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Digenea, Plagiorchiida

Hemiurata Skrjabin & Guschanskaja, 1954 (Suborder)

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Phylum Platyhelminthes

Class Trematoda

Subclass Digenea

Order Plagiorchiida

Suborder Hemiurata

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Chapter 40

Hemiurata Skrjabin & Guschanskaja, 1954 (Suborder)

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Suborder Hemiurata Skrjabin & Guschanskaja, 1954

The suborder Hemiurata represents one of the most diverse groups of digeneans, which usually occurs in the stomach and intestine mainly of marine teleost fishes but also occurs in freshwater teleosts, elasmobranchs, amphibians, and reptiles (Gibson and Bray, 1979). This group has a wide geographical distribution as it is found in the Great Barrier Reef of Australia, the Indian Ocean, and the Atlantic Ocean (Gibson and Bray, 1986).

Typically, members of Hemiurata have a 2- or 3-host life cycle in which marine gastropods act as the first intermediate host, crustaceans or other invertebrates as the second intermediate host (in the 3-host life cycles), and fishes as the final host. These life cycles are characterized by the fact that eggs are eaten by the first intermediate host.

Although, the systematic status of Hemiurata has been somewhat controversial, its taxonomic position within Plagiorchiida was well-supported by Olson et al. (2003), except for 2 superfamilies (Azygioidea and Hemiuroidea) in this suborder.

Superfamily Azygioidea Lühe, 1909

This group was erected by Lühe (1909) as a subfamily (Azyigiinae) and used at the family rank by Odhner (1911). La Rue (1957) included this group of digeneans in the superfamily Azygioidea. The superfamily was, thereafter, recognized by Gibson (2002l).

Members of this superfamily are parasitic in the stomach or body cavity of freshwater and marine fishes, mainly elasmobranchs, teleosts, and holosteans (Cribb et al., 2003; Gibson, 2002l). Eggs of azygioids have to be ingested by the first intermediate host (which are gastropods). Fork-tailed cercariae are produced in rediae in the gastropod. The cercarial body is withdrawn into the tail after emergence and the definitive host becomes infected by ingesting the cercariae directly. In some cycles, cercariae emerge with an egg already formed in the uterus. In another cycle, a second intermediate host is intercalated (Cribb et al., 2003).

The superfamily Azygioidea is monotypic and contains only 1 family: Azygiidae.

Family Azygiidae Lühe, 1909

This family contains 2 subfamilies and 4 genera, *Azygia* being the type genus. Subfamilies are differentiated on the basis of the position of the testes, specifically, whether they are post-ovarian (Azygiinae) or pre-ovarian (Leucerothrinae). The subfamily Azygiinae includes 3 genera (*Proterometra, Otodistomum*, and *Azygia*) which are differentiated by the structure of the testes, uterus, and vitelline follicles (Gibson 2002m). Subfamily Leucerothrinae only includes 1 genus (*Leuceruthus*) characterized as mentioned above, by the pre-ovarian position of the testes.

Superfamily Hemiuroidea Lühe, 1909

The Hemiuroidea, with a somewhat controversial taxonomy, constitute a huge and diverse group of digeneans that are commonly parasites the gut—mainly the stomach—of fishes. They are especially found in marine teleosts, but also occur in freshwater teleosts, elasmobranchs, and occasionally in amphibians and reptiles (Gibson, 2002m). In addition to the gut, species or entire groups are known from tissues, gallbladder, swimbladder, body cavity, lungs, and skin.

The life cycles of Hemiuroidea present specialized fork-tailed cercariae known as cystophorous cercariae, which are peculiar and highly modified forms possessing a tail with a caudal cyst into which the body of the worm can be withdrawn and a delivery tube through which the cercarial body is injected into the second intermediate host after the cercaria is released from the mollusc (Figure 1). Cercariae are produced in sporocysts or rediae in the first intermediate host gastropods or, rarely, scaphopods or bivalves. After ingestion of cercariae by the second intermediate host, a specialized structure

