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Bothriocephalidea Kuchta et al., 2008 (Order)

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Phylum Platyhelminthes

   Class Cestoda

    Subclass Eucestoda

      Order Bothriocephalidea

Chapter 21

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Introduction

Members of Bothriocephalidea are included among the bothriate groups of cestodes in which the attachment organs are not separated from the surrounding tissue by a well-demarcated plasma membrane (Kuchta et al., 2008a). The name of this order is derived from the Greek terms **bothrion** (small pit) and **kephalē** (head), which refer to the presence of dorsal and ventral longitudinal grooves, named bothria, along the scolex. What characterizes these organisms is that the strobila are generally segmented completely, and are craspedote and anapolytic; also, the adult worms often are intestinal parasites of Actinopterygii (ray-finned fishes, mainly from marine environments), although they are occasionally found in amphibians, particularly newts (Kuchta et al., 2008a). The species richness of this order is moderate, but the group has a worldwide distribution, with the majority of species described from the Atlantic Ocean (Kuchta et al., 2008a).

Based on morphological and molecular evidence, Bothriocephalidea arises from the suppression of the former order Pseudophyllidea. It was separated from Diphyllobothriidea based on several traits, mainly: 1) The position of the genital pore located dorsally, dorsolaterally, or laterally in the proglottid, posterior to the ventral uterine pore in Bothriocephalidea, versus the ventral position of the genital pore, anterior to the uterine pore in Diphyllobothriidea; 2) the presence of an external seminal vesicle in Diphyllobothriidea, but which is absent in the Bothriocephalidea; 3) the lack of a uterine sac in Diphyllobothriidea, but which is present in Bothriocephalidea; and 4) due to members of both orders parasitizing different groups of hosts. Bothriocephalidea is found mainly in actinopterygians and is never found in homoeothermic vertebrates, while Diphyllobothriidea infects tetrapods, commonly mammals (Kuchta et al., 2008a; Kuchta and Scholz, 2017).

Species of 48 genera included in this order belong to 3 families: Bothriocephalidae (16 genera), Echinophallidae (8 genera), and Triaenophoridae (24 genera). In addition, 1 species (*Dactylobothrium choprai*) is considered to be a species of doubtful indentity also known in Latin as species inquirenda. As of 2017, 132 species of bothriocephalidean cestodes were described (Kuchta and Scholz, 2017) (see, for example, images of *Clestobothrium cristinae* in Figure 1).

Main Morphological Characteristics

Species included in this order of bothriate cestodes are all characterized by having a scolex that is composed of 2 elongated bothria (dorsal and ventral longitudinal grooves) as the attachment organs on the anterior end of the animal.

The shape of the scolex is quite variable among the genera; they can have an apical disc and either have hooks or the hooks may be absent. Hooks, when present, vary in size, shape, and number. In some bothriocephalideans the scolex might be what is called a pseudoscolex or it might be highly modified, sometimes called a deformed scolex, which is sometimes referred to as scolex deformatus. Scanning electron micrographs of the scolexes of species representing several genera have revealed the presence of microtriches and lumpy globular surface structures. A neck may be present or absent.

