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Eucestoda

Trypanorhyncha Diesing, 1863 (Order)

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Phylum Platyhelminthes

Class Cestoda

Subclass Eucestoda

Order Trypanorhyncha

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Chapter 23

Trypanorhyncha Diesing, 1863 (Order)

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Introduction

The members of the order Trypanorhyncha are within the subclass Eucestoda. Trypanorhynchs are common cestode parasites of marine fish, but this group is also among the most enigmatic groups of cestodes. The order Trypanorhyncha was established by Diesing in 1863, and it was then considered to be a putative chaotic order within the phylum Plathyhelminthes. However, taxonomically this order is only a complex group, like many other orders of cestodes.

To date, the species of the order Trypanorhyncha are grouped into 4 superfamilies that currently include 315 species within 81 genera (Beveridge et al., 2017). The adults of these species are typically found infecting the stomach and the spiral intestine of elasmobranchs (sharks and rays) as their definitive hosts. Larval trypanorhynchs infect a wide variety of marine invertebrates and teleost fish (Palm, 2004; 2010; Palm et al., 2009). There are larval trypanorhynchs that have been used for descriptions of species but the morphology of the adults of those species is unknown. In contrast, larvae of other orders of cestodes (for example, Tetraphyllidea) typically have not been identified to the specific level based on morphological criteria because is not possible to do so with the few apparent structures (Jensen and Bullard, 2010).

Morphology of Trypanorhyncha Larva

As described above, trypanorhynchs go through larval developmental stages, including plerocercus, plerocercoid, and merocercoid (Sakanari and Moser, 1989; Palm and Caira, 2008; Palm et al., 2009). These stages all look very different from one another, which makes it difficult to trace out the patterns of life cycles. The morphology of each stage is described briefly below (Table 1).

Morphology of Trypanorhyncha Adults

The body of adult trypanorhynchs consists of 2 main regions, the **scolex** and the **strobila**.

Scolex

Members of the subclass Eucestoda exhibit an amazing variety of forms of the scolex. The scolex is the anterior part of the adult cestode, often highly specialized for adhesion to the host's intestine. The scolex of trypanorhynchs (Figure 1A) is divided into 3 regions: 1) **Pars bothrialis**, anterior end to the hind margin of the bothridia; 2) **Pars vaginalis**, anterior end to the posterior end of the tentacular bulbs; and 3) **Pars bulbosa**, extends the length of the bulbs at the tentacle base.

Trypanorhynchs have 2 or 4 bothridia and the tentacular apparatus consists of 4 retractile tentacles. Each tentacle has hooks and each is attached to a retractor muscle that is within a muscular bulb (Figure 1A and 1B) (Jones et al., 2004; Palm et al., 2009; Jones, 2000; Beveridge et al., 2017).

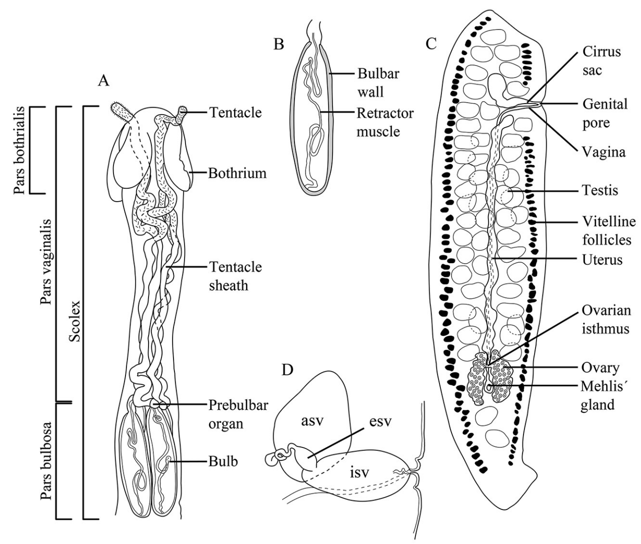

Figure 1. General morphology of a trypanorhynch: A) Scolex; B) Bulb; C) Mature proglottid; D) Terminal genitalia. Abbreviations: asv = accessory seminal vesicle; esv = external seminal vesicle; isv = internal seminal vesicle. Source: Modified from Beveridge and Justine, 2006. License: CC BY-NC-SA 4.0.

