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## DIGENEA, PLAGIORCHIIDA

## XIPHIDIATA

# Opecoelidae Ozaki, 1925 (Family): The Richest Trematode Family

*Storm B. Martin*

Phylum Platyhelminthes
  Class Trematoda
    Subclass Digenea
      Order Plagiorchiida
        Family Opecoelidae

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# Chapter 46

# Opecoelidae Ozaki, 1925 (Family): The Richest Trematode Family

Storm B. Martin
School of Biological Sciences, University of Queensland,
Brisbane, Queensland, Australia
storm.martin@uqconnect.edu.au

## Introduction

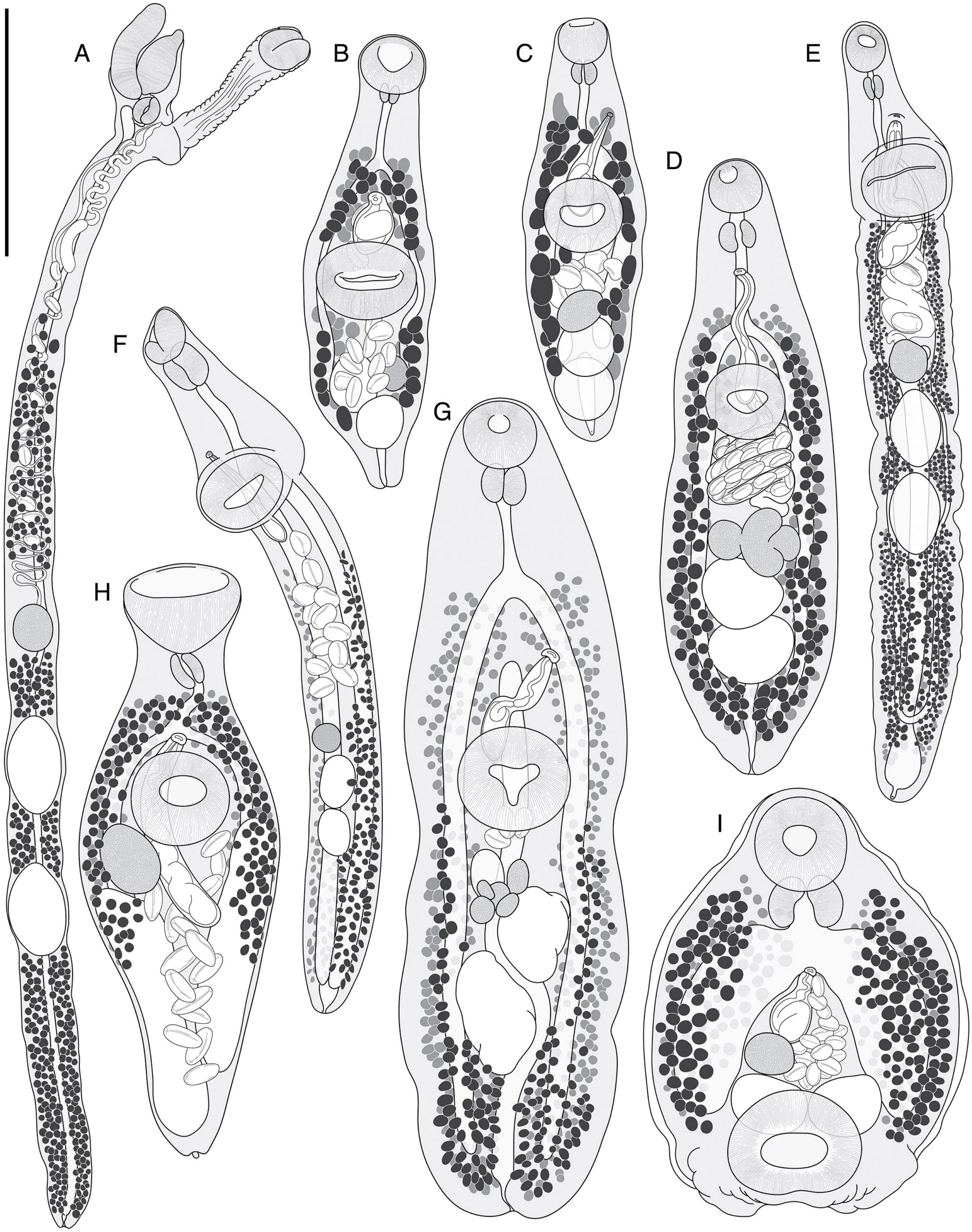
The Opecoelidae Ozaki, 1925 is the richest of all trematode families. It comprises over 1,000 described species presently arranged into about 100 genera. Adult opecoelids are benign endoparasites, typically residing in the intestines, pyloric ceca, or rectum of phylogenetically and ecologically diverse teleost fishes worldwide. They exploit both marine and freshwater fishes and are among the best represented trematode lineages known from polar and deep sea fishes (Bray, 2004; Faltýnková et al., 2017; Martin et al., 2018d). Therefore, although no opecoelids are known to have any economic importance, they are often among the lineages of trematodes most frequently encountered by ichthyoparasitologists in the field.

