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Eucestoda

Lecanicephalidea Hyman, 1951 (Order)

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Class Cestoda

Subclass Eucestoda

Order Lecanicephalidea

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Chapter 26

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Introduction

Lecanicephalidea (the name derived from Greek, **lekane** = dish or pot and **kephalē** = head) is an order of cestodes remarkably diverse in its morphology. They are mainly parasites of the spiral intestine of batoid elasmobranchs distributed around the world (Jensen et al., 2016). The main diagnostic trait of this group is the presence of an apical structure on the scolex, called a myzorhynchus or, more recently, termed the apical organ, which is found in a wide variety of forms. Other important characteristics of this group include: The presence of 4 suckers (also termed bothridia), proglottids with the vagina opening posterior from the cirrus sac into the genital atrium (Jensen et al., 2017), and a sizeable vas deferens often expanded into a sacciform external seminal vesicle that extends from the level of the ovarian isthmus to the cirrus sac (Jensen et al., 2016).

They were discovered in the 1890s. The first valid species described for this order was *Polypocephalus radiatus* Braun, 1897; however, the ordinal status of Lecanicephalidea has been questioned (their elevation to this level was even invalidated by Butler (1987)) and its species were often included in the order Tetraphyllidea (Jensen et al., 2017). Currently, based on molecular data analyses, Lecanicephalidea is considered the earliest diverging lineage among the acetabluate cestode orders (Jensen et al., 2017).

According to Jensen and colleagues (2017), Lecanicephalidea contains 8 families with 29 genera and 90 described species, as well as 7 incertae sedis species and 66 species inquirendae. *Polypocephalus* is the genus with the highest number of species (16 species; see Figure 1), while *Adelobothrium*, *Cephalobothrium*, *Collicocephalus*, *Rexapex*, *Anthemobothrium*, *Corrugatocephalum*, and *Quadcuspibothrium* are monotypic.

Main Morphological Characteristics

The strobila of this group of polyzoic cestodes is relatively small since the smallest worm measures less than 500 mm (Jensen, 2005) and only a few species have strobila measuring up to 6 cm, according to Butler (1987). Lecanicephalideans are generally euapolytic, but some species can be anapolytic, apolytic, and hyperapolytic. The proglottids

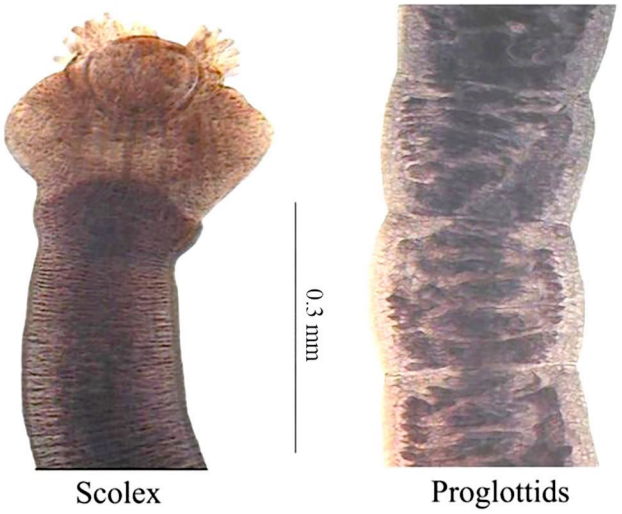

Figure 1. Scolex and proglottids of *Polypocephalus moretonensis* Butler, 1987, holotype specimen from the Queensland Museum, South Brisbane, Queensland, Australia. See https://www.gbif.org/occurrence/1066763010 for more information about this specimen. Source: Queensland Museum, 2023. License: CC BY.

tend to be craspedote (or may rarely be acraspedote) and may be laciniated (fringed in the posterior end) or not (Jensen et al., 2016).

With the exception of *Aberrapex* and *Paraberrapex*, which lack an apical structure in the scolex, the remaining lecanicephalideans are distinguished from most other orders of cestode parasites of elasmobranchs by having this structure (Jensen, 2005). The apical organ can be external or entirely internal; its morphology varies from a foldable sheet to an oval muscular pad or may present as an inverted cone with papilliform projections. In families such as Cephalobothriidae, there can be a glandular sphere. In others, such as Polypocephalidae, the apical organ is divided into tentacles. The tentacles can be retractable (or not) and some are invaginable. The scolex is also characterized by having 4 uniloculate acetabula or bothridia (and are biloculate only in Zanobatocestidae and diamond-shaped only in *Quadcuspibothrium*). Immature proglottids may be laterally expanded or not, and may form a trough (although only in Eniochobothriidae) (Jensen et al., 2016).