Table 1. Types of hooks and patterns of distribution in tentacles of trypanorhynchs.

Armature pattern of the tentacle	Description
Typical	Tentacle without intercalary hooks (Figure 3A).
Atypical	Tentacle with intercalary hooks (Figure 3B).
Convergent	Tentacle in which there are no distinct spaces at the beginning of the rows of principal hooks.
Divergent	Tentacle with distinct space between the beginnings of the rows of principal hooks.
Heteroacanthous	Tentacle with hooks arranged in half spiral rows around the tentacle (Figures 3A–C).
Homeoacanthous	Tentacle with hooks arranged in complete spirals surrounding the tentacle (Figure 3E).
Heteromorphous	Tentacle with hooks of different shape.
Homeomorphous	Tentacle with hooks of similar shape.
Intercalary hook	Tentacle with interpolated microhooks between rows of principal hooks.
Principal hook	Tentacle with enlarged hooks arranged in half spiral rows around the tentacle.
Poeciloacanthous	One tentacle surface bears characteristic hooks arranged in 1–3 longitudinal files along the tentacle, forming a chain of hooks that differs in form and/or size from principal and intercalary hooks (Figure 3D).

Ultrastructures of the tegument of the scolex

Cestodes entirely lack a digestive system and instead absorb nutrients through the tegument. On the tegument of the scolex are **microtriches**, which may help in the absorption of nutrients (Chervy, 2009). Scanning electron microscopy (SEM) reveals different kinds of microtriches across the entire surface of the tegument of the different groups of cestodes (Chervy, 2009; Faliex et al., 2000; Caira et al., 1999). There are different forms of microtriches in the different groups of trypanorhynchs, such as capilliform, papilliform, palmate, filiform, and others (Figure 2) (Whittaker, 1985; Palm, 2008; Caira et al., 2010; Menoret and Ivanov, 2015; Haseli et al., 2016).

Scolex armature

The retractile tentacles have hooks (armature) that are highly variable. The type (size, curvature, etc.) of hooks and the armature pattern is used in the classification of the groups. The armature patterns are classified as described by Palm et al. (2009) (Table 1 and Figure 3).

Strobila

Strobila refers to the set of proglottids located posteriad to the border of the posterior margin of the scolex. The reproductive organs are located in the proglottids or segments. There are various types of proglottids in the strobila of a cestode: 1) Immature proglottids in the anterior part of the strobila; the anlagen (the beginning primordia of the genitalia) are found here; these lack distinct internal structures; these lack distinct internal structures; 2) mature proglottids, in which at least 1 reproductive system is functional (male, female, or both) (Figure 1C); and 3) gravid proglottids, in which fertilization has occurred and the uterus is filled with eggs.