## Identifying the Opecoelidae

Although opecoelids are a hugely speciose and evolutionarily derived group, they are neither diverse nor specialized in their morphology relative to other trematode lineages. Nevertheless, opecoelids are usually readily recognizable, even under stereomicroscope in the field, by the combination of some general characters together with the absence of certain specialized characters that are seen in other groups (select opecoelids depicted in Figure 1). Most species are 1–5 mm in length, although a few apparently never exceed 1 mm, for example, *Choerodonicola arothrokoros* Martin et al., 2018 (Martin et al., 2018a), species of *Fairfaxia* Cribb, 1989 (Cribb, 1989; Hassanine and Gibson, 2005), and some species of *Plagioporus* Stafford, 1904 (Fayton et al., 2017; 2018), and specimens of some species may exceed 5 mm, for example, species of *Macrourimegatrema* Blend et al., 2004 (Blend et al., 2017) and some species of *Hamacreadium* Linton, 1910 (see Bray and Justine, 2016; Martin et al., 2017b). Most opecoelids are dorsoventrally flattened and elongate-oval, oval, or linguiform. The body may also be elongate and subcylindrical or squat and robust to almost round. The tegument is never spinous, although species of *Poracanthium* Dollfus, 1948 (subfamily Opecoelinae) possess specialized spines surrounding the genital pore (Cribb, 2005a). In some other species, especially those of the subfamily Opistholebetinae, the tegument may be thick, wrinkled, or rugose, and in *Scorpidotrema longistipes* Aken'Ova & Cribb, 2003 and species of *Holsworthotrema* Martin et al., 2018 (subfamily Stenakrinae), it is covered by small, fine projections (Martin et al., 2018d).

Opecoelids have 2 usually-large suckers. The oral sucker is always anteriorly terminal or subterminal and the ventral sucker is usually larger and typically situated in the anterior half of the body. In species of several unrelated genera, the ventral sucker is supported by a long peduncle, while in others it may protrude prominently from the ventral body surface, be surrounded by fleshy tegumental folds or obvious muscle fibers, or be provided with papillae (Cribb, 2005a). In species of some genera belonging to the subfamily Opistholebetinae, the ventral sucker is situated in the posterior half of the body (such as *Heterolebes* Ozaki, 1935 and *Pseudoheterolebes* Yamaguti, 1959) or even near the posterior extremity, such as *Opistholebes* Nicoll, 1915 and *Parallelolebes* Martin et al., 2018 (see Martin et al., 2018e). Opecoelids always have a well-developed pharynx and a bifurcated intestine. The ceca usually reach near to the posterior extremity and may be blind, open into separate ani, or may unite, in which case they may form a cyclocoel, open into a common anus, or open into the excretory vesicle to form a uroproct (Cribb, 2005a). The excretory vesicle is probably always tubular, although in many opecoelids it has not been described and in others it has been reported as Y-shaped. *Pacificreadium serrani* (Nagaty & Abdel Aal, 1962) is exceptional in that its excretory vesicle is diverticulate anteriorly. The length of the excretory vesicle is important for distinguishing some genera; in most opecoelids it terminates anteriorly at about the level of the ovary, but in some species, especially freshwater taxa belonging to the subfamily Plagioporinae, it is shorter, and in others it enters the forebody. The excretory pore is usually terminal posteriorly, sometimes subterminal.

