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Phyllobothriidea Caira et al., 2014 (Order)

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Phylum Platyhelminthes

Class Cestoda

Subclass Eucestoda

Order Phyllobothriidea

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Chapter 28

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Introduction

These acetabulate cestodes are parasites of the spiral valve or spiral intestine of sharks and occasionally batoid rays. Previously included in the Tetrathyllidea (Caira and Jensen, 2014), this order is named after the genus *Phyllobothrium* (from the Greek **phyllon** = leaf-shaped and **bothros** = trench) and was not formally recognized until the phylogenetic analysis with molecular data conducted by Caira and colleagues (2014). These worms are characterized by unarmed bothridia harboring apical suckers, their body size (which can be from small to medium), and their spectacular ornamentation on the scolex (Caira and Jensen, 2014; Ruhnke et al., 2017). Only the members of the former Phyllobothriidae are included in this order, bearing 73 species in 24 described and valid genera, plus 3 genera yet to be described. *Paraorygmatobothrium*

is the most speciose and geographically widespread genus, with 25 formally described species and 4 still-undescribed taxa (Cutmore et al., 2017; Ruhnke et al., 2017). In general, these cestodes exhibit a cosmopolitan distribution, but the records are less common at higher latitudes (Caira and Jensen, 2014).

Main Morphological Characteristics

Phyllobothriidea Caira, Jensen, Waeschenbach, Olson & Littlewood, 2014 are polyzoic worms of small to medium size. They are hermaphroditic. Most of the species are eupolytic or anapolytic; just a few exceptions are hyperapolytic. They may be craspedote or acraspedote with spinitriches restricted to the bothridial surfaces, often being serrate or gongylate. The neck and the strobilar surfaces are filled with filitriches distributed in scutes or in leaf-like structures. The scolex has 4 unarmed muscular bothridia and an anterior accessory sucker. Stalks are absent and an accessory sucker lacks lateral muscular projections. They do not include facial loculi, although some can show marginal loculi. Some species can present lacinated proglottids. There is 1 set of reproductive organs on each proglottid. They have 2 pairs of lateral osmoregulatory canals; in general, the ventral canals are wider than the dorsal ones. There are numerous testes, and a post-poral field is almost always present. The vas deferens is convoluted. An external seminal vesicle may be present or absent. The cirrus is armed with spinitriches. The genital pore is lateral and alternates irregularly, and is mainly located in the anterior half of the proglottid. The vagina opens anterior to the cirrus sac into the genital atrium. The vitellarium is follicular and the follicles are usually arranged in lateral fields, occasionally circumcortically or circummedullarily. The uterus lacks lateral diverticula (Ruhnke, 2010; Caira et al., 2014; Ruhnke et al., 2017).

Description and Summary of a Representative Species

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

Paraorygmatobothrium prionacis (Yamaguti, 1934) Ruhnke, 1993

These tetrabothridiated worms of medium body size (7.2–19.3 mm-long with a maximum width of 400–750 mm at the level of the scolex), and they are craspedote and apolytic. The number of segments is variable, from 11 to 29. The scolex measures from 430 to 620 mm-long and the apical area is covered with filitriches. The bothridia measure from 420 to 620 mm-long and 270 to 440 mm-wide. Each bothridium bears a single loculus and a round, anterior apical sucker (80–118 mm in diameter). The proximal surfaces of the bothridia

are covered with serrated spinitriches and filitriches. On the distal locular surface and distal surface of the apical sucker, the serrated spinitriches are slender and filitriches are also present. The neck varies from 1.8 to 4.6 mm-long; its dorsal and ventral surfaces are scutellated with small (< 500 nm) overlapping triangular structures covering the surface.

The mature segments are longer than they are wide (generally 3 times), with dorsal and ventral pairs of excretory ducts. A pair of nerve chords is situated laterally. The testes are arranged in 2 irregular longitudinal rows, from 2–4 in number in a horizontal row above the genital pore and 2–3 in number in a horizontal row below the genital pore; they are medullar, 1 row deep in cross section. The genital pores are lateral and alternate irregularly. The vagina is median, extending anteriorly from the ovary to the mid-level of the segment, then laterally along the anterior margin of the cirrus sac to the genital pore. The ovary is near the posterior end of the proglottid and is H-shaped in the frontal view and tetralobed in cross section. The uterus is ventral to the vagina and extends from the anterior margin of the ovary to the posterior margin of the cirrus sac in mature proglottids. A uterine duct is present, median, parallel, and dorsal to the uterus. The vitellarium is follicular and arranged in 2 lateral fields, each constituting 1–2 dorsal and 1–2 ventral columns, interrupted by the ovary and the cirrus sac. The eggs are spindle-shaped (Ruhnke, 2010).