Reproductive Structures

Lecanicephalideans are hermaphroditic.

The female reproductive system is markedly heterogeneous; it consists of the following structures. It contains an ovary that is variable in form (it may be H-shaped, bi-lobed, tetra-lobed in cross section, digitiform, irregularly lobed with each lobe divided in 3 sub-lobes, etc.). It includes a vagina, which may be positioned medially, laterally, or sub-laterally (or may even be absent), opening into a genital atrium posterior to the cirrus sac. It includes a follicular vitellarium, generally arranged in 2 lateral bands. The vitellarium may reach the posterior end of the proglottids or only the anterior border of the ovary, and they do not exceed the anterior limit of the testicular field. The vitellarium may be distributed in 3 fields (1 posterior to the ovary, 1 between the genital atrium and the anterior margin of the ovary, and a field consisting of 2 lateral bands before the cirrus sac) or may present in 2 lateral bands from the middle of the cirrus sac to the level of the ovarian isthmus. It includes a uterus that is medial, saccate, or bisaccate (and constricted to the level of the genital atrium), and is variable in extent, from the anterior of the ovary to the genital pore, or almost occupying the entire length of the proglottid (Jensen, 2005; Jensen et al., 2016).

In contrast, the morphology of the male reproductive system is more homogeneous: The number of testes varies from 4 (in *Seusapex karybares*) to more than 40 (in *Tetragonocephalus kazemii*) that are distributed commonly in 1 to 2 columns, located anteriorly to the genital pore, ovary, or cirrus sac (Russell and Jensen, 2014; Jensen et al., 2016; Roohi and Malek, 2017). Internal and external seminal vesicles may be present or absent. The cirrus sac is pyriform (or elliptical in some Polycephalidae). The cirrus is unarmed (although it is armed in Tetragonocephalidae and Eniochobothriidae and rarely in Polycephalidae and Lecanicephalidae). The genital pore is lateral (or sub-lateral in Polycephalidae), alternating irregularly (Jensen, 2005; Jensen et al., 2016).

Description and Summary of a Representative Species

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

***Aberrapex senticosum* Jensen, 2001**

These are small, euapolytic worms, 1.48–6.33 mm-long, with a maximum width of 31–38 mm at the ends of the strobila. The scolex consists of 4 bothridiated acetabula. There is apical modification of the scolex proper and an apical organ is absent. The acetabula and scolex proper are partially covered with large blade-like spiniform microtriches and long filiform microtriches. A cephalic peduncle is absent. The strobila has long filiform microtriches, becoming wider toward the posterior margins of the proglottids. The proglottids are craspedote and laciniate. There are 29–36 immature proglottids with 1 or 2 proglottids containing 20–40 testes arranged in a single field from the anterior margin of the proglottid to the anterior limit of the ovarian isthmus. The external seminal vesicle is wide and saccate, while an internal seminal vesicle is absent. The cirrus sac is pyriform and the cirrus is unarmed. The ovary is H-shaped in the dorsoventral view and tetra-lobed in cross section. It is also lobulated and symmetrical. The vagina runs laterally from the ootype zone to the genital pore; it is open posterior to the cirrus sac into the genital atrium. The genital pore is lateral, pre-equatorial, and alternates irregularly. The uterus is saccate, extending along the midline of the proglottid, almost reaching the anterior margin of the proglottid. A uterine pore is absent. The vitellaria are follicular, medullar, and lateral. The follicles are distributed along the entire length of the proglottid, only interrupted by the ovary (Jensen, 2001).

Taxonomic summary.

Type host: Bat eagle ray *Myliobatis californica* Gill, 1865 (Rajiformes, Myliobatidae).

Type locality: Santa Rosalía (27° 81′ 99″ N, 112° 81′ 79″ W), Baja California, Mexico.

Site of infection: Spiral intestine.

Type specimens are listed here and additional details can be found in the original paper where this species was described: Holotype (CNHE 4188) and 2 paratypes (CNHE 4189); 3 paratypes (USNPC 91208); 2 paratypes (HWML 16374); 7 paratypes (LRP 2152–2158).