Opecoelids are simultaneous hermaphrodites. The male reproductive system consists of the testes connected via the vas deferens to the terminal genitalia. The testes are always situated in the posterior half of the body and are usually 2, although species belonging to 2 probably unrelated genera, *Decemtestes* Yamaguti, 1934 and *Helicometrina* Linton, 1910, have approximately 10. The male terminal genitalia include the seminal vesicle, a sperm storage organ, and the cirrus, an eversible copulatory organ, all of which may (or may not) be entirely or partially enclosed in a muscular, or sometimes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membranous, cirrus sac (Cribb, 2005a). The ejaculatory duct runs through the cirrus and opens, together with the uterus, into a common genital atrium. The genital pore is always ventral and in the forebody (that is, anterior to the ventral sucker). The single ovary may be smooth to deeply lobed and round to irregular. It is usually situated anterior to the testes, although in species of *Hysterogonia* Hanson, 1955, *Pseudoplagioporus* Yamaguti, 1938, *Sphaerostoma* Rudolphi, 1809, and *Urorchis* Ozaki, 1927 it is between the testes and in *Orthodena tropica* Durio & Manter, 1968 it lies beside the testes. The ovarian complex may or may not include a canalicular seminal receptacle, a specialized envagination of the Laurer's canal. The vitellarium includes fields of typically numerous, dense follicles. These are usually extensively distributed and the precise distribution is frequently important for distinguishing genera and species. The uterus is usually restricted in distribution to the intercecal zone between the gonads and cirrus sac, although in species of some genera it may extend beyond the ceca laterally or between or beyond the testes posteriorly. Eggs are tanned, operculate, and unembryonated. Exceptionally small eggs, < 30 μm-long, are diagnostic for 2 genera, *Choerodonicola* and *Diplobulbus* Yamaguti, 1934 (see Cribb, 2005a). Likewise, filamented eggs are a defining characteristic of the subfamily Helicometrinae, but bifilamented eggs also occur in species *Diplobulbus*.

In the field, it is often necessary to distinguish opecoelids from taxa belonging to the Fellodistomidae Nicoll, 1909, Lecithasteridae Odhner, 1905, Lepocreadiidae Odhner, 1905, Monorchiidae Odhner, 1911 and Zoogonidae Odhner, 1902, other rich and frequently encountered groups exploiting the intestine of teleost fishes. Lepocreadiids, monorchiids, and zoogonids have a spinous tegument. The ventral sucker in lepocreadiids and monorchiids is also usually much smaller relative to that of most opecoelids and remnant eye spot pigment is often visible in the forebody. The fellodistomids and lecithasterids have a smooth tegument and usually a large ventral sucker similar to that of opecoelids. Distinguishing these groups from opecoelids requires assessment of some internal characters and can therefore be more difficult. Typically, compared with most opecoelids, the distribution of the vitelline follicles in both fellodistomids and lecithasterids is highly restricted and the distribution of the uterus is much more extensive. This distinction also usually applies to the Monorchiidae and Zoogonidae.

Smaller groups exploiting fishes which may potentially be confused with opecoelids are the Acanthocolpidae Lühe, 1906, Allocreadiidae Looss, 1902, Apocreadiidae Skrjabin, 1942 and Enenteridae Yamaguti, 1958. All acanthocolpids and many apocreadiids have a spinous tegument. However, in some acanthocolpids, specifically of the genus *Acanthocolpus* Lühe, 1906, the spines are easily lost during handling and fixation of the specimens and may be mistakenly identified or described as opecoelids (see Bray and Gibson, 1991; Martin et al., 2018c). Some enenterids are highly similar to some opecoelids, but they are a small group specializing mainly in 1 small family of herbivorous fishes, the drummers (Perciformes: Kyphosidae) (Bray and Cribb, 2001). Likewise, the allocreadiids are now recognized as a relatively small group restricted to freshwater fishes (Cribb, 2005b). Many allocreadiids can be distinguished from opecoelids by the presence of a remnant eye spot pigment, a papillate oral sucker, or an extensive uterus, but others are less distinctive and more closely resemble generalized opecoelids.

The unspecialized morphology of opecoelids is perhaps best exemplified by comparison to species of *Biospeedotrema* Bray et al., 2014 and *Zdzitoweickitrema incognitum* Sokolov et al., 2018. These taxa are known only from deep sea fishes and are morphologically indiscernible from the opecoelids (Bray et al., 2014; Sokolov et al., 2019). However, phylogenetic analyses suggest closer affinity with the Gorgoderoidea (Sokolov et al., 2019). Thus, these enigmatic taxa are presently without a suitable family designation.