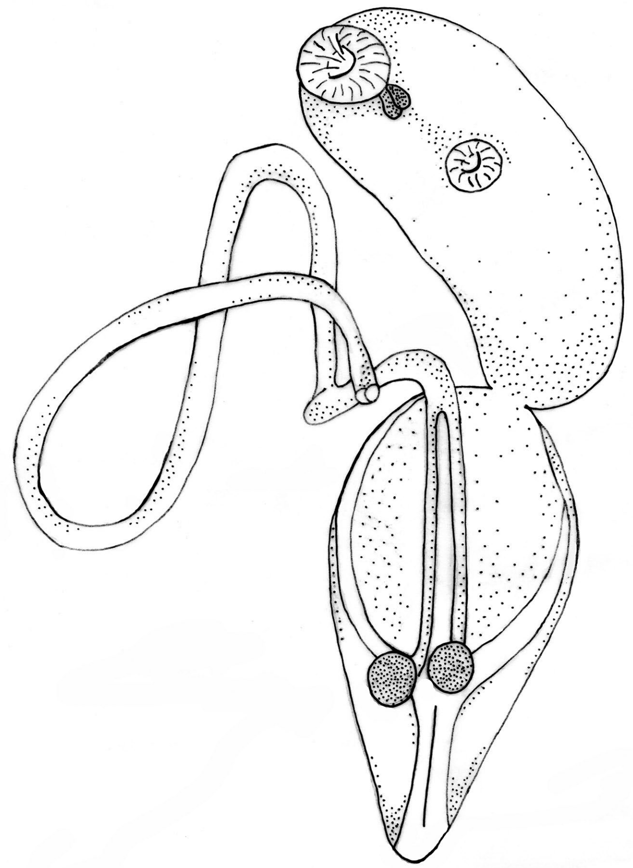

Figure 1. General scheme of a cystophorous cercariae. Source: L. Acosta Soto, B. Fried, and R. Toledo. License: CC BY-NC-SA 4.0.

(the delivery tube) everts, penetrating the host gut where unencysted metacercariae are formed. The final host becomes infected after ingestion of metacercariae (Cribb et al., 2003). In some life cycles of hemiuroids, a fourth host can be included, by intercalation of this extra host between the second intermediate and the definitive host. In contrast, other life cycles can be abbreviated with all larval stages occurring within the gastropod (Cribb et al., 2003).

The main morphological features of this family are a genital pore that is mid-ventral, male and female terminal ducts that normally fuse to form a hermaphroditic duct with, commonly, a hermaphroditic intromittent organ (sinus organ) and a surrounding muscular sac, and characterized by the absence of a pre-pharynx, a tegument devoid of spines, and a Y-shaped excretory vesicle with arms bonding dorsally in the forebody (Gibson, 2002m). Moreover, there are a number of other specialized structures in certain families of Hemiuroidea (Cribb et al., 2003), including:

- **Ecsoma**: Name given to the posterior region of the body of a digenean when it is capable of being retracted within the body, which appears to be associated with the inhospitable environment (the cardiac stomach, which these worms inhabit) in that it is believed to be a feeding organ protruded only when the pH and/or osmolarity are suitable (Gibson and Bray, 1979)
- **Plications**: Regular backwardly directed thickenings of the tegument which surround, partly or completely, the body transversally.
- **Juel's organ**: A sac containing an amorphous granular material on which Laurer's canal opens dorsally.
- **Manter's organ**: A tubular vesicle lined with an epithelium and usually surrounded by bundles of muscle, occurring dorsally to the excretory vesicle into which it opens close to the excretory pore.
- **Fistchal's organ**: A round vesicle of unknown function, lined with epithelial cells and surrounded by a mass of gland cells opening dorsally to the right of Mehlis' gland.

Using these morphological features, (Gibson and Bray, 1979) classified the Hemiuroidea on the basis of 3 transformational series: 1) The seminal storage and disposal apparatus in the female reproductive system, with emphasis on the presence or absence of Juel's organ; 2) the form of the vitellarium; and 3) the structure of the terminal genitalia (Figure 2). On this basis, a total of 14 families were admitted. Blair et al. (1998) first used molecular and morphological matrices for phylogenetic reconstructions of Hemiuroidea. The main conclusion of this study was that molecular and morphological matrices for a large group of digeneans are not incongruent, leading to the belief that both kinds of data are of value in inferring relationships within this group. Based on the data reported by Blair et al. (1998), Gibson (2002m) admitted a total of 12 families within the Hemiuroidea.

