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Eucestoda

Relics of “Tetraphyllidea” van Beneden, 1850 (Order)

Berenice Adán-Torres, Omar Lagunas-Calvo,

Brenda Atziri García-García, and Luis García-Prieto

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Chapter 30

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Berenice Adán-Torres
Departamento de Zoología, Instituto de Biología,
Universidad Nacional Autónoma de México,
Mexico City, Mexico
bere.ada@ciencias.unam.mx

Omar Lagunas-Calvo
Departamento de Zoología, Instituto de Biología,
Universidad Nacional Autónoma de México,
Mexico City, Mexico
omarlagunas77@gmail.com

Brenda Atziri García-García
Laboratorio de Vertebrados, Departamento de Biología
Comparada, Facultad de Ciencias, Universidad Nacional
Autónoma de México, Mexico City, Mexico
atziri.garcia@ciencias.unam.mx

Luis García-Prieto
Laboratorio de Helmintología, Instituto de Biología,
Universidad Nacional Autónoma de México,
Mexico City, Mexico
luis.garcia@ib.unam.mx

Introduction

The cestodes referred to the "Tetraphyllidea" (from the Greek **tetra** = 4, and **phyllon** = leaf-shaped) are so allocated because of the morphological characteristics of the scolex (the attachment organs) found in the spiral intestine and occasionally the stomach of species representing all orders of elasmobranch fishes. This group was proposed by van Beneden in 1850 to accommodate the family "Tetraphyllidés." This family included cestode parasites with 4 lobes of the scolex that live in elasmobranchs. Under this name, van Beneden established 3 subgroups: Phyllobothriens (now Phyllobothriidea), phyllacanthiens (now Onchoproteocephalidea), and phyllorhynchiens (now Trypanorhyncha) (Euzet, 1994). Although van Beneden (1850a; 1850b) made the first taxonomic analysis of the group, he never considered it to be an order (Euzet, 1994). Subsequent to van Beneden, Braun (1894–1900) was the first author that considered Tetraphyllidea to be an order consisting of 4 families (Onchobothriidae, Lecanicephalidae, Phyllobothriidae, and Ichthyotaeniidae). Since then, the "Tetraphyllidea" has included cestode species that lack exclusive diagnostic characteristic as the other cestode orders hosted by elasmobranchs (Caira et al., 2017). For this reason, orders such as Onchoproteocephalidea, Trypanorhyncha, Cathetocephalidea, Lecanicephalidea, Litobothriidea, Phyllobothriidea, and Rhinebothriidea have been derived from this group (Braun, 1894–1900; Olson and Caira, 2001; Caira et al., 2005; 2014; Healy et al., 2009). Despite all these changes, "Tretraphyllidea" remains the most problematic order of Cestoda, because it is not a monophyletic group and contains cestodes with morphology that varies remarkably from one another. Consequentially, the remaining taxa of "Tetraphyllidea" require a phylogenetic analysis to establish accurate relationships (Caira and Jensen, 2014; Caira et al., 2014).

Main Morphological Characteristics

"Tetraphyllidea" are polyzoic cestodes. The scolex of all species of "Tetrapyllidea" has 4 sessile or pedunculated bothridia, but present in a great variety of forms. Some species of this order have hooks, loculi, or combinations of these. For example, species of *Pedibothrium* have 1 pair of anterior hooks that are bipronged, while in *Yorkeria*, *Pachybothrium*, and *Spiniloculus* the pair of hooks is unipronged (Caira and Pritchard, 1986; Caira et al., 2007; Desjardins and Caira, 2011). In contrast, species of *Calliobothrium, Symcallio, Erudituncus*, and *Biloculuncus* have 2 pairs of hooks; other species of "Tetraphyllidea" lack hooks. In genera such as *Erudituncus* and *Biloculuncus*, each bothridium is divided into 2 loculi, while in *Calliobothrium* and *Symcallio*, each bothridium is divided into 3 loculi (Nasin et al., 1997; Healy and Caira, 2001; Bernot et al., 2015). Bothridia of *Dioecotaenia cancellata* and *D. campbelli* have 3 columns of facial loculi (Schmidt, 1969; Mayes and Brooks, 1980; Caira et al., 2017). This feature is also present in *Glyptobothrium zwerneri* in which bothridia are divided into 3 longitudinal rows of loculi and separated into 3 parallel longitudinal rows of 10–12 loculi (Pulido-Flores and Monks, 2014). Members of other genera, such as *Ceratobothrium* and *Dinobothrium*, possess an apical pad (Caira et al., 2017); in species of Rhoptrobothriidae, the cephalic peduncle bears 4 stalked extensions, termed remi by Jensen and Caira (2006); this feature is unique to this family.