Figure 1. Select representative taxa belonging to the Opecoelidae: A) *Pseudopecoeloides tenuis* Yamaguti, 1940 (subfamily Opecoelinae), original ex. *Priacanthus macracanthus* Cuvier, the spotted bigeye, collected in Moreton Bay, Australia; B) *Fairfaxia lethrini* Cribb, 1989 (subfamily uncertain), original ex. *Lethrinus nebulosus* (Forsskål), the spangle emperor, collected off Lizard Island, Australia; C) *Plagioporus ictaluri* Fayton et al., 2018 (subfamily Plagioporinae); D) *Helicometra* sp. cf. *H. fasciata* (Rudolphi, 1819) Odhner, 1902 (subfamily Helicometrinae), original ex. *Thalassoma lunare* (Linnaeus), the moon wrasse, collected off Heron Island, Australia; E) *Bathycreadium brayi* Pérez-del-Olmo et al., 2014; F) *Polypipapiliotrema citerovarium* Martin et al., 2018 (subfamily Polypipapiliotrematinae), original ex. *Chaetodon quardimaculatus* Gray, the fourspot butterflyfish, collected off Ra'ivāvae, Austral Archipelago, French Polynesia; G) *Hamacreadium* sp. cf. *H. mutabile* Linton, 1910 (subfamily uncertain) (original ex. *Lutjanus carponotatus* (Richardson), the Spanish flag snapper, collected off Heron Island, Australia; H) *Hexagrammia longitestis* Schell, 1973 (subfamily Stenakrinae); I) *Opistholebes amplicoelus* Nicoll, 1915 (subfamily Opistholebetinae), original ex. *Tetractenos hamiltoni* (Richardson), the common toadfish, collected in Moreton Bay, Australia. Scale bar: 0.5 mm. Sources: A, B, D, F, G, I) S. B. Martin; C) Adapted from Fayton et al., 2018; E) Adapted from Pérez-del-Olmo et al., 2014; H) Adapted from Schell, 1973. License: CC BY-NC-SA 4.0.

## Systematics and Taxonomy

The morphological similarity between allocreadiids and opecoelids is reflected in the confused taxonomic history of these groups. Many opecoelid genera were originally proposed in the Allocreadiidae and, until recently, most authors considered the Opecoelidae and Allocreadiidae to be closely related, belonging to the superfamily Allocreadioidea Looss, 1902, together with the Acanthocolpidae and Brachycladiidae Odhner, 1905 (see Cribb, 2005a; 2005b). Although phylogenetic relationships among families within the Xiphidiata are not yet entirely resolved, combined evidence from recent analyses (Olson et al., 2003; Bray et al., 2005; 2009; Curran et al., 2006; Littlewood et al., 2015) demonstrate that true allocreadiids are not especially closely related to opecoelids. Instead, they resolve as sister to the Gorgoderidae Looss, 1899 and, thus, the Allocreadioidea is best considered synonymous with the Gorgoderoidea Looss, 1899 (see Littlewood et al., 2015). The Acanthocolpidae and Brachycladiidae are closely related and are now combined into the superfamily Brachycladioidea Odhner, 1905. The opecoelids appear to be closer to this group than to the gorgoderoids (Olson et al., 2003), but are sufficiently distinctive such that they were recognized by Littlewood and colleagues (2015) in a separate superfamily, the Opecoeloidea Ozaki, 1925. However, the establishment of Opecoeloidea is not a new concept; the separation between the Opecoelidae and Allocreadiidae was appreciated much earlier by some taxonomists, specifically Cable (1956) and Dollfus (1959).

## Life Cycles

Opecoelid life cycles, where known, usually involve 3 hosts (Figure 2). Eggs are passed with feces of the definitive host, which is always a teleost fish, and miracidia hatch from the eggs and seek and penetrate the first intermediate host, which is always a gastropod (Cribb, 2005a). Within the gastropod, the miracidium develops into a mother sporocyst which produces more sporocysts. These may be mother sporocysts themselves or may be daughter sporocysts, which produce cercariae (Cribb, 1985).

Opecoelid cercariae lack eye spots, possess a penetration stylet, and, usually, have a stumpy, cup-shaped tail. These cercariae do not swim, but crawl in a leech-like manner (Cribb, 2005a). However, one cercaria, that of *Helicometra gibsoni* Meenakshi et al., 1993, has a very long tail (Meenakshi et al., 1993). It belongs to what is potentially the most basal opecoelid lineage, the subfamily Helicometrinae, leading to intriguing speculation as to the original tail condition in the earliest opecoelids.