Family Hemiuridae Looss, 1899

The Hemiuridae is a group of digeneans which usually occur in the stomach of marine teleosts, although forms are known from freshwater teleosts and the lung of piscivorous sea snakes. Gibson and Bray (1979) characterized the members of this family by their possession of a terminal ecsoma or "tail," which is capable of being retracted within the body. However, in later works, the ecsoma has not been considered to be the primary apomorphy of the group (Gibson and Bray, 1986; Gibson, 2002e; Atopkin et al., 2017). This structure is thought to be associated with the inhospitable environment (the cardiac stomach, which these worms inhabit) in that it is believed to be a feeding organ protruded only when the pH and/or osmolarity are suitable (Gibson and Bray, 1979).

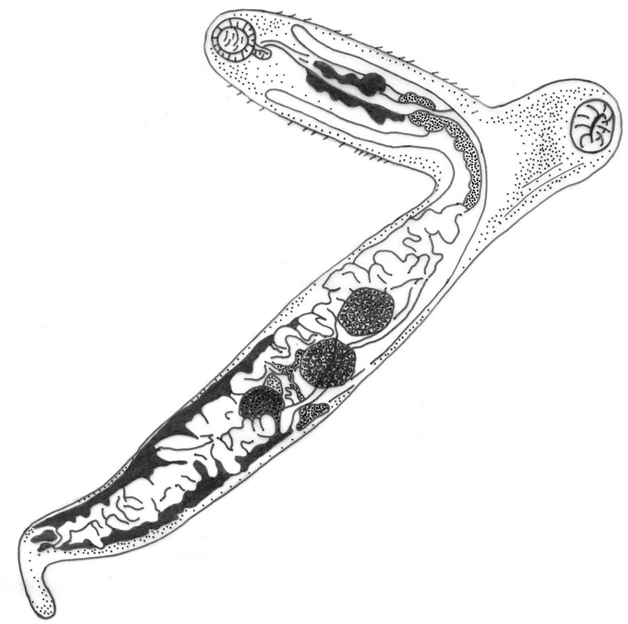

Figure 2. General scheme of an adult specimen of *Accacoelium* sp. (Accacoeliidae). Source: L. Acosta Soto, B. Fried, and R. Toledo. License: CC BY-NC-SA 4.0.

The life cycle of most hemiurids is poorly known, but it is likely that they follow the typical hemiuroid pattern (Gibson and Bray, 1986), which includes the following stages. Embryonated eggs passed by the fish in its feces are swallowed by gastropod molluscs and hatch in the gut, releasing the miracidium. Within the tissues of the mollusc the miracidium is transformed into a mother-sporocyst which normally gives rise to a generation of rediae (on rare occasions daughter-sporocysts). Within these parthenitae develop cystophorous cercariae. The metacercaria, which is unencysted, usually occurs in the hemocoel of planktonic organisms, such as copepods and chaetognaths. Chaetognaths acquire the parasites by feeding upon infested copepods, but it is not known for certain that hemiurids cannot be acquired directly by these hosts. The definitive hosts become infected either directly, in the case of young fish, small fish, and filter feeders, or indirectly by feeding upon small, infected fishes. In some cases, such as some lecithochiriines, immature forms may occur encapsulated in the body cavity of fishes which appear to act as obligate third intermediate hosts.

Although the composition of taxa within hemiuridae is somewhat confusing, Gibson (2002e) accepted a total of 12 subfamilies (Glomericirrinae, Lecithochiriinae, Plerurinae, Pulmoverminae, Lethadeninae, Hemiurinae, Elytrophallinae, Dinurinae, Ophasthadeninae, Theletrinae, Bunocotylinae, and Aphanurinae) and a total of 53 nominal genera, with *Hemiurus* being the type genus. Subfamilies are mainly differentiated on the basis of the presence or absence of an ecsoma, ejaculatory vesicle, sinus sac, and uterine seminal receptacle and the structure of the seminal vesicle and body surface (Gibson, 2002e).

Family Accacoeliidae Odhner, 1911

Members of the family Accacolediiae are easily recognized by the presence of an anterior extension to the pharynx, which penetrates the base of the oral sucker. Although several species of fishes can be infected by accacoelids, most of the taxa occur in a single fish species, *Mola mola*. This is related to the fact that *M. mola* is medusaophagus and the metacercariae of this family occurs in nektonic organisms, especially cnidarians and ctenophores (Gibson, 2002a). Accacoelids are commonly parasites in the gut but, occasionally, they can inhabit the gill of fishes as monogeneans. Various classifications have been proposed for the family Accacoelediiae. Gibson (2002a) included 2 subfamilies: Accacoelinae including 7 genera (*Accacoelium, Rhynchopharynx, Accacladium, Accacladocoelium, Odhnerium, Tetrotechtus*, and *Orophocotyle*); and the monotypic subfamily Paraccacladiinae that only comprises the genus *Paraccacladium*. *Accacoelium* is the type genus.