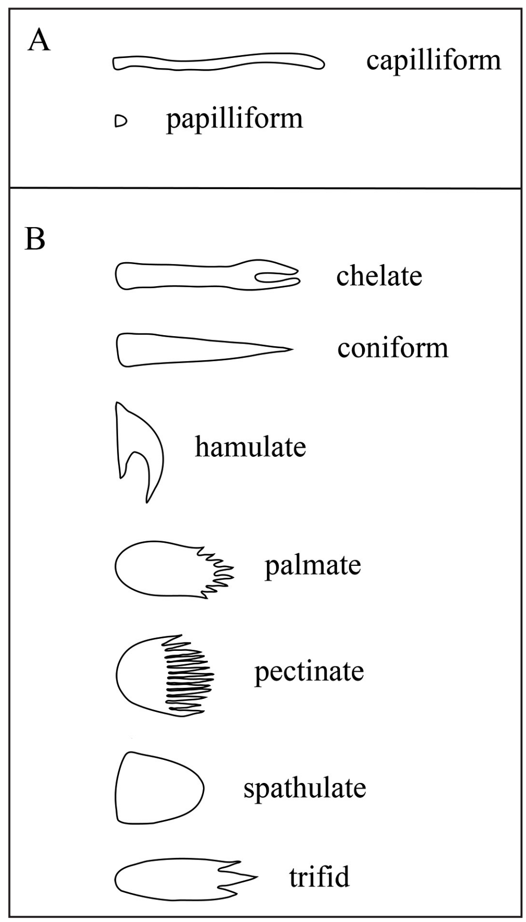

Figure 2. Schematic representation of some ultrastructural features of the scolex reported for trypanorhynchs. **Microtriches** with basal widths ≤ 200 nm are considered to be **filitriches** (A); in contrast, microtriches with basal widths > 200 nm are considered to be **spinitriches** (B). Source: Modified from Chervy, 2009. License: CC BY-NC-SA 4.0.

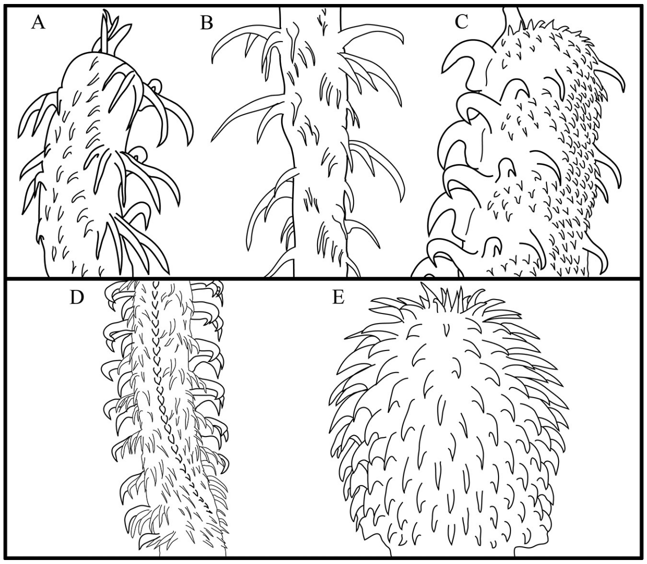

Figure 3. Armature patterns of tentacles of some trypanorhynchs. A) Typical heteroacanthous tentacular armature; B) Atypical heteroacanthous tentacular armature; C) Multiatypical heteroacanthous tentacular armature; D) Poeciloacanthous tentacular armature; E) Homeocanthous tentacular armature. Source: Modified from Beveridge et al., 2017. License: CC BY-NC-SA 4.0.

In all members of the subclass Eucestoda, apolysis refers to the loss of the most-posterior proglottids from the strobila. The terms used to describe the apolysis of the proglottids are as follows. **Hyperapolytic** refers to a strobila that never possesses proglottids that are either mature or gravid. **Euapolytic** refers to a mature terminal proglottid without gravid proglottids. **Apolytic** refers to a strobila that has some gravid proglottids. **Anapolytic** refers to a strobila containing gravid proglottids along with older, degenerated proglottids (Caira et al., 1999; Franzese and Ivanov, 2018).

The anatomy of the proglottid of Trypanorhyncha is similar to other orders of cestodes (for example, Rhinebothriidea, Tetraphyllidea, and Onchoproteocephalidea). The trypanorhynchs are hermaphroditic and the proglottids include both male and female reproductive organs (Figure 1C). There are numerous testes. The ovary is composed of 4 lobes and it is positioned in the posterior part of the proglottid. The vitellarium is follicular with vitelline follicles and, in some species, the vitelline follicles form lateral bands. The genital pores usually alternate irregularly and are located in the lateral part of the proglottid. The uterus is saccate in gravid proglottids. The vagina opens posteriorly to the cirrus sac and it is positioned ventrally (Figure 1C). In addition, the Trypanorhyncha as a whole exhibit remarkable variation in the arrangement of their terminal genitalia, which may include accessory, internal, and external seminal vesicles, and a hermaphroditic duct or vesicle (Palm et al., 2009; Beveridge et al., 2017) (Figure 1D).