The morphology of the strobila is very similar to members of Trypanorhyncha and Lecanicephalidea (Schmidt, 1986). Some species are euapolytic (such as *Yorkeria hilli*, *Y. kelleyae*, *Caulopatera pagei*, and *Pedibothrium cabrali*) (Caira and Tracy, 2002; Caira et al., 2004; Cutmore et al., 2010), hyperapolytic (such as *Calliobothrium australis* (Ivanov and Brooks, 2002), or apolytic (such as *Symcallio barbarae*) (Ivanov and Brooks, 2002). The proglottids can be acraspedote (Cutmore et al., 2010; 2018) (specifically, *Yorkeria*, *Caulopatera*, and *Carpobothrium*, according to Caira and Tracy (2002); Koontz and Caira (2016)) or craspedote (specifically, *Calliobothrium* and *Symcallio*; see Ivanov and Brooks, 2002; Bernot et al., 2016). The genital pores are lateral or sublateral (as in *Duplicibothrium*; Williams and Campbell, 1978; Ruhnke et al., 2000) and alternate irregularly. There are numerous testes and the vagina opens anterior to the cirrus sac. The ovary is posterior and bi-lobed or tetra-lobed in cross section. The vitelline follicles are arranged in 2 lateral bands.

Currently, "Tetraphyllidea" includes 6 families and 4 clades, as recognized by Caira et al. (2014) and described by Caira et al. (2017): Balanobothriidae is the family with the most species with 38, distributed in 5 genera, followed by Calliobothriidae (26 species and 4 genera), Clade 4 (9 and 3, respectively), Clade 2 (8 and 1, respectively); Rhoptrobothriidae and Serendipidae (both with 6 species and 3 genera); Clade 3 (with 3 species of *Carpobothrium* and the monotypic *Caulopatera*; Gastrolecithidae with the genera *Cerabothrium* (1 species) and *Dinobothrium* (3 species); Clade 1 (with 3 monotypic genera), and, finally, Dioecotaeniidae with the genus *Dioecotaenia*, constituting 2 species. Up until the latest classifications, "Tetraphyllidea" included 106 species and 27 genera (Caira et al., 2017).

Description and Summary of a Representative Species

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

***Duplicibothrium cairae* Ruhnke et al., 2000**

The worms are slightly craspedote and euapolytic. The scolex of this species has 4 pyriform bothridia. The dorsal and ventral bothridia are paired and fused. The bothridia each have 27–33 loculi arranged in 5 or 7 anterior rows of 3, 1 posterior row of 5, and the last posterior row with 7. The scolex is covered with round microtriches; the cephalic peduncle is covered with dense microtriches.

There are 20 to 35 proglottids per strobila, progressively becoming longer than wider. The last segments have dorsal and ventral pairs of excretory ducts. The mature segments have 28–43 testes distributed in a post-ovarian field. In cross section, there are 4–10 medullary testes in 2 irregular deep rows. The cirrus is armed with spiniform microtriches. The cirrus sac is oval. The genital pore is positioned within 80–96% of the proglottid length, irregularly alternating and sublateral. The vagina is weakly developed in the mature proglottids. The ovary is digitiform in cross section. The uterus is median and poorly developed in the terminal proglottids. There are 8–12 vitelline follicles that are convergent in a dorsal field and are not found at the level of the ovary and cirrus sac (Ruhnke et al., 2000).