Taxonomic summary.

Type host: Blue shark *Prionace glauca* Linnaeus, 1758 (Carcharhiniformes).

Site of infection: Spiral intestine.

Type locality: Pacific coast, Japan.

Type specimens deposited: Unknown.

Phyllobothriidea Caira et al., 2014 Taxonomy

The taxonomic history of this group has been difficult to ascertain since some of the genera and species were originally only loosely defined (Ruhnke, 2010). Morphologically, the genus *Paraorygmatobothrium* is defined by the possession of bothridia with a single apical sucker and an undivided oval posterior loculus; likewise, this genus has serrate gladiate spinitriches on the proximal bothridial surface, the subterminal and terminal proglottids are longer than they are wide, they possess post-vaginal testes, and have vitelline follicles that are distributed in 2 lateral fields (Cutmore et al., 2017). Among the 25 species that belong to the genus, *Paraorygmatobothrium prionacis* has an apical sucker of 80 to 118 µm in diameter, a range that is similar to those registered from *P. exiguum*, *P. janinae*, *P. triacis*, *P. sinclairtaylori*, and *P. ullmanni* (Ruhnke, 2010; Cutmore et al., 2017). From

these 5 species, *P. prionacis* can be distinguished due to its body size (7.2–19.3 versus 35–46 mm in *P. triacis*); from *P. janinae*, because this species has more proglottids (59–104 versus 11–29). Two other species have remarkable differences in relation to the number of testes: *P. prionacis* only has from 34 to 62 testes, while the number of testes is higher (57–152 and 86–116 testes, respectively) in *P. sinclairtaylori* and *P. ullmanni*. Finally, it can be separated from *P. exiguum* by the position of the genital pore along the proglottids (from 74–83% in this species versus 48–59% in *P. prionacis*) (Ruhnke, 2010; Cutmore et al., 2017). According to Cutmore and colleagues (2017), it is essential to analyze the molecular data for the *Paraorygmatobothrium* genus in order to understand their relationships; the description of species on the basis of morphological data alone is considerably problematic. However, the last analysis published by them using molecular evidence, does not show this genus as a monophyletic group (see Cutmore et al., 2017).

Despite the fact that the molecular data analysis is derived from the elevation of this family to the order level, the phylogenetic relationships among the Phyllobothriidea with respect to the other acetabulated clades such as Onchoproteocephaliidea, the residual tetraphilideans, and the clade that comprises mainly cestodes of terrestrial hosts (Cyclophyllidea, Tetrabothriidea, Nippotaeniidea, and *Mesocoestoides*) requires further investigation and expansion of the collecting sites as well as an increase in the number of species examined because fewer than 30% of the valid taxa have been put into a molecular phylogenetic context (Caira and Jensen, 2014; Caira et al., 2014; Ruhnke et al., 2017; Waeschenbach et al., 2017).

Life Cycles

The Carcharhiniformes sharks harbor the majority of species of this cestode group, but they can also parasitize species of the Pristiophoriformes, Squaliformes, Orectolobiformes, and Lamniformes. Just a few phyllobothriideans have been found inhabiting the spiral valve of batoids (Myliobatiformes, Torpediniformes, and Rajiformes). Some authors have considered that this occurrence underlies a host-capture event, particularly since *Chimaerocestos* has been found to parasitize Chimaeriformes. In spite of the great richness of hosts, these worms are considered to be oioxenous (Ruhnke and Workman, 2013; Caira and Jensen, 2014; Caira et al., 2014; Ruhnke et al., 2017). The recent discovery of species of this group from the Southern African marine realm by Ruhnke and colleagues (2017) expanded the distribution to all 12 marine realms considered by Spalding and colleagues (2007), making this group of parasites cosmopolitan.

According to Caira and Reyda (2005), the life cycle of the marine cestodes lacks free-living stages and the transmission