Table 2. Genera within the superfamily Eutetrarhynchoidea.

Genera	Number of species
Cetorhinicola Beveridge and Campbell, 1988	1
Didymorhynchus Beveridge and Campbell, 1988	1
Dollfusiella Campbell and Beveridge, 1994	30
Eutetrarhynchus Pintner, 1913	4
Fellicocestus Campbell and Beveridge, 2006	1
Halysiorhynchus Pintner, 1913	1
Hemionchos Campbell and Beveridge, 2006	3
Hispidorhynchus Schaeffner and Beveridge, 2012	3
Mecistobothrium Heinz and Dailey, 1974	6
Mixodigma Dailey and Vogelbein, 1982	1
Mobulocestus Campbell and Beveridge, 2006	3
Nataliella Palm, 2010	1
Oncomegas Dollfus, 1929	4
Parachristianella Dollfus, 1946	10
Paroncomegas Campbell, Marques and Ivanov, 1999	3
Poecilorhynchus Schaeffner and Beveridge, 2013	1
Prochristianella Dollfus, 1946	21
Progrillotia Dollfus, 1946	3
Pseudochristianella Campbell and Beveridge, 1990	3
Rhinoptericola Carvajal and Campbell, 1975	1
Shirleyrhynchus Beveridge and Campbell, 1988	3
Tetrarhynchobothrium Diesing, 1854	5
Trigonolobium Dollfus, 1929	2
Trimacracanthus Beveridge and Campbell, 1987	2
Trygonicola Beveridge and Campbell, 1998	1
Zygorhynchus Beveridge and Campbell, 1988	4

Table 3. Genera within the superfamily Tentacularoidea.

Genera	Number of species
Heteronybelinia Palm, 1999	15
Kotorella Euzet and Radujkovic, 1989	1
Kotorelliella Palm and Beveridge, 2002	1
Mixonybelinia Palm, 1999	6
Nybelinia Poche, 1926	29
Paranybelinia Dollfus, 1966	1
Pseudonybelinia Dollfus, 1966	1
Tentacularia Bosc, 1797	1

Life Cycle of the Trypanorhyncha

In general, the life cycles of species of cestodes that parasitize marine hosts are poorly known. In agreement with Sakanari and Moser (1989), Palm and Caira (2008), and Palm et al.

Table 4. Genera within the superfamily Gymnorhynchoidea.

Genera	Number of species
Aporhynchus Nybelin, 1918	4
Chimaerarhynchus Beveridge and Campbell, 1989	1
Deanicola Beveridge, 1990	2
Gilquinia Guiart, 1927	4
Gymnorhynchus Rudolphi, 1819	2
Hepatoxylon Bosc, 1811	2
Heterosphyriocephalus Palm, 2004	2
Molicola Dollfus, 1935	3
Nakayacestus Caira, Kuchta and Desjardins, 2010	2
Pintneriella Yamaguti, 1934	4
Plesiorhynchus Beveridge, 1990	3
Sagittirhynchus Beveridge and Justine, 2006	1
Sphyriocephalus Pintner, 1913	4
Vittirhynchus Beveridge and Justine, 2006	1