Taxonomic summary.

Type host: Pacific cownose ray *Rhinoptera steindacheneri* Evermann and Jenkins, 1891.

Site of infection: Spiral intestine.

Type locality: Puertecitos (28° 85′ 50″ N, 113° 83′ 20″ W), Baja California, Gulf of California, Mexico.

Type specimens are listed here and additional details can be found in the original paper where this species was described: Holotype (CNHE 3846); paratypes (CNHE 3847; USNM (USNPC) 89726, 89727; HWML (15275, 15276).

"Tetraphyllidea" van Beneden, 1850 Taxonomy

To date, *Duplicibothrium* contains 3 species: *D. cairae*, *D. minutum*, and *D. paulum*, all of them parasites of rays of the genus *Rhinoptera* (Caira et al., 2017). *Duplicibothrium* is characterized by the possession of 4 bothridia, the dorsal and ventral fused lengthwise into 2 pairs; the bothridial surfaces are divided into loculi by muscular septa or horizontal and longitudinal septa, showing a digitiform ovary and sublateral genital pore (Williams and Campbell, 1978; Ruhnke et al., 2000). *Duplicibothrium cairae* possesses a pair of longitudinal septa on each bothridium, while in *D. minutum* and *D. paulum* this feature is absent. Each septum is bifurcated in the posterior third of the bothridia, forming 5 or 7 anterior horizontal rows and ending with 1 row of 5 loculi and 1 more-posterior row of 7 loculi. *Duplicibothrium cairae* differs from the other 2 species by the number of segments: *D. paulum* has 3–11 proglottids, *D. cairae* has 20–35 proglottids, and *D. minutum* has 6–14 proglottids. In addition, *D. cairae* can be distinguished from *D. paulum* and *D. minutum* by the number of loculi in the bothridia; *D. paulum* has 57–63 loculi per bothridia, and *D. minutum* has 6–8 loculi per bothridia versus 27–33 per bothridia in *D. cairae* (Williams and Campbell, 1978; Ruhnke et al., 2000).

In the latest phylogenetic analysis of *Duplicibothrium*, the represented species nested with *Glypthobothrium* and *Serendip*, which are included in Serendipidae (Caira et al., 2017). According to this, the phylogenetic position of *Duplicibothrium* is strongly supported by morphological and molecular evidence, due the 3 genera of Serendipidae being characterized by the presence of facial loculi in the bothridia (Ruhnke et al., 2000).

"Tetraphyllidea" does not represent a monophyletic group. All phylogenetic analyses, both with morphological or molecular data that included species of this order, conducted since 1981 by Euzet and colleagues (1981) through Caira and colleagues (2014), indicate that this order is paraphyletic (Olson and Caira, 1999; Caira et al., 1999; 2001; Waeschenbach et al., 2007; 2012). The resolution of this paraphyly is essential to understand cestode evolution and describe the phylogenetic relations of species currently included in "Tetraphyllidea" (Caira et al., 2014). The last analysis with molecular data of "Tetraphyllidea" shows that this group is non-monophyletic since its species were distributed across trees in different clades (Caira et al., 2014; 2017). For this reason, Caira and colleagues (2014; 2017) retained these species as members of "Tetrapyllidea" and suggested that more exhaustive studies should be conducted.

Finally, according to Caira and colleagues (2014; 2017), "Tetraphyllidea" contains 10 independent groups (see above). Interestingly, Clade 1 of this analysis is the sister taxon of Rhinetobothriidea and Clade 3 of Cyclophyllidea.

