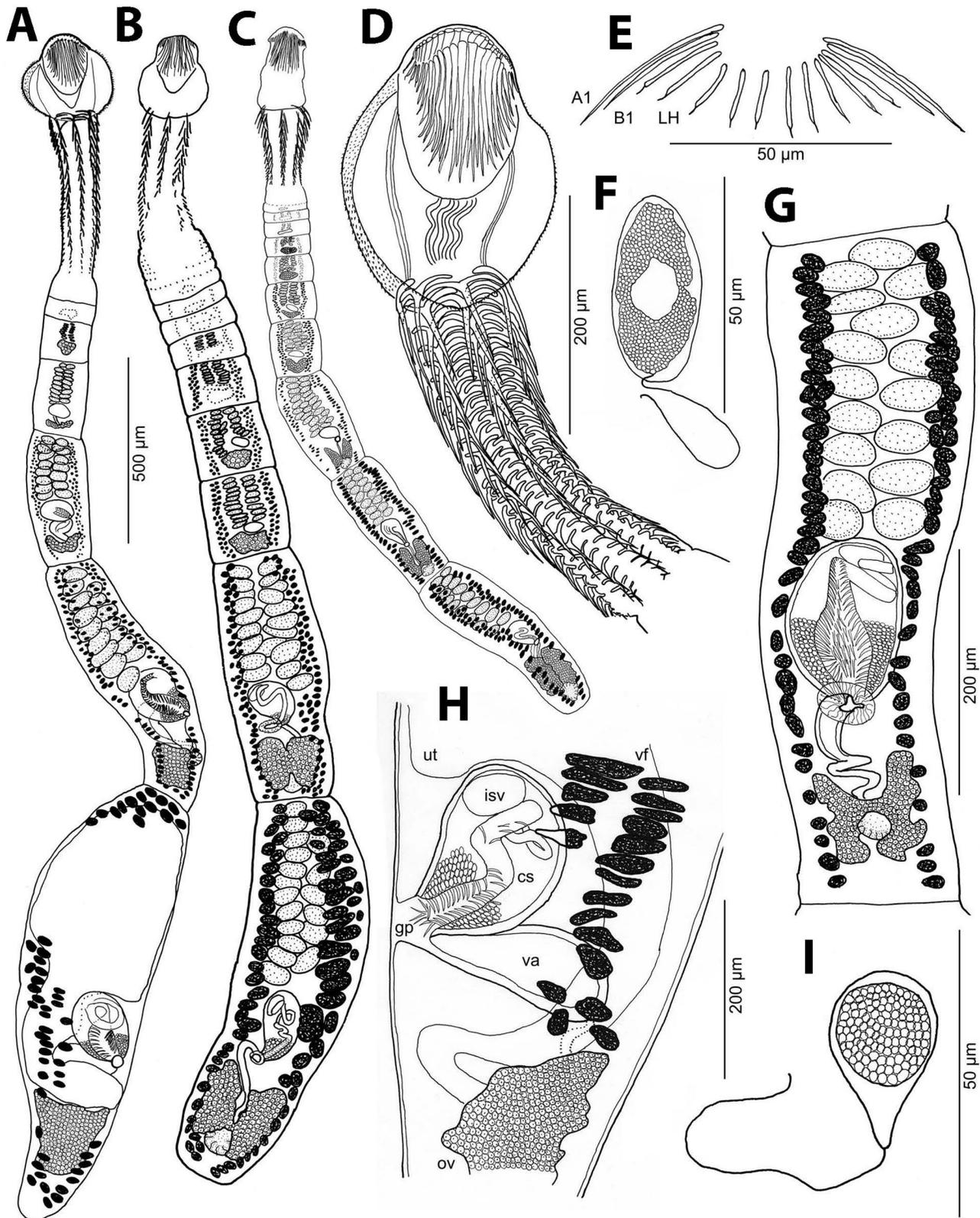


Figure 1. Line drawings. A, D–H) *Echinobothrium nataliae* A) Whole worm; D) scolex; E) L lateral hooklets; F) egg. G) mature proglottid; H) detail of terminal genitalia, lateral view; B) *Echinobothrium reginae*, whole worm; C, I) *Echinobothrium vojtae*; C) whole worm; I) egg. Abbreviations: A1) First A (anterior) hook; B1) First B (posterior) hook; cs) cirrus sac; gp) genital pore; isv) internal seminal vesicle; LH) lateral hooklets; ov) ovary; ut) uterus; va) vagina; vf) vitelline follicles. Source: Kuchta and Caira, 2010. License: CC BY.

projection, such as *Echinobothrium harfordi*, and some have a polar filament, *Echinobothrium affine* (Ivanov and Hoberg, 1999; Tyler, 2006).