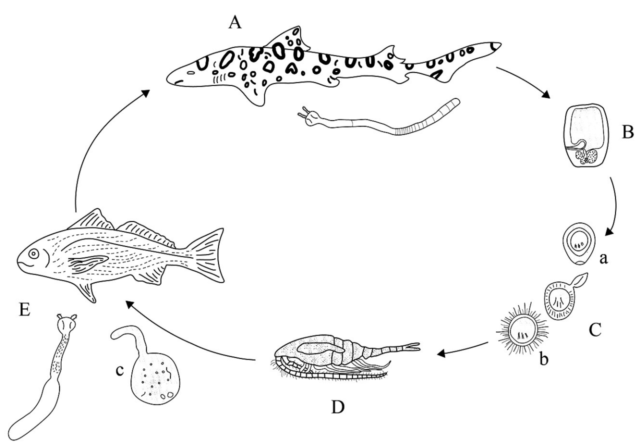

Figure 4. Life cycle of *Lacistorhynchus dollfusi* Beveridge and Sakanari, 1987. A) Adult trypanorhynch in the spiral valve of *Triakis semifasciata* Girard, 1855 (leopard shark); B) Gravid proglottids pass out with the feces and release eggs into the water; C) Coracidium larva (b) hatch from operculate eggs (a); D) The coracidium larvae are eaten by *Tigriopus californicus* (Baker, 1912) (copepod) in which the procercoids are developed; E) The infected copepods are ingested by teleosts such as *Genyonemus lineatus* (Ayres, 1855) (white croaker), in which the plerocercus form inside blastocysts (c). The life cycle is completed when *T. semifasciata* eats an infected *G. lineatus* individual. Source: Modifed from Sakanari and Moser, 1989. License: CC BY-NC-SA 4.0.

(2009; 2017), trypanorhynchs share a general pattern of life cycle. In this general cycle, the first intermediate host (often a copepod) becomes infected when it consumes an oncosphere or a coracidium larva (free-swimming larva). Inside the first intermediate host, the zygote develops into a procercoid larva. The

Table 5. Genera within the superfamily Lacistorhynchoidea.

Genera	Number of species
Ancipirhynchus Schaeffner, Gasser and Beveridge, 2011	1
Bathygrillotia Beveridge and Campbell, 2012	2
Bombycirhynchus Pintner, 1931	1
Callitetrarhynchus Pintner, 1931	2
Campbelliella Palm, 2004	1
Cavearhynchus Schaeffner and Beveridge, 2012	1
Dasyrhynchus Pintner, 1928	5
Diesingium Pintner, 1929	3
Diplootobothrium Chandler, 1942	1
Floriceps Cuvier, 1817	2
Fossobothrium Beveridge and Campbell, 2005	1
Grillotia Guiart, 1927	17
Grillotiella Palm, 2004	1
Hornelliella Yamaguti, 1954	1
Iobothrium Beveridge and Campbell, 2005	1
Lacistorhynchus Pintner, 1913	2
Microbothriorhynchus Yamaguti, 1952	2
Otobothrium Linton, 1890	12
Paragrillotia Dollfus, 1969	3
Parotobothrium Palm, 2004	2
Poeciloacanthum Palm, 1995	1
Poecilancistrium Dollfus, 1929	1
Pristiorhynchus Schaeffner and Beveridge, 2013	1
Proemotobothrium Beveridge and Campbell, 2001	3
Protogrillotia Palm, 2004	2
Pseudogilquinia Bilqees and Khatoon, 1980	5
Pseudogrillotia Dollfus, 1969	6
Pseudolacistorhynchus Palm, 1995	5
Pseudotobothrium Dollfus, 1942	2
Pterobothrioides Campbell and Beveridge, 1997	2
Pterobothrium Diesing, 1850	15
Stragulorhynchus Beveridge and Campbell, 1988	1
Symbothriorhynchus Yamaguti, 1952	2

first intermediate host is consumed by the second intermediate host. These include a wide array of marine animals (invertebrates and teleost fish). The definitive host, an elasmobranch, is infected when it consumes the infected second intermediate host (Palm et al., 2017).

Although the full life cycles are unknown, partial life cycles of the trypanorhynchs were described by Sakanari and Moser (1989) in the 1980s. Figure 4 shows an example of the complete life cycle of a trypanorhynch that was completed by these authors in a laboratory setting.