The strobila of species of cestodes included in this order ranges from small to large. Segmentation may be complete, incomplete, or completely absent in species of some genera while in all species in the order, the proglottids are craspedote, rectangular, and anapolytic. The osmoregulatory canals are paired, with the ventral canals usually being wider than the dorsal pair. Most of the bothriocephalideans have 1 set of reproductive organs per segment, but some may have 2 symmetrical sets. The testes are numerous and usually found in the middle of the segment and, in general, they are distributed in 2 lateral fields (in the middle of the segments). The genital pores are located on the dorsal surface of the proglottids (or segments) and from anterior to posterior, the genital pores can be located submarginally, marginally, or medially, alternating irregularly. A cirrus sac is present, either with or without an internal seminal vesicle. There are coiled sperm ducts and there is no external seminal vesicle. The cirrus is smooth with tegumental bumps (folds) or with spinitriches. The ovary is located in the middle of the segment, posterior and is commonly bi-lobed and may be either compact,
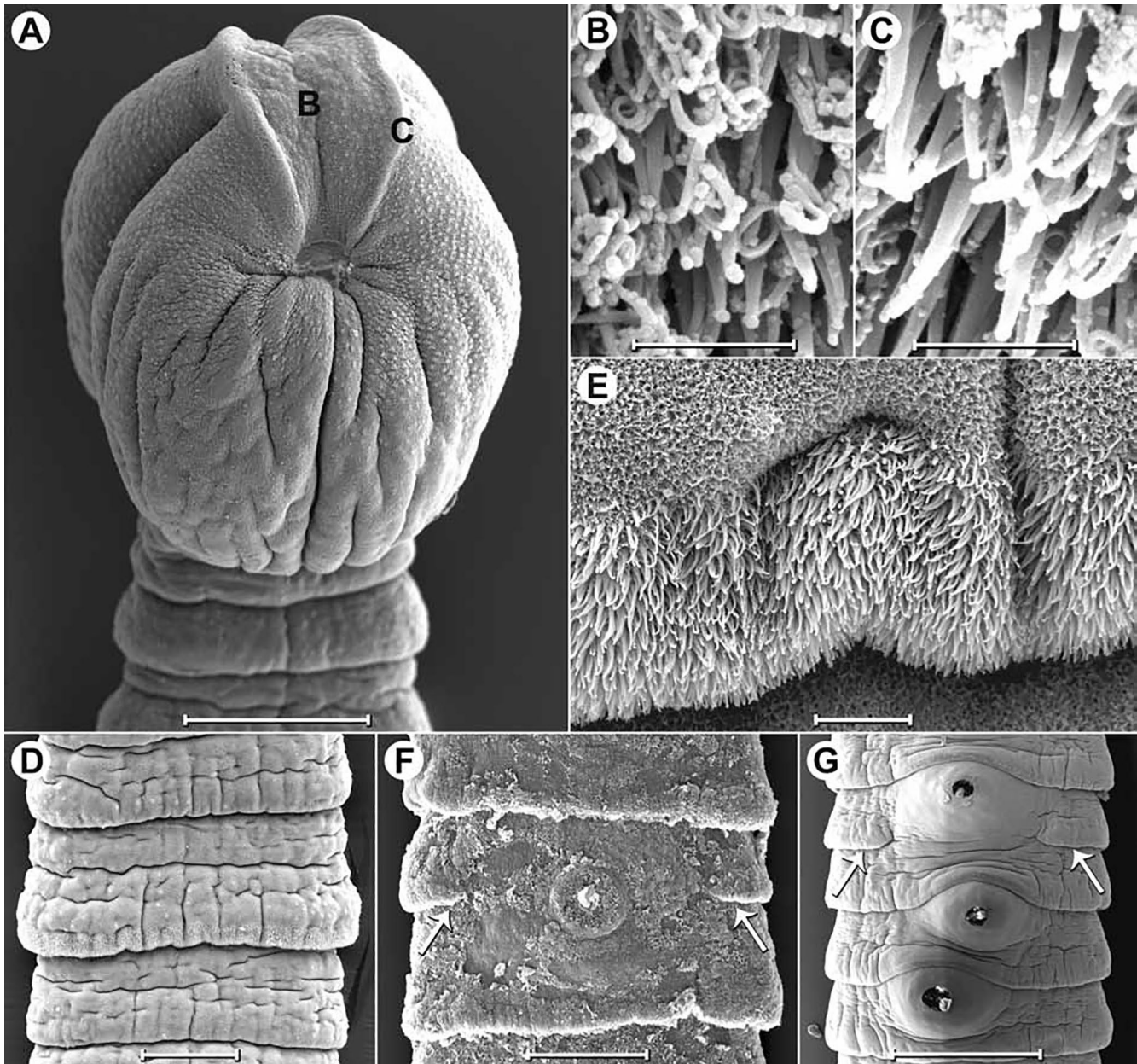
Figure 1. *Clestobothrium cristinae* from *Merluccius hubbsi*, scanning electron micrographs. A) Dorsoventral view of scolex showing tumuli; the surfaces of B and C are shown at high magnification; B) Central surface between lips; C) Marginal surface of lips; D) Piece of immature strobila; E) Surface of middle and posterior part of immature proglottis; F) Piece of mature strobila showing position of genital pore relative to spurious articulation (white arrows), dorsal view; G) Piece of gravid strobila showing uterine pore, eggs, and spurious articulation (white arrows); ventral view. Scale bars: A = 200 µm; B, C = 2 µm; D = 100 µm; E = 10 µm; F, G = 500 µm. Source: Gilde Pertierra et al., 2011. License: CC BY 4.0.

follicular, or dendritic. The vagina may be armed or not, with or without a muscular sphincter and the terminal end of the vaginal canal opening may be posterior, anterior, at the same level, or alternating in relation to the cirrus sac. The vitellarium is follicular and extensive, and there is rarely just a single one. The vitellarium may be cortical, medullary and cortical, or exclusively medullary in cross section. The uterus may be compact or lobed; the uterine duct may be coiled or elongated and the uterine sac may be compact or branched; and a uterine pore may be present or absent, and is ventral, if present. The eggs, whether operculated or not, may contain an intrauterine embryo; in non-embryonated eggs, there may be a free ciliated coracidium (Kuchta et al., 2008b; Kuchta and Scholz, 2017).