Family Bathycotylidae Dollfus, 1932

Bathycotylidae is a monotypic family that includes only 1 genus (*Bathycotyle*). They are parasites on gills and probably the stomach of pelagic marine teleosts. The most relevant features of this family are the presence of an intertesticular ovary, the absence of a sinus sac, and that they inhabit the gills (Gibson, 2002b).

Family Derogenidae Nicoll, 1910

This family includes parasites usually in the intestinal system (normally the stomach) of freshwater and marine teleosts, but occasionally recorded from amphibians, reptiles, and freshwater shrimp. Members of the family Derogenidae are characterized by the absence of constant seminal storage and the presence of a disposal apparatus in the female (Gibson and Bray, 1979). Gibson and Bray considered that these morphological variations were related to the fact that derogenids have evolved around the time the first modifications of the primitive arrangement of the seminal storage and disposal apparatus began to occur.

Gibson (2002c) accepted the previous classification of the family by Gibson and Bray (1979) including 3 subfamilies: Gonocercinae (including 2 genera), Halipeginae (including 16 genera), and Derogeninae (including 5 genera). Subfamilies are differentiated on the basis of the position of the testes with respect the ovary and vitellarium and the character of the life cycle (marine or freshwater) (Gibson, 2002c). *Derogenes* is the type genus.

Family Dictysarcidae Skrjabin & Guschanskaja, 1955

The family Dictysarcidae comprises parasites in the swimbladder of marine physostomatous teleosts. Gibson (2002d) included 3 subfamilies within the Dictysarcidae: Albulatrematinae, comprising the genera *Albulatrema* and *Elongoparorchis*, Dictysarcinae, including the genera *Dictysarca* and *Aerobiotrema*, and the monotypic Cylindrorchiinae, comprising only the genus *Cylindrorchis*. Differentiation of the subfamilies is based on position of the uterus (whether it is pre- or post-ovarian) and the structure and shape of the ovary, vitellarium, and hermaphroditic duct. The type genus is *Dictysarca*.

Family Hirudinellidae Dollfus, 1932

Members of the family Hirudinellidae are very large hemiuroids that parasitize the stomach of large marine teleosts; and immature forms are occasionally present in salmonids (Gibson and Bray, 1979). They can be differentiated from other hemiuroids by the absence of a hermaphroditic duct, and the possession of a form of cirrus and cirrus sac that are different from other digeneans. This structure almost certainly developed independently of the sinus sac, but it does appear to be analogous and not homologous. (The sinus sac is a muscular sac that surrounds the base of the genital atrium.) Such a structure probably developed in this group because its ancestors lost, or did not develop, a hermaphroditic duct, with the result that the copulatory organ (the cirrus) did not contain the female duct. In this group, therefore, both the male and the female ducts have developed their own finger-like projections from the wall of the genital atrium (Gibson and Bray, 1979).

The Family Hirudinellidae contains 1 subfamily (Hirudinellinae) and 3 genera (*Lampitrema*, *Hirudinella*, and *Botulus*) that are differentiated by the body shape and the position of the uterus and the vitellarium (Gibson, 2002f).

Family Isoparorchiidae Travassos, 1922

This is a monotypic family that only contains 1 genus, *Isoparorchis*, that parasitize the swimbladder of physostomatous freshwater teleosts in Asia and Australia. The species of *Isoparorchis* differ from other parasites of the swimbladder in that they occur in freshwater rather than marine environments, and due to the possession of Laurer's canal, a tubular vitellarium, and an ovary and well-developed muscular sinus sac (Figure 3) (Gibson and Bray, 1979; Gibson, 2002g).