Unlike most other orders of cestodes, the final stage of the larva of trypanorhynch (namely, plerocercoid,

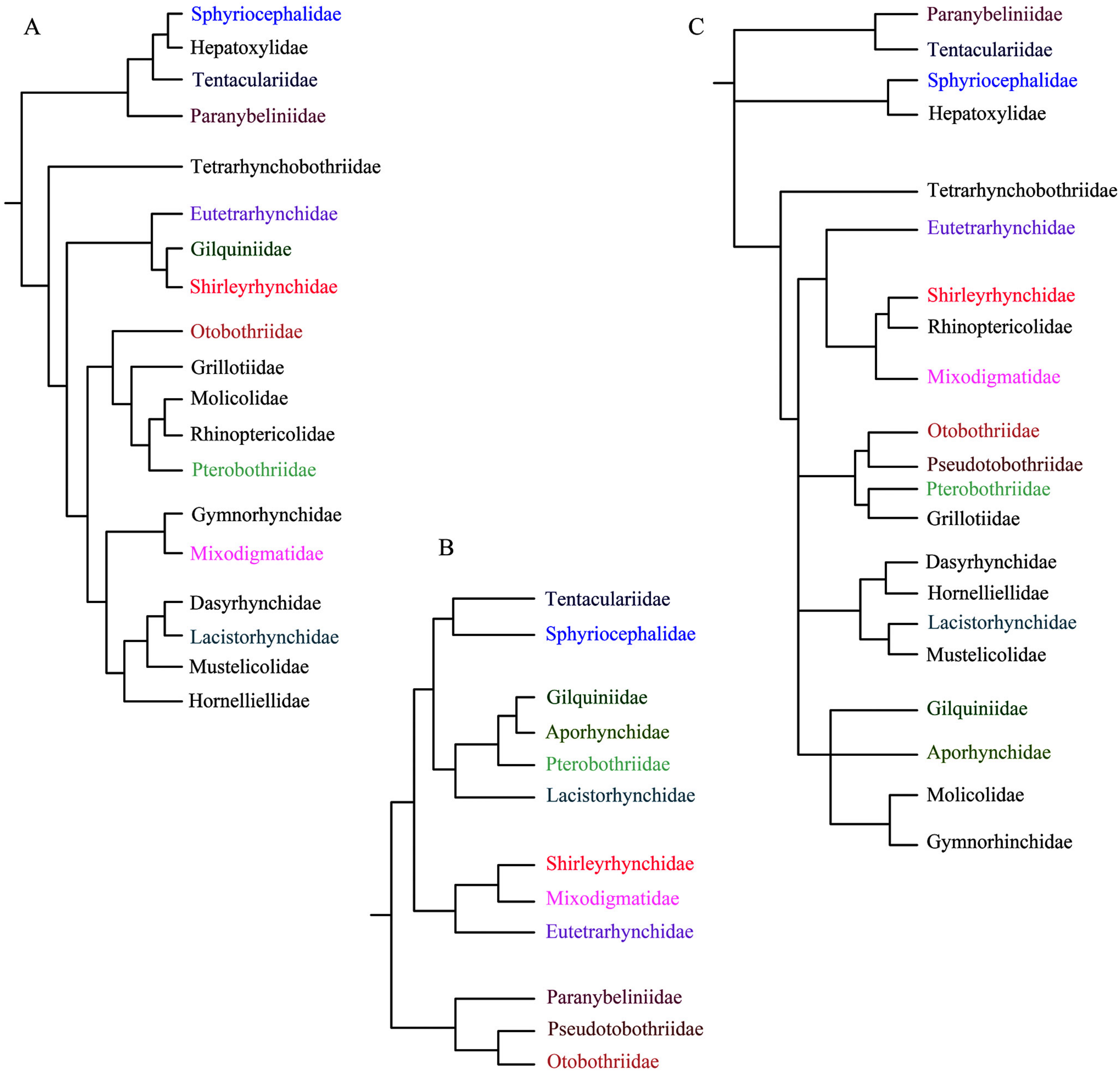

Figure 5. Classification of the order Trypanorhyncha to the family level using morphological characters. A) Hypothesis by Campbell and Beveridge, 1994; B) Hypothesis by Palm, 1997; C) Hypothesis by Beveridge et al., 1999. Source: Modified from Beveridge et al., 1999. License: CC BY-NC-SA 4.0.