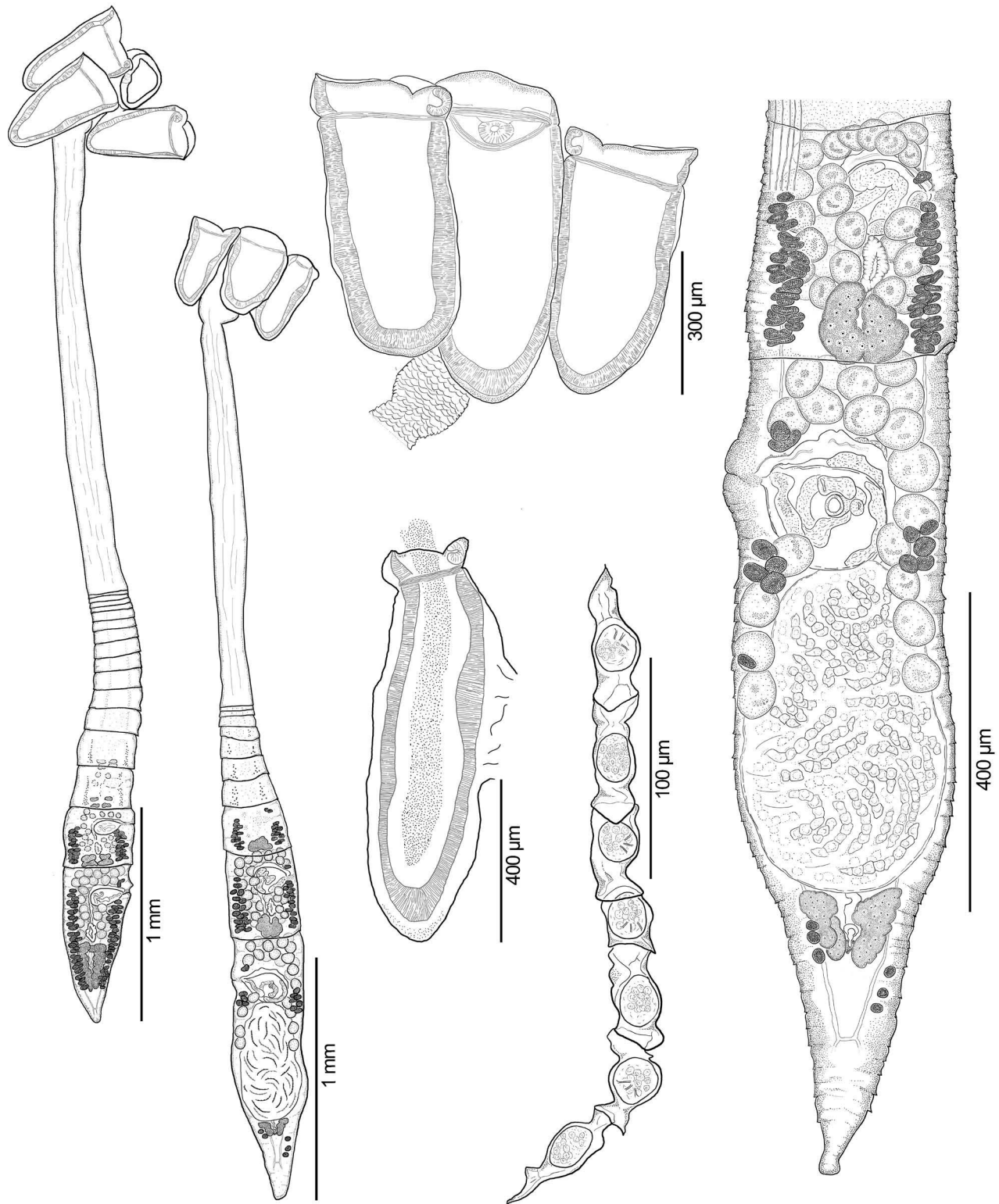


Figure 1. *Guidus francoi* sp. n. from *Bathyraja magellanica* (Philippi), line drawings. A) Entire mature worm (holotype MACN-Pa No. 739); B) entire gravid worm (paratype MACN-Pa No. 746/6); C) scolex (paratype MACN-Pa No. 743); D) bothridium attached to host tissue, muscular bothridial sphincter contracted (paratype MACN-Pa No. 741/1); E) terminal portion of gravid strobila, ventral view (paratype MACN-Pa No. 746/6), longitudinal muscles partially drawn to allow the view of internal organs; F) cocoon. Source: Menoret and Ivanov, 2021. License: CC BY 4.0.