Description and Summary of a Representative Species

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

Schyzocotyle acheilognathi **(Yamaguti, 1934) Brabec et al., 2015**

According to Scholz (1997a), this cestode is unusual in its extreme morphological variability. Following is a brief characterization of this species based on the morphological information compiled by Scholz based on material collected from Europe, Asia, and Africa. The scolex is generally heart-shaped with short, deep bothridia, directed anterolaterally, with non-creanulate margins. The terminal disc is weakly developed and unarmed. A neck is absent; the first proglottids are immediately posterior to and narrower than the scolex. The strobila is acraspedote (meaning that the segments connect without a velum or without overlapping parts) and are relatively short (22–32 mm-long) but can reach up to 1,000 mm (= 1 m); both mature and gravid proglottids are elongated (length/width ratios 1:7–8 and 1:3–4.5, respectively). There are 33–100 testes distributed in 2 lateral fields that are located in the middle of the segment (medullary) and are spherical to oval. The cirrus sac is spherical and is situated anterior to the ovary. The cirrus is unarmed. The genital pore is median, opening into a common genital atrium while the ovary is median, and transversally bi-lobed, near the posterior margin of the proglottids. The vagina is tubular, opening posterior to the cirrus sac into the genital atrium. The vitelline follicles are circumcortical. The uterus is spherical, near the anterior part of the proglottids. The uterine pore is median andhe eggs are operculate and unembryonated within the proglottid (Scholz, 1997b; Brabec et al., 2016).

Taxonomic summary.

Type host: Kanehira, *Acheilognathus rhombea* (Cyprinidae).

Site of infection: Intestine.

Type locality: Lake Ogura (37° 24′ 01″ N, 139° 57′ 51″ W), Honshu, Japan; however, Choudhury and Cole (2012) considered the Amur River (eastern Asia) as the original distribution area of this cestode species, and other authors, such as Scholz et al. (2012), suggest that the parasite's origin is Africa.

Type specimens deposited: Unknown.

Schyzocotyle **Genera**

The genus *Schyzocotyle* currently comprises 2 species, including: *S. acheilognathi* and *S. nayarensis*, both characterized by the possession of a heart-shaped scolex (Brabec et al., 2015). However, the inadequate original description of *S.*

nayarensis (Brabec et al., 2016) as well as the extreme morphological variability of *S. acheilognathi* (Scholz, 1997b), makes it difficult to identify. Traits of *S. nayarenis* such as body size (12–27 mm), number of testes (52–78), or egg diameter (10–46 μm) (Malhorta, 1983) are included in the characteristics provided by Scholz (1997b) for *S. acheilognathi* obtained in fish collected from several sites in Europe, Asia, Africa, and the Americas. Interestingly, specimens that are designated as holo- or paratypes are not known to exist in any collections (Brabec et al., 2016), which limits the knowledge of this species. The study of phylogenetic relationships among the members of this group of cestodes has been addressed on several occasions. Bray and colleagues (1999) conducted a preliminary morphological cladistic analysis based on 16 species representing the type-genera, and they considered it reasonable to divide the Pseudophyllidea into 2 suborders: Bothriocephaloidea and Diphyllobothrioidea. Similar conclusions were reached by Mariaux (1998) when studying the molecular phylogeny of the Eucestoda in general, noting that the species included in the Pseudophyllidea at the time were clearly paraphyletic. The suppression of the order Pseudophyllidea with its formal separation into 2 orders (Bothriocephaliidea and Diphyllobothriidea) was inferred by Kuchta and colleagues (2008a) based on molecular evidence. As a result of this study, Kuchta and colleagues (2008a) considered that Bothriocephalidea may be a sister-group to the tetrafossate cestodes, which are generally considered to have derived characters. Brabec and colleagues (2015) confirmed the monophyly of Bothriocephalidae, a family constituted of a single clade of freshwater worms and several marine clades.

Life Cycles

The life cycle of species from the order Bothriocephalidea includes 1, or occasionally 2, intermediate hosts with procercoids in copepods and plerocercoids in fishes that eat the infected copepods. The adult stage is mainly found in the intestine of fishes and a few are found in newts (Kuchta et al., 2008b). For example, the life cycle of *Bothriocephalus claviceps*, a specific parasite of eels (*Anguilla* spp.), was studied by Scholz (1997a) under experimental conditions where he found that the development of the worm takes 4 months to complete (at 22–24 °C). The spontaneous hatching of ciliated, motile coracidia from the eggs occurs in 2 days in experimental conditions.