plerocercus, or merocercoid) generally helps identify the species because the adult hook pattern is evident. Some trypanorhynchs use a paratenic host following the final intermediate host; this paratenic host serves to bridge the food web between types of organisms that normally do not come into contact with one another (Palm et al., 2017). As adults, trypanorhynchs parasitize the spiral intestine of sharks and rays (Palm et al., 2017).

General Characteristics of Each Superfamily of the Order Trypanorhyncha

Since its inception, the order Trypanorhyncha has had many changes in its taxonomic classification (Campbell and Beveridge, 1994; Palm, 1995; 1997; 2004; Beveridge et al., 1999). However, Beveridge and colleaagues (2017) can serve as a basis for a summary of the general characteristics of the superfamilies of trypanorhynchs, as follows.

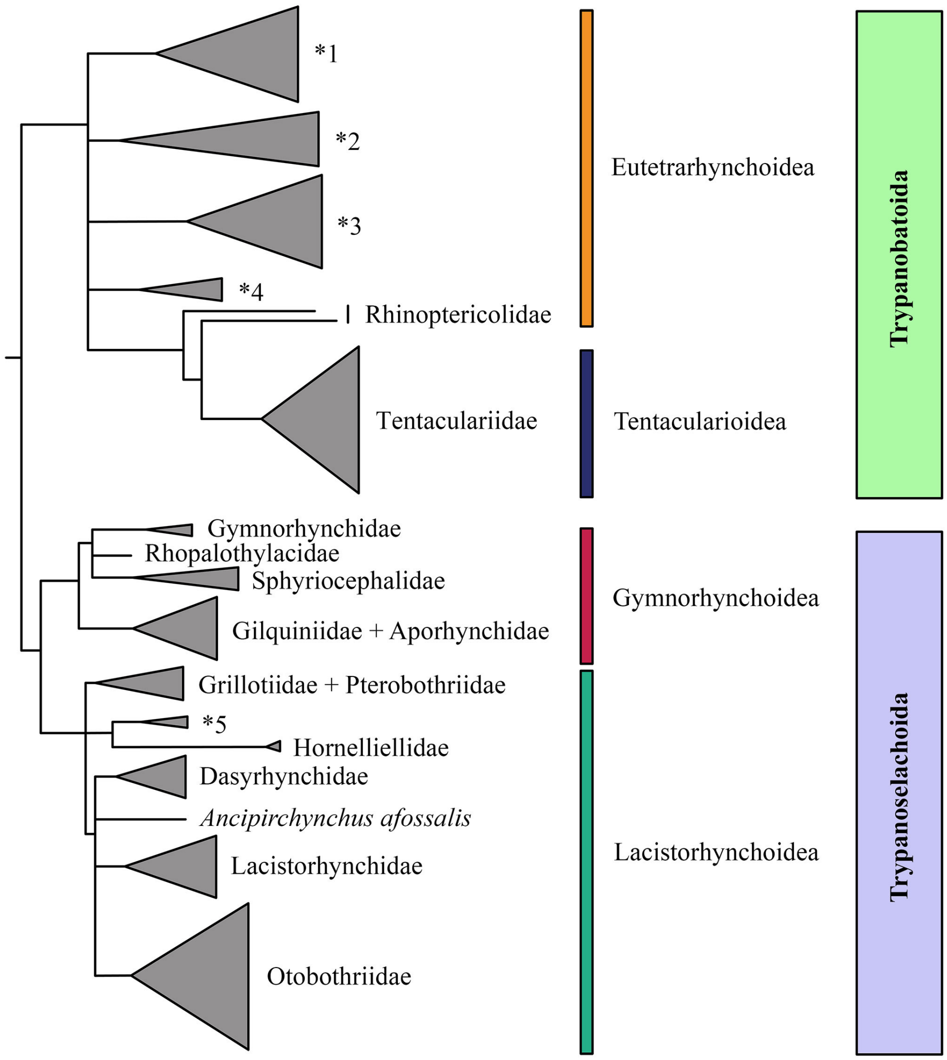

Figure 6. Schematic molecular phylogeny of Trypanorhyncha with recognized suborders, superfamilies, and families. Note: The clades marked with an asterisk * followed by a number are new clades for which there is no existing a name for the family. Source: Modified from Beveridge et al., 2017. License: CC BY-NC-SA 4.0.

Currently, the order Trypanorhyncha is divided into 2 suborders: **Trypanobatoida** and **Trypanoselachoida** (Olson et al., 2010). The suborder Trypanobatoida is divided into 2 superfamilies (**Eutetrarhynchoidea** (6 families) and **Tentacularioidea** (1 family)) and the suborder Trypanoselachoida is also divided into 2 superfamilies (**Gymnorhynchoidea** (5 families) and **Lacistorhynchoidea** (8 families)).

Superfamily Eutetrarhynchoidea

The species within this superfamily are characterized by the presence of prebulbar organs and gland cells within the bulbs. It comprises 118 species within 26 genera (Table 2). Of these genera, only the species within *Prochristianella* do not have prebulbar organ glands and gland cells within the bulbs.

Superfamily Tentacularioidea

The species within this superfamily are characterized by a ventro-submarginal genital pore and a uterus that develops laterally from the end of the uterine duct. There are 55 species within the 8 genera of the superfamily (Table 3).

Superfamily Gymnorhynchoidea

The species within this superfamily are characterized by the retractor muscle originating near the middle of the tentacular bulb (Olson et al., 2010) and, typically, a heteroacanthus armature (Palm, 2004). There have been 35 species reported within 14 genera (Table 4).