Opecoelid cercariae penetrate and encyst as metacercariae in a wide variety of second intermediate hosts, including crustaceans, aquatic insects, oligochaetes, echinoids, gastropods, scleractinian anthozoans, and fishes (McCoy, 1930; Meenakshi et al., 1993; Aeby, 1998; Jousson et al., 1999; Cribb, 2005a; Yoshida and Urabe, 2005; Yano and Urabe, 2017; Martin et al., 2018b). The metacercariae reach the definitive host via trophic transmission. This transmission is usually passive, however, in the case of *Polypipapiliotrema stenometra* (Pritchard, 1966) (subfamily Polypipapiliotrematinae Martin et al., 2018), infection with metacercariae increases the chance of the second intermediate host, reef-building corals of the genus *Porites*, being preyed upon by the definitive hosts, corallivorous butterflyfishes (Chaetodontidae) (Aeby, 1998; 2002). Infection of the coral polyp by the metacercaria triggers a growth response (possibly an immune response) which causes pink discoloration and abnormal growth such that the polyp may be unable to retract into its calyx (Cheng and Wong, 1974; Aeby, 1998). Thus, infected polyps are both more vulnerable and more nutritious, and this change in condition is prominently advertised to the butterflyfishes, which preferentially prey on the infected polyps (Aeby, 2002).

Facultatively progenetic life cycles, where eggs are produced and released by precocial metacercariea within the second intermediate host, have been documented for at least 9 opecoelid species belonging to 6 genera (Lefebvre and Poulin, 2005). In these species, the definitive host may be skipped. Exceptionally, in the life cycle of *Plagioporus sinitsini* Mueller, 1934, the second intermediate host, or even both the second intermediate and definitive host, may be facultatively skipped (Barger and Esch, 2000). In this species, cercariae may develop into metacercariae within the daughter sporocyst which emerges from the gastropod and is consumed directly by the definitive teleost host. However, the metacercariae may also develop into adult worms which produce eggs within the daughter sporocyst; the sporocyst emerges from the gastropod and releases miracidia ready to infect the next gastropod (Barger and Esch, 2000).

The nature of the opecoelid life cycle means that definitive teleost hosts are overwhelmingly predators or omnivores, but several opecoelid species belonging to genera in the Opecoelinae and Helicometrinae subfamilies have been reported from herbivorous perciform fishes, namely Acanthuridae (surgeonfishes), Blenniidae (blennies), Girellidae (luderick), Scaridae (parrotfishes), and Siganidae (rabbitfishes). Some opecoelids even appear to specialize in such fishes. Two species of *Choerodonicola* and 3 species of *Diplobulbus* are known only from fishes of the family Scaridae (Yamaguti, 1934; 1942; 1952; Martin et al., 2018a), and species of *Holsworthotrema* and *Scorpidotrema* (monotypic) (subfamily Stenakrinae) are known only from species of Kyphosidae (drummers) and a species of Scorpidiidae (sweep),