The zooplanktonic coracidia are ingested by copepods of species in the genera *Macrocyclops*, *Cyclops*, or *Acanthocyclops*. In these crustaceans procercoids develop after 8–12 days at 22–24 °C and the fish definitive hosts become infected through ingestion of infected copepods. Egg production in the fish then begins around 3 months post infection. Some

small fishes, such as *Perca fluviatilis* and *Poecilia reticulata*, can act as paratenic hosts of *B. claviceps*. In *P. reticulata*, the plerocercoid survives up to 14 days after exposure and they develop into adults in the definitive host after the paratenic host is consumed.

Host Range

Host range of bothriocephalideans is usually narrow; however, *Schyzocotyle acheilognathi* is a parasite with a very wide host range and is among the most generalist species of all helminths worldwide. Members of the order Bothriocephalidea are commonly found in perciform fishes, particularly Centrolophidae. Most of the species (65%) parasitize marine fishes, while 32% are found in freshwater fishes. Three species, including: *Eubothrium acipenserium*, *E. crassum*, and *E. salvelini*, may live in both types of environments (see Kuchta et al., 2018).

Zoogeography

The geographic distribution of bothriocephalideans is heterogeneous. Data on the marine species of this order probably do not totally agree with their actual distribution because the sampling effort by scientists looking for species in this group has been relatively low in the marine environment. About 38% of the known species richness has been reported from hosts from the Atlantic Ocean and 29% from the Pacific Ocean, while around 17% of the species were reported from the Indian Ocean. In addition, some species are only found in deep sea teleost fishes. In contrast, freshwater bothriocephalidean species are distributed mainly in Eurasia (27 species) and North America (18 species). On other continents, the representation of this group of cestode is very low, being especially scarce in fishes from South America (Kuchta et al., 2017).

Schizocotyle acheilognathi (Asian Fish Tapeworm)
Prevalence

Schizocotyle acheilognathi, also known as the Asian fish tapeworm (AFT), was described as *Bothriocephalus acheilognathi* (Yamaguti, 1934) from the cyprinid fish *Acheilognathus rhombeus* from Lake Ogura, Japan. Since then, *S. acheilognathi* has become the most successful globally invasive parasite of freshwater fish, infecting a broad spectrum of hosts. According to Kuchta and colleagues (2018), until now the number of fish hosts parasitized by this tapeworm is 312 (belonging to 38 fish families and 14 orders), as well as 11 non-fish vertebrate host species including the amphibians *Ambystoma dumerilii* and *Lithobates megapoda*, and the snake *Thamnophis melanogaster* in Mexico (see Pérez-Ponce

de León et al., 2018). This cestode has been found in 74% of Cyprinidae fishes examined (170 species), mainly in the common carp *Cyprinus carpio*. *Schizocotyle acheilognathi* is distributed throughout the world, except in Antarctica, but the highest concentrations are found in North America, Asia, and Europe (Kuchta et al., 2018).

Since the first discovery of AFT in Mexico, parasitizing the grass carp *Ctenopharyngodon idella* (López-Jiménez, 1981), the number of fish species known to be infected by this worm has increased to 110, which represents 22% of the freshwater fish fauna in Mexico; therefore, Mexico probably has the greatest prevalence of this parasite in the world (Pérez-Ponce de León et al., 2018).

The success of *Schizocotyle acheilognathi* as an invasive species was discussed by Kuchta and colleagues (2018), highlighting 3 factors: 1) Synanthropic association (probably this cestode was initially introduced anthropogenically via aquaculture practices and has continued through the natural dispersal of its hosts); 2) efficient resource use and wide environmental/physiological tolerance (note that *S. acheilognathi* is able to exploit important resources, and is capable of invading numerous species of copepods (first intermediate host) and almost any species of fish (final host) through a wide range of water temperatures); 3) life history strategy, reproductive style, capacity, and timing. In the vocabulary of population biology, the AFT is evidently an r-strategist with a reproductive potential that is adapted to produce a huge number of eggs dispersed by water currents before they hatch; hatched larvae are also dispersed by water currents. Kutcha and colleagues (2018) also point out that the existence of a niche available in the most common host groups for *S. acheilognathi* (for example, Ciprododontoides), due to the lack of their own typical cestode adult fauna, perhaps allowed the invasion of this cestode. However, they do not exclude the possibility of primary adaptation to the physiological conditions of the intestine of these fish.

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