Superfamily Lacistorhynchoidea

The species of this family possess a hermaphroditic duct. It is composed of 107 species within 33 genera (Table 5).

Phylogenetic Relationships of the Trypanorhyncha

The relationship between Trypanorhyncha and the other orders of cestodes is not clear (see Brooks et al., 1991; Hoberg et al., 1997; Mariaux, 1998). One of the first to try to relate the species of Trypanorhyncha was Dollfus (1942), who considered the number of bothridia and the tentacular armature to be the most important characters. Succeeding works (Beveridge and Campbell, 1988; Campbell and Beveridge, 1994; Palm, 1995; 1997) have culminated in the preliminary cladistic analysis for the order by Beveridge et al. (1999). However, this provided evidence that conflicted with previous classifications (Figure 5). The hypothesis presented by Beveridge and colleaguea (2017) detailing the relationships of species of Trypanorhyncha uses molecular data from various species from each of the superfamilies (Figure 6). The classification provided in this chapter is based on the hypothesized relationships of that study. These authors (Beveridge et al., 2017) have suggested that this order of cestodes requires a more detailed review using both molecular and morphological characters. To learn more about the phylogenetic hypotheses, ecology, or biogeography of different groups of helminth parasites, the work of Brooks and McLennan (1991; 1993; 2002) covers these aspects in greater detail.

Zoogeography

The distribution of each species of parasite is determined by and limited, at least in part, to the distribution of its host or hosts. The trypanorhynchs are, obviously, restricted to the localities where elasmobranchs are distributed. This linked relationship between the distributions of host and parasite is a continuing area of study (see, for example, Brooks and McLennan, 1991, for further information on host-parasite coevolution and cospeciation). According to Last and colleagues (2016), there are 34 families comprising approximately 516 valid species of sharks and 26 families of rays with 636 valid species. The number of species of trypanorhynchs that have been reported from those species of elasmobranchs is low and this information shows the relative scarcity of known species that parasitize elasmobranchs. This suggests that a very large amount of work with these groups remains to be done. Let's get to it!

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