Lecanicephalidea Hyman, 1951 Taxonomy

In addition to *Aberrapex senticosum*, 6 more species of the genus parasitizing myliobatiform batoids from tropical and temperate waters have been described to date: *A. arrhynchum* (Brooks, Mayes, and Thorson, 1981) Jensen, 2001; *A. ludmilae* Menoret, Mutti & Ivanov, 2017; *A. manjajiae* Jensen, 2006; *A. sanmartini* Menoret, Mutti & Ivanov, 2017; *A. vitalemuttiorum* Menoret, Mutti & Ivanov, 2017; and *A. weipaensis* Koch, Jensen & Caira, 2012 (Menoret et al., 2017). *Aberrapex senticosus* can be distinguished from the other species included in the genus since it has the highest number of testes (20–40 versus 18–25, 24–31, 10–19, 11–16, 15–21, and 10–17, respectively). In addition, *A. ludmilae* and *A. arrhynchum* lack an external seminal vesicle (while it is present in *A. senticosum*). In the remaining species, hastate spinitriches are entirely absent in the acetabular surface (*A. weipaensis*), restricted to the central region of the acetabula (*A. manjiajae*) or cover only two-thirds of the distal acetabular surface (*A. sanmartini* and *A. vitalemuttiorum*) while in *A. senticosus* hastate spinitriches cover the entire distal acetabular surface (Jensen, 2001; 2006; Koch et al., 2012; Menoret et al., 2017).

The first phylogenetic studies on lecanicephalids were based on morphological data (Caira et al., 1999; 2001; Jensen, 2005). In such studies, this group of cestodes was generally nested as a clade by the presence of an apical structure in the adult stage. When authors such as Jensen (2005) included some species lacking apical structure, they were positioned as the first divergent lineages of the order. Relative to its relationship with other orders of cestodes, Caira and colleagues (1999; 2001) detected possible affinities with cyclophyllideans.

Almost simultaneously, several works based on molecular evidence established Lecanicephalidea as the earliest lineage among the acetabulate cestode orders (Olson and Caira 1999; Olson et al., 2001; Caira et al., 2005; Waeschenbach et al., 2007).

The most recent and comprehensive analyses on the relationship among lecanicephalidean cestodes was conducted by Jensen and colleagues (2016); these authors confirmed the monophyletic nature of the order and recognized 8 major groups as independent families: 4 previously existing (Lecanicephalidae, Polypocephalidae, Tetragonocephalidae, and Cephalobothriidae) and 4 new families (Aberrapecidae, Eniochobothriidae, Paraberrapecidae, and Zanobatocestidae).

Life Cycles

Life cycles of cestodes of the order Lecanicephalidea are poorly known; however, according to Caira and Reyda (2005) larvae of these cestodes have been registered in some groups of invertebrates, mainly bivalves (molluscs) and crustaceans, as well as in few actinopterygians. Based on the scarce available information on the developmental stages of lecanicephalideans, Caira and Reyda (2005) suggested that they lack a coracidium (that is, a hexacanth embryo is inside the egg); plerocerci have been found in bivalves and gastropod molluscs and plerocercus, their terminal larval stage, in actinopterygians such as *Scomberoides commersonnianus* from the Arabian Gulf (Bannai et al., 2014).

Lecanicephalideans have circumglobal distribution; currently, members of this cestode order have been described from 8 of the 12 marine biogeographic realms, with the greatest concentration of species (69%) recorded in the central Indo-Pacific (Jensen et al., 2017).

Additional Notes about the Morphology

As noted above, Lecanicephalidea is an order of cestodes remarkably diverse in its morphology. For example, many lecanicephalideans possess additional features of proglottid anatomy that are unusual for other cestodes hosted by elasmobranchs (Jensen et al., 2017). For example, the genus *Hexacanalis* was erected by Perrenoud (1931) based on the presence of 6 excretory vessels, while the most common condition in the cestodes is the presence of 2 dorsal and 2 ventral excretory vessels. Jensen and colleagues (2016) pointed out that the different number of pairs of excretory vessels (1, 3, or more) is so particular, that it can be considered a diagnostic trait of the family Lecanicephalidae. In the same way, 1 species included in this genus (*Hexacanalis folifer*) is unique among lecanicephalideans by having a U-shaped ovary in cross section and proglottids with prominent posterior dorsoventral processes in the form of large lappets (Cielocha and Jensen, 2011).

On the other hand, despite the scarce knowledge about the gravid proglottids of the members of this order, it has been determined that the morphology of the eggs shows drastic variations, even among the congeneric species: In *Anteropora comica*, the eggs are covered with numerous small, regularly-spaced surface protuberances without polar filaments, while in *A. klosmamorphis*, the eggs have a corrugated surface and bipolar filaments (Jensen et al., 2011). Something similar occurs with the cocoons, since in some species (for example, *Zanobatocestus major*), cocoons contain only 2 eggs while in others (such as *Z. minor*), these are arranged in cocoons with hundreds of eggs (Jensen et al., 2014).

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