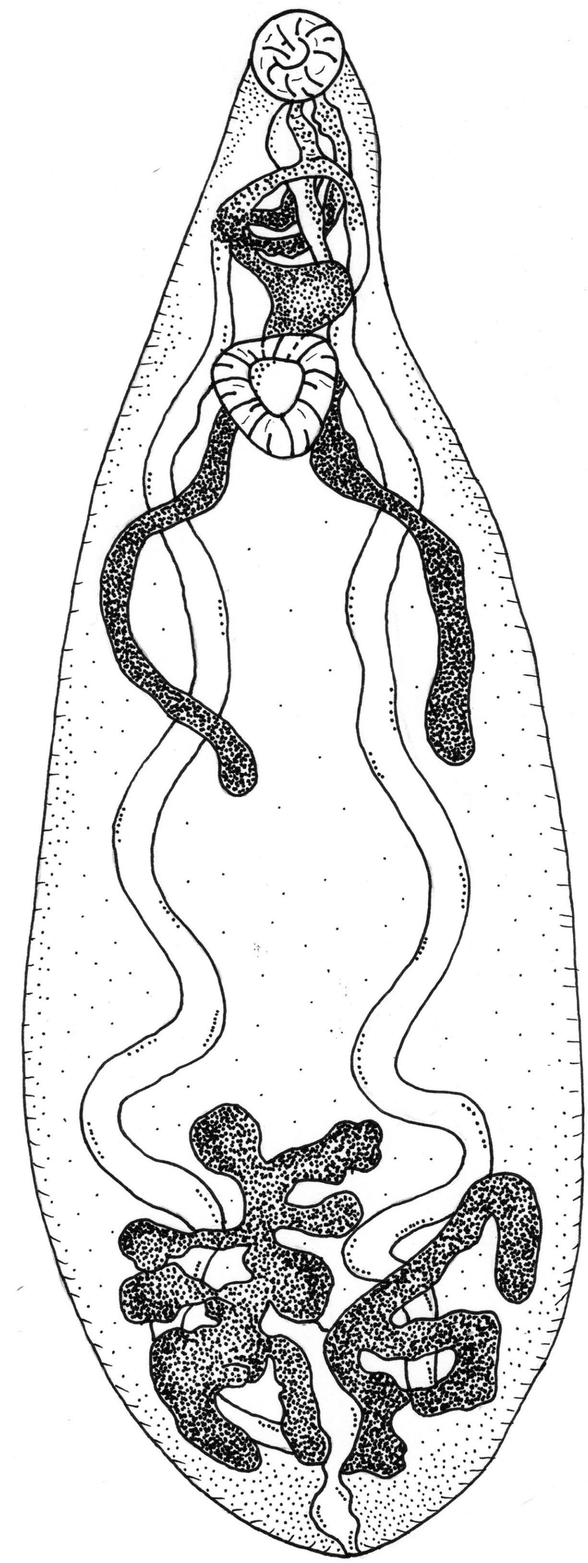

Figure 3. General scheme of an adult specimen of *Isoparorchis* sp. (Isoparorchiidae). Source: L. Acosta Soto, B. Fried, and R. Toledo.

Family Lecithasteridae Odhner, 1905

This family contains parasites in pyloric cecae and the anterior intestines of marine teleosts, mainly in the waters of the Great Barrier Reef off the coast of Australia. This group is characterized by a hermaphroditic duct that is relatively tubular, with a distinct gap, usually filled with fibrous connective tissue and gland cells between the wall of the hermaphroditic duct and the wall of the sinus sac. Species of Lecithasteridae retain both a uterine seminal receptacle and a rudimentary seminal receptacle. Moreover, the uterine distribution and structure of the vitellarium has taxonomic value (Gibson and Bray, 1979; Gibson, 2002h). Gibson (2002h) included a total of 5 subfamilies and 19 genera within the Lecithasteridae: Lecithasterinae (with the genera *Monorchiaponorus, Lecithaster, Lecithophyllum*, and *Aponorus*), Hysterolecithinae (including *Thulinia, Hysterolecitha, Hysterolecithoides*, and *Machidatrema*), Macradenininae (*Monorchimacradena, Dichadena, Neodichadena, Acanthuritrama, Macradenina*, and *Macradena*), Quadrifoliovariinae (comprising the genera *Unilacinia, Quadrifoliovarium*, and *Bilacinia*), and Trifoliovariinae (including *Trifoliovarium* and *Assitrema*), with *Lecithaster* serving as the type genus. Subfamilies are mainly differentiated by characters such a as the presence or absence of a uterine vesicle, blind seminal vesicle, and sinus sac, the structure of the uterus and the hermaphroditic duct, or the position of the seminal vesicle (Gibson, 2002h).

