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Eucestoda

Litobothriidea Dailey, 1969 (Order)

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Class Cestoda

Subclass Eucestoda

Order Litobothriidea

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Chapter 27

Litobothriidea Dailey, 1969 (Order)

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Introduction

The order Litobothriidea was established by Dailey (1969) to accommodate 2 new species recovered from the bigeye thresher shark *Alopias superciliosus*, from the California coast. This proposal was based on the unique holdfast features; according to Dailey (1969), the scolex consists of an apical sucker with an auxiliary holdfast modification of the anterior segments of the strobila. The name Litobothriidea, derived from the Greek word **lito** (= simple) and **bothros** (= trench), reflects the simplicity of the scolex. Caira and colleagues (1999) pointed out that the region posterior to the apical sucker can be constituted of up to 5 pseudosegments, a subset of which is cruciform in cross section.

Considering the 9 orders of cestodes parasitizing elasmobranchs, Litobothriidea is the second-least speciose group after Cathetocephalidea (constituting 6 species) (Caira et al., 2017b). The 9 species included in the order, all belonging to the genus *Litobothrium*, infect the spiral intestine of Lamniformes sharks from Mexico and Taiwan (Caira et al., 2017a) in the tropical eastern Pacific to the central Indo-Pacific marine ecoregions, according to Spalding and colleagues (2007).

Main Morphological Characteristics

They are medium-sized worms with a body length ranging from 1.65 mm (as in *Litobothrium alopias*) to 32.8 mm (as in *L. aenigmaticum*). The scolex comprises a single and well-developed apical sucker and 3–5 cruciform pseudosegments (but which is dome-shaped in *L. aenigmaticum* with an extensive cephalic peduncle and special tissue composition). Bothridia and a neck are absent. They have dorsoventrally flattened strobila with numerous craspedote proglottids (13–88 in number) that may be laciniated or not. They are apolytic, anapolytic, euapolytic, or extremely hyperapolytic (the latter a feature only of *L. aenigmaticum*). They are hermaphroditic with a single set of reproductive organs by segment, medullary located. The genital pores are lateral and alternate irregularly. The cirrus sac is pyriform, and the cirrus may be armed or not. There are numerous testes (15–84) that are medullary and preovarian, in general, arranged in 2 columns. They extend from the anterior end of the proglottid to the anterior margin of the ovary, rarely overpassing it. The vagina opens into the genital atrium anterior to or at the level of the cirrus sac. The ovary is usually an inverted U-shape and is medial and posterior. The vitellaria are follicular, encircling a medullary parenchyma, with the exception of *L. amsichensis*, in which it is circumcortical. The uterus commonly reaches the posterior margin of the cirrus sac and is armed at the base in *L. amsichensis*. The eggs do not reach the oncosphere stage while in the uterus (Dailey, 1969; 1971; Kurochkin and Slankis, 1973; Caira and Runkle, 1993; Olson and Caira, 2001; Caira et al., 2014a). The structure of the reproductive organs of *L. aenigmaticum* remain unknown because mature and gravid proglottids have not been found in specimens from that group (Caira et al., 2014a).

Description and Summary of a Representative Species

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

Litobothrium amplificum (Kurochkin and Slankis, 1973) Euzet, 1994

These are cestodes with a short body (3.3–6.8 mm). The scolex consists of a cup-shaped apical and muscular sucker

and 4 cruciform pseudosegments. The first pseudosegment has inconspicuous dorsomedial and ventromedial projections; pseudosegments 2 and 3 have well-developed projections, and in the last pseudosegment, the projections are highly modified. The lateral margins are divided into 3 projections: 1 small central, 1 large dorsal, and 1 large ventral, and the last 2 are recurved medially. The first 2 pseudosegments are armed with a single row of spine-like structures that are embedded in its posterior margins.

The first 3 segments of the strobila are highly laciniated, with the laciniations of the first reaching the posterior end of the third segment. The body is covered with filitriches, which are longer in reproductive segments than those in the immature proglottids.

The strobila is euapolytic and consists of 13–19 craspedote segments, 12–19 immature segments that gradually become longer than they are wide and with 0–2 mature segments that are longer than they are wide. There are 53–84 oval to round testes. The cirrus sac is pyriform and extends approximately to the median line of the segment. The cirrus is highly coiled and is armed with spiniform microtriches. The vas deferens is anterior to the cirrus sac and is bifurcated prior to the ovary. The ovary is inverted, U-shaped, posterior, and bi-lobed in cross section.

The genital pore is located at 60–78% of the segment length from the posterior end and alternates irregularly. Mehlis' gland is posterior to the ovary in the segment. The uterus extends from the ovarian isthmus to the posterior margin of the cirrus sac. The vitellarium is follicular and is positioned across the length of the segment, interrupted by the ovary and cirrus sac.

Taxonomic summary.

Host: Pelagic thresher shark *Alopias pelagicus* Nakamura, 1935.

Site of infection: Spiral intestine.

Type locality: Gulf of Tehuantepec, Oaxaca, Mexico.

Additional localities: Bahía de los Ángeles (28° 55′ N, 113° 32′ W) and Santa Rosalía (27° 19′ N, 112° 17′ W), Gulf of California, Mexico.

Type specimens: Unknown.

This species was described by Kurochkin and Slankis (1973) as *Renyxa amplifica* from 2 specimens of *Alopias superciliosus* from the Gulf of Tehuantepec in Oaxaca, Mexico (but according to Olson and Caira (2001), this shark was misidentified and probably belongs to *A. pelagicus*). Subsequently, *Litobothrium amplificum* was redescribed by Olson and Caira (2001) based on 17 worms obtained from *A. pelagicus* from the Gulf of California. This new record extends the geographic distribution of this cestode.