Description and Summary of a Representative Species

Note: This is not intended for the purposes of zoological nomenclature.

Halysioncum mexicanum (Tyler & Caira, 1999) Caira et al., 2013

These are short-bodied worms (1.16–0.27 mm length), consisting of 4–10 segments, and are longer than they are wide as they reach maturity. Generally, the last segment is the widest portion of the body (0.11–0.44 mm). The scolex is constituted of 2 large oval bothridia (1 ventral and 1 dorsal) and an apical rostellum armed with 2 groups of 23 large apical hooks, 1 dorsal and 1 ventral. The hooks are flanked by 1 continuous row of 10–13 small lateral hooklets on each side. The surface of the bothridia is covered with palmate microtriches, with the number of digits varying along bothridia (3 or 4 at the anterior-most proximal area and 6 at the posterior region). They include short filiform microtriches spread along the proximal surfaces. The microtriches change from palmate to slender filiform abruptly, limiting the border between the distal and proximal surfaces of the bothridia. The cephalic peduncle is large and wide at the middle point, armed with 8 longitudinal columns of 23–40 spines with a triradiate base. The base length decreases from the anterior to the posterior region of the cephalic peduncle, which is covered by short filiform microtriches. The strobila is acraspedote, formed by 1–3 mature segments and 1 gravid proglottid. The testes (10–20 in number) are arranged in 2 or 3 columns at the anterior half of each segment. The cirrus sac is expanded, and is armed along its length with robust curved spines. The ovary is bi-lobed and H-shaped. The ovarian isthmus is stout. Mehlis' gland is prominent. The vagina is robust, ventral, and positioned immediately adjacent to the genital atrium. The genital pore is situated mid-ventrally. The uterus is dorsal, extending from the ovarian isthmus to the anterior margin of a gravid segment. A uterine pore is absent. The follicular vitellaria are arranged in 2 wide lateral bands uninterrupted along the proglottid, and are joined posterior to the ovary. There are small filamented eggs. The excretory ducts are lateral.

Taxonomic summary.

Type host: Snouted eagle ray, *Myliobatis longirostris*.

Site of infection: Spiral intestine.

Type locality: Bahía de Los Ángeles, Gulf of California, Mexico (28° 55' N, 110° 25' W).

Type specimens are listed here and additional details can be found in the original paper where this species was described: Holotype (CNHE 3343); paratypes (CNHE 3344–3345; USNPC 88220–88221; HWML 39912–39914).

Members of the Order Diphyllidea van Beneden in Carus, 1863 in Relation to Each Other

Of the 15 additional species described for the genus *Halysioncum*, *H. mexicanum* has 23 apical hooks on its scolex. Therefore, *H. mexicanum* can be distinguished from 6 of the other species because these have a smaller number of hooks: *H. fautleyae* (11 hooks), *H. pigmentatum* (20 hooks), *H. bonasum* (11 hooks), *H. hoffmanorum* (19–21 hooks), *H. californiense* (21 hooks), and *H. kishiense* (10–11 hooks), and from an additional 6 species because they have a greater number of hooks (between 25 and 29): *H. nataliae* (27–29 hooks), *H. reginae* (29 hooks), *H. vojtaei* (29 hooks), *H. euzeti* (25 hooks), *H. megacanthum* (27 hooks), and *H. gibsoni* (27 hooks). Finally, the number of apical hooks on the scolex of *H. mexicanum* is similar to that of *H. raschii* (23–25 hooks) and identical to the number of hooks contained within *H. arafuerense* and *H. rayallemangi*. However, the length of the strobilus in *H. raschii* is considerably greater (8.6–21.5 mm) than that of *H. mexicanum* (1.16–5.27 mm) and the number of digits in the microtriches of *H. raschii* can be up to 15 while in the Mexican species its number ranges from 3–6. The number of spines of the cephalic peduncle is another trait that makes it possible to differentiate *H. arafuerense* and *H. rayallemangi* from *H. mexicanum*, since this number ranges from 20 to 24, 2 to 5 and 23 to 40, respectively. Additionally, the number of testes of *H. rayallemangi* is considerably lower (4–6) than that of *H. mexicanum* (10–20) (see Tyler, 2006; Kuchta and Caira, 2010; Ivanov and Caira, 2013; Moghadam and Haseli, 2014).