Family Ptychogononimidae Dollfus, 1937

This is a small family of hemiuroids that contains only 2 genera, *Ptychogononimus* and *Melagonimus*, which are differentiated by the presence of a uroproct, the position of the uterus, and the structure of the wall of the genital atrium (Gibson, 2002h). Ptychogononimidae is characterized by an unusual life cycle in that its members use a scaphopod as the first intermediate host and transmission to the second intermediate host is affected by means of a motile parthenita (a unisexual stage in an intermediate host).

Family Sclerodistomidae Odhner, 1927

The family Sclerodistomidae is a controversial and small group of trematodes that are generally parasites of the gut (mainly the stomach) and are occasionally found in the body cavities of marine teleosts. This family only contains 4 subfamilies and 5 genera: Sclerodistominae (with the genus *Sclerodistomum*), Kenmackenziinae (including *Kenmackenzia*), Prosogonotrematinae (containing the genus *Prosogonotrema*), and Prosorchiinae (comprising *Prosorchis* and *Prosorchipsis*). Probably the most relevant feature of the members of this family is the presence of 1 or 2 Manter's organs (an accessory excretory organ) which occurs dorsal to the excretory vesicle, into which it opens posteriorly (Gibson, 2002i). Subfamilies are differentiated on the basis of the structure of Manter's organ, and the position of the testes and ovary. The type genus is *Sclerodistomum* (Gibson, 2002i).

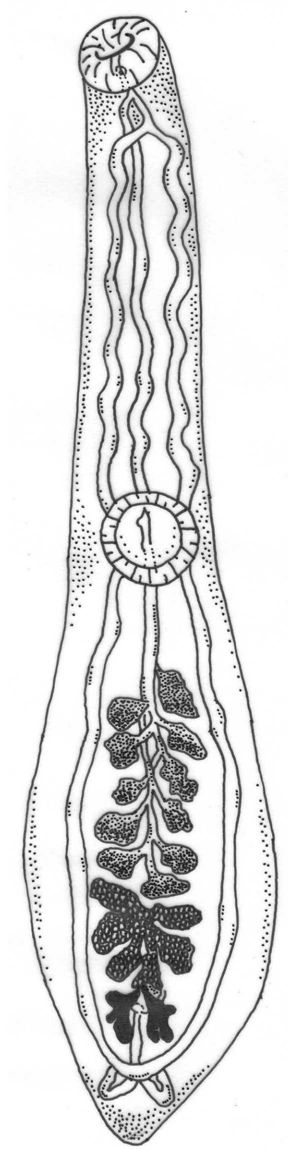

Figure 4. General scheme of an adult specimen of *Syncoelium* sp. (Syncoeliidae). Source: L. Acosta Soto, B. Fried, and R. Toledo. License: CC BY-NC-SA 4.0.

Family Sclerodistomodiidae Gibson and Bray, 1979

The family Sclerodistomodiidae was established by Gibson and Bray (1979) to allocate *Sclerodistomoides pacificus*, which is currently the only species in the family. These authors considered the genus *Sclerodistomoides* to be different from other hemiuroids based on the structure of the pharynx, the absence of Manter's organ, and the orientation of the main collecting ducts of the vitelline system (Gibson and Bray, 1979; Gibson, 2002i).

Family Syncoeliidae Looss, 1899

The Syncoeliidae is a marine family of robust digeneans with 11 species distributed across 2 subfamilies (Syncoeliinae and Otiotrematinae) and 4 genera, including: *Syncoelium* and *Copiatestes* (belonging to Syncoeliinae) and *Otiotrema* and *Paronatrema* (included in Otiotrematinae), with *Syncoelium* which is the type genus (Figure 4). Subfamilies are differentiated on the basis of the structure of the ovary and vitellarium (Gibson, 2002k). This family is closely related to Hirudinellidae (Calhoun et al., 2013). Adults of Syncoeliidae are usually found associated with the gills, stomach, or buccal cavity of elasmobranchs or teleosts (Gibson and Bray, 1979; Gibson, 2002k; Curran and Overstreet, 2000). Pelagic, benthopelagic, and benthic fishes serve as definitive hosts and the metacercaria for a syncoeliid species (Calhoun et al., 2013). Since many of the 11 species of syncoelliids use definitive hosts that occur in benthic or bentho-pelagic habitats, it is likely that vertical migration of crustaceans or the use of paratenic hosts may play a role in the life history of the Syncoeliidae.

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