Life Cycle

The life cycle of tetraphyllidean cestodes is poorly known. Caira and Reyda (2005) and Caira and Jensen (2014) have suggested that species of "Tetraphyllidea" likely parasitize 2 or 3 intermediate hosts and 1 species of elasmobranch as definitive host. The adults of "Tetraphyllidea" have been reported as hosts of all orders (8 of sharks and 4 of batoids) of Elasmobranchii. At the family level, tetrapyllideans are parasites of 23 families (Caira et al., 2017). The larval stages have been recorded in crustaceans, molluscs, and fishes (Jensen and Bullard, 2010). To date, only the life cycle of the tetraphyllidean *Calliobothrium verticillatum* has yet been described; as an adult, it is a parasite of the spiral valve of the smooth dogfish *Mustelus canis* (Cherry et al., 1991). The plerocercoid larvae have been found parasitizing the lumina of the anterior and midgut ceca of the hermit crab *Pagurus pollicaris* (Cherry et al., 1991). This crab is an important component of the dogfish's diet (Montemarano et al., 2016). In general, the life cycle of *C. verticillatum* begins when worms reach maturity in the spiral valve of *M. canis.* These cestodes produce hexacanth embryos that are released from gravid proglottids and are eaten by the hermit crab, where the procercoids and plerocercoids are developed. Finally, the hermit crabs are ingested by sharks that act as definitive hosts (McDermott et al., 2010).

According to Jensen and Bullard (2010), one factor that contributes to the scarcity of information on life cycles is that the larval stages lack the morphological characteristics of adults, which makes taxonomic identification difficult. Although molecular data have been used to match the larval stages with the adult forms, analyses are scarce. For this reason, there are many records of "Tetraphyllidea" larvae without specific identifications (Álvarez et al., 2002; Palm and Klimpel, 2008; Klimpel et al., 2010; Carballo et al., 2011; Montoya-Mendoza et al., 2014; Centeno-Chalé et al., 2015; Constela et al., 2015; Dallarés et al., 2017; Morales-Serna et al., 2017). The most complete analysis using molecular characters for taxonomic identification of larvae was conducted by Jensen and Bullard (2010). In this analysis the authors identified larvae of *Duplicibothrium minutum*, *Anthobothrium* spp., and possibly *Pedibothrium* spp. The larval stages of *D. minutum* were collected from bivalves and gastropods (that is, *Melongena corona* and *Angulus versicolor*); larvae of *Pedibothrium* spp., were found in the fishes *Opsanus beta* and *Lutjanus campechanus*, and the larval stages of *Anthobothrium* spp. were found in fish such as *Ariposis felis, Trichiurus lepturus, Peprilus burti*, and *Diplectrum formosum*. According to Jensen and Bullard (2010), these organisms act as intermediate hosts for this group of cestodes since they are an important component of the diet of sharks. In addition, some species exhibit heteroxenous associations which allows them to parasitize more than 1 species of host (for example, *Calliobothrium verticillatum*), while other species of "Tetraphyllidea" exhibit oxioenus associations with their hosts. For example, some species of the genus *Symcallio* only parasitize sharks of the genus *Mustelus* (Bernot et al., 2015).

Caira and colleagues (2017) pointed out that the geographical distribution of members in this order is determined by the geographical distribution of their hosts, although these cestodes only have been recorded between 60° N and 60° S latitudes, mainly in tropical localities, such as the Gulf of California (specifically, *Duplicibothrium cairae* (Runhke et al., 2000)).

Additional Relevant Details about the Order "Tetraphyllidea" van Beneden, 1850

Species of *Calliobothrium* and *Symcallio* present different site specificity along the spiral intestine (Bernot et al., 2015). Cislo and Caira (1993) analyzed the parasites of *Mustelus canis* and observed that *S. lintoni* and *C. verticillatum* each have a different site of attachment along the spiral intestine. *Symcallio lintoni* was found in the anterior of the spiral intestine whereas *C, verticillatum* was found in the posterior region.

The majority of species of Cestoda are hermaphroditic; however, there are few exceptions, such as species of *Dioecotaenia*. These species are the unique dioecious cestodes of "Tetraphyllidea," and in both species, the strobila has separate sexes (the proglottids only have male genital organs or only female genital organs) (Schmidt, 1969; Mayes and Brooks, 1981). This feature is also present in some Cyclophyllidea as members of Dioecocestidae, parasites of charadriiform birds, and in the progynotaeiid *Gynandrotaenia*, which are parasites of flamingos (Olson and Caira, 1999; Mariaux et al., 2017).

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