In the first phylogenetic study about the intrageneric relationships of Diphyllidea, based on morphological traits, Ivanov and Hoberg (1999) recognized monophyly of the order. However, the results suggested that 2 of the 3 formerly recognized genera (*Macrobothridium* and *Echinobothrium*) could be considered synonyms, validating the independence of *Ditrachibothridium*, a proposal ratified by Tyler (2006). The molecular confirmation of this hypothesis was made by Caira and colleagues (2013), who also erected 2 new genera (*Halysioncum* and *Coronocestus*) based on species previously included in *Echinobothrium*. In the same work, the authors identified a new genus of parasite provisionally termed *Leucoraja*, which was formally described a year later and named *Andocandoncum* (Abbott and Caira, 2014).

Life Cycle

The complete life cycle of species of Diphyllidea is poorly known (Tyler, 2001; Bray and Olson, 2004). According to Caira and Reyda (2005) the diphyllidean cestodes follow the same pattern of life cycles as other elasmobranch cestodes. In this pattern the life cycle appears to involve 2 intermediate hosts and 1 elasmobranch as the definitive host. The intermediate hosts are species of Mollusca, Arthropoda, and Actinopterygii. There are many records of larvae in teleost fishes and invertebrates such as crustaceans and molluscs (Bray and Olson, 2004). For example, Cake (1976) reports larvae from 1 species of *Echinobothrium* from the gastropod *Cantharus cancellarius* and *Narrasius vibex* from the northern Gulf of Mexico; Jones and Beveridge (2001) collected a single plerocercoid of *Echinobothrium chisholmae* from the decapod *Penaeus longistylus* from Heron Island, Queensland, Australia, and Muñoz and colleagues (2001) found larvae in the intestine of the fish *Notothenia c.f. angustata* in the Gulf of Arauco, Chile. The adults of this order parasitize mainly batoids (skates and stingrays) (Tyler, 2001) although some species of *Coronocetus* have been recorded in sharks of the genera *Mustelus* and *Iago* (Ivanov, 1997; Haseli and Azad, 2015). Finally, Tyler (2006) suggests that diphyllidean species follow this pattern of life cycle: Eggs are shed with the feces of the definitive host, and posteriorly ingested by a first intermediate host (an invertebrate) such as an amphipod. In the intestine, the eggs hatch, releasing a hexacanth larva which then develops a proceroid. Then, the amphipod is ingested by the second intermediate host (a crab or a shrimp). Into this host the proceroid encysts in the liver and develops a plerocercoid. Finally, this stage is eaten by a definitive host (a shark or batoid) in which the cestodes reach sexual maturity. In some cases, the plerocercoid can be ingested by another type of host (a teleost fish), acting as a paratenic host (which is an organism that carries the immature stage of parasites).

Additional Notes about the Morphology

Diphyllidea and Trypanorhyncha are the only 2 orders of parasites of elasmobranchs in which metacestodes harbored by the last intermediate host bear the diagnostic taxonomic characters of the adult scolex (Beveridge et al., 2017; Caira et al., 2017). This allows identification of the metacestodes to the species level using morphology only.

The morphology of the scolex in Diphyllidea shows a wide range of modification in terms of the presence or absence and arrangement of structures. These variations oscillate from the total absence of spines in the cephalic peduncle and hooks in the scolex-proper of *Ditrachybothridium* (Faliex et al., 2000), to the lack of spines on the cephalic peduncle in some species of *Echinobothrium* and *Ahamulina* (Tyler,

2006; Marques et al., 2012), or may have between 100 and 107 spines along each of 8 longitudinal rows disposed in the cephalic peduncle, as is found in *Halysioncum euzeti* (Campbell and Carvajal, 1980).

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