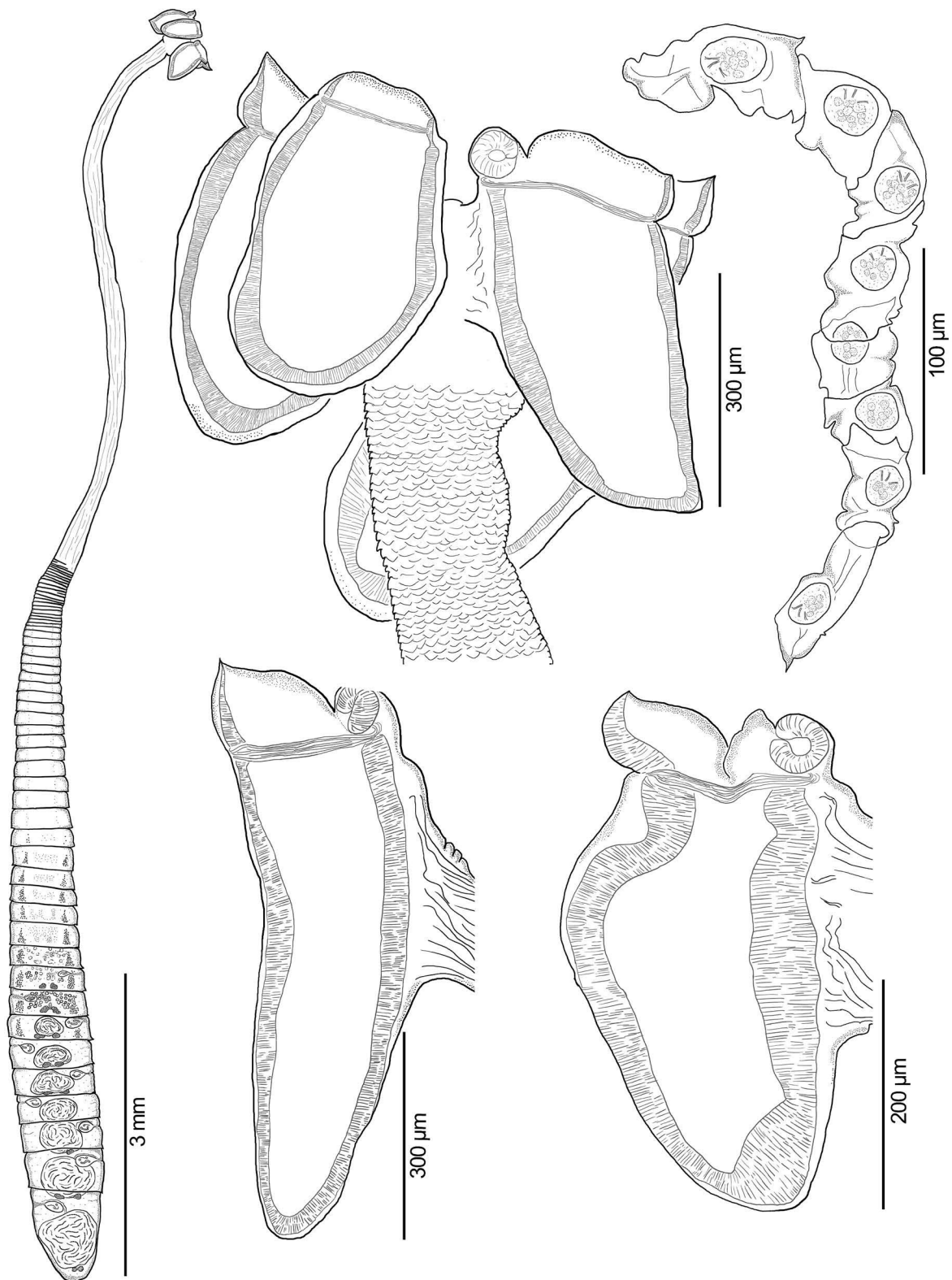


Figure 2. *Guidus magellanicus* from *Bathyraja magellanica* (Philippi), line drawings. A) Entire gravid worm (holotype MACN-Pa No. 747); B) scolex (holotype MACN-Pa No. 747); C) cocoon; D) bothridium, muscular sphincter relaxed (paratype MACN-Pa No. 748/2); E) bothridium, muscular sphincter contracted (paratype IPCAS No. C-888). Source: Menoret and Ivanov, 2021. License: CC BY 4.0.

between hosts depends on the particular food web dynamics. However, it is known that at least 2 or 3 intermediate hosts are involved. The work conducted by Jensen and Bullard (2010) allowed the identification of larval forms that could be assigned to what are now recognized as phyllobothriidean genera; these larvae were found only on teleost fishes that they considered to be acting as intermediate hosts involved in the life cycle of these parasites. Notwithstanding, recent observations have suggested the possibility that pinnipeds and cetaceans also serve as intermediate hosts of some species of this group, particularly in geographical regions where they represent the preferred prey of adult sharks (Klotz et al., 2018). This may help ratify the proposal about the high complexity of the web of intermediate-definitive hosts in the life cycle of these cestodes (Jensen and Bullard, 2010).

Additional Comments on the Taxonomy of the Group

There is no doubt about the position of this group as an order of elasmobranch-hosted cestode. As mentioned before, this group was named after *Phyllobothrium*, the type genus of Phyllobothriidae. Curiously, the taxonomic status of this genus remains problematic: The majority of species (21) are considered incertae sedis, and only 5 species are considered to be valid (including the type species *P. lactuca*) (Ruhnke, 2010; Ruhnke et al., 2017) (see Figures 1 and 2). Further investigation should be conducted on these species to understand their relationships inside the order.

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