Litobothriidea Dailey, 1969 Taxonomy

Litobothrium amplificum was originally described as a member of *Renyxa* by Kurochkin and Slankis (1973). However, Euzet (1994) considered this genus to be a synonym of *Litobothrium*.

Litobothrium amplificum can be distinguished from 5 of the 8 remaining species included in the genus by having 4 cruciform pseudosegments in the scolex while *L. amsichensis* (see Figure 1), *L. daileyi*, and *L. nickoli* each have 5, and *L. coniformis* and *L. gracile* each have 3 pseudosegments. *Litobothrium alopias* and *L. janovyi* share the same number of pseudosegments with *L. amplificum*; however, the fourth cruciform pseudosegment of *L. amplificum* has recurved laciniations and medial projections that are absent in the other 2 species (Olson and Caira, 2001). *Litobothrium aenigmaticum*, the most recently described species for the genus, differs from all the other species because it has a dome-shaped, grooved scolex, while in the other species, the scolex is constituted of an apical sucker and several cruciform pseudosegments without glandular tissue (Olson and Caira, 2001; Caira et al., 2014a).

The establishment of this order was strongly supported by molecular phylogenetic analyses that included broad sampling of cestodes belonging to several orders (Waeschenbach et al., 2012; Caira et al., 2014b). In both studies, litobothriideans were recovered as the sister taxon of the clade that includes the acetabulate cestode orders and as a monophyletic order. Intraorder relationships show that the clade formed

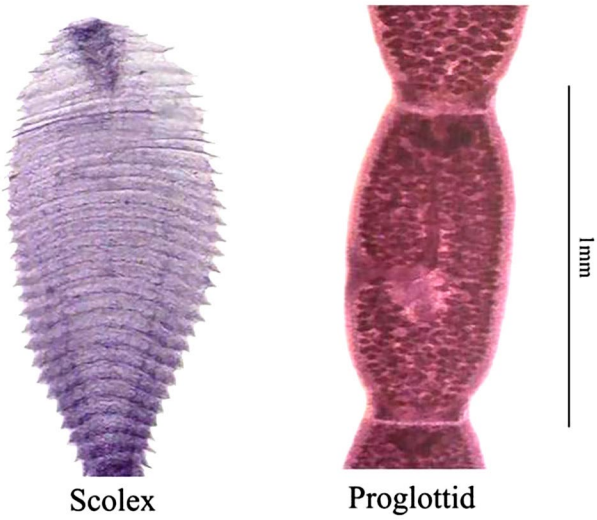

Figure 1. Scolex and proglottids of *Litobothrium amischensis* Caira & Runkle, 1993, holotype specimen from the Queensland Museum, South Brisbane, Queensland, Australia. See https://www.gbif.org/occurrence/1066761304 for more information about this specimen. Source: Queensland Museum, 2023. License: CC BY.

by *Litobothrium aenigmaticum* + *L. amplificum* was robustly supported as the sister taxon of *L. nickoli*. This is interesting because all the members of this clade parasitize pelagic thresher sharks and have *L. janovyi* as a sister taxon, whose host is a different species (the bigeye thresher shark). In this context, future molecular phylogenetic studies could reveal that *L. alopias*, *L. daileyi*, and *L. coniformis* are closely related to *L. janovyi* since they share the same host species. On the other hand, *L. gracile* (hosted by the sand shark) and *L. amsichensis* (a parasite of the goblin shark) could constitute independent groups of the other 7 species.

It is important to mention that the sequences of partial 28S rDNA (D1–D3) obtained from *Litobothrium aenigmaticum* and *L. amplificum* by Caira and colleagues (2014a) were identical; so, inclusion of other molecular markers is necessary for future studies.

Life Cycles

The life cycles of elasmobranch cestodes are practically unknown (Caira and Jensen, 2014); however, authors such as Caira and Reyda (2005) suggested that the life cycle of this group follows a pattern similar to other elasmobranch cestodes. The life cycle can include 2 or 3 intermediate hosts and larvae are trophically transmitted. In some cases, they can infect paratenic hosts (Caira and Jensen, 2014). Particularly, litobothriidean species only have been found parasitizing 4 species of lamniform sharks, among them members of Alopiidae (thresher sharks), Mitsukurinidae (goblin shark), and Odontaspididae (sand tiger sharks) (Caira and Jensen, 2014).

Additional Notes about the Morphology

The litobothriidean scolex consists of an apical sucker followed by a series of pseudosegments, a subset of which are cruciform (Caira and Jensen, 2014). However, these features are not present in most recently described species for the genus, namely, *Litobothrium aenigmaticum*. In contrast, this species exhibits a scolex consisting of a dome-shaped, grooved scolex proper and an extensive cephalic peduncle. In addition, the analysis of histological sections has revealed 4 distinct tissue types not seen in other litobothriideans.

When Caira and colleagues (2014a) described *Litobothrium aenigmaticum*, they pointed out that this species was the only hyperapolytic one so far in the order; nevertheless, these authors suggested that this material could represent a larval stage due to the lack of mature proglottids. The correspondence of microtriche distribution between adults and early juveniles corroborates that type specimens truly represent adult stages and ratify the hyperapolysis in this group for the first time (Caira et al., 2017a).

In spite of the remarkable morphological differences between *Litobothrium aenigmaticum* and the remaining 8 species included in this genus, molecular data robustly place it among the species in this order (Caira et al., 2014a).

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