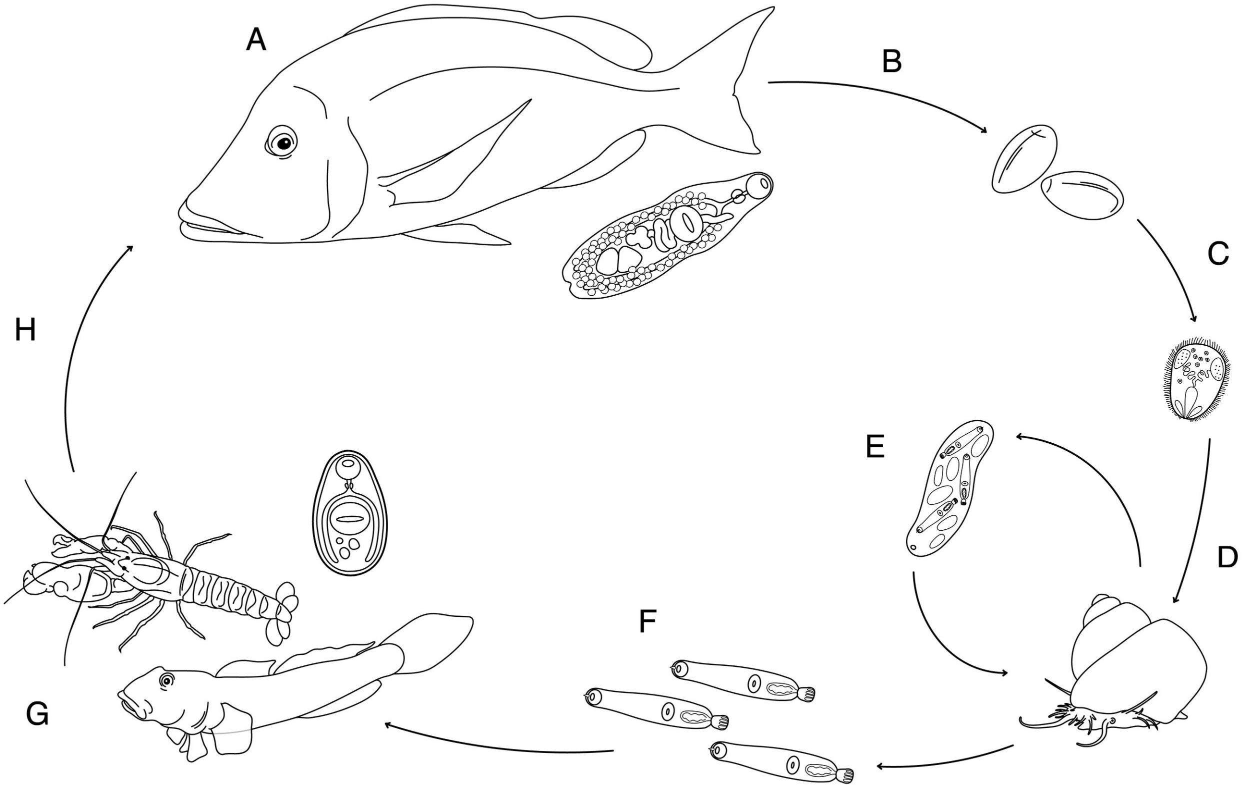

Figure 2. Generalized opecoelid life cycle. A) Adult opecoelids reside within the intestines of teleost fishes; B) Opecoelid eggs are passed to the environment in definitive host feces; C) Eggs hatch in the environment, giving rise to the ciliated miracidia larvae; D) Miracidia seek and penetrate the first intermediate host, which is always a gastropod; E) Within the gastropod, the miracidia sporocyst. Asexual reproduction produces generations of sporocysts, some of which produce cercariae; F) Cercariae emerge from the first intermediate host and seek and penetrate the second intermediate host using a stylet. Most opecoelid cercariae have a stumpy tail and do not swim but crawl; G) Various groups of invertebrates, and sometimes vertebrates, are exploited as intermediate hosts. The cercaria encysts within host tissue and develops into the metacercaria; H) Metacercariae are transmitted to the definitive host when they prey on an infected second intermediate host. If this fish is an appropriate (physiologically compatible) definitive host, the metacercariae may mature into reproductive adults. Source: S. B. Martin. License: CC BY-NC-SA 4.0.

respectively (Martin et al., 2018d). It is not known how these trematodes reach their definitive hosts. Presumably they penetrate invertebrates living among algae which are incidentally ingested by the definitive fish hosts, but it is also possible that they have secondarily adopted a 2-host life cycle with direct encystment of metacercariae onto algae or the substrate. This strategy is known for other trematode families specializing in herbivorous fishes such as the Atractotrematidae (Huston et al., 2018), Gorgocephalidae (Huston et al., 2016), Gyliauchenidae (Al-Jahdali and Hassanine, 2012), Haplosplanchnidae (see the Haplosplanchnata chapter for more information), and Microscaphidiidae (Hassanine et al., 2016). Intriguingly, the cercaria has been described for one of the species of *Choerodonicola* and, unlike most other opecoelid cercariae, it lacks a stylet, the specialized organ used to penetrate the second intermediate host (Martin et al., 2018a).

**Host Range**

The host range of opecoelids across various species of fishes is variable and a complete understanding of patterns within the family, as in many other trematode groups, is hampered by a multitude of dubious or unsubstantiated records, poor descriptions, and the persistence of many polyphyletic genera (these are genera in which species are lumped by researchers even though there is no phylogenetic/evolutionary ancestor descendant relationships among the species). However, it seems that for the most part, host range is very low, especially for species from tropical marine systems. For example, on the Great Barrier Reef, Australia, only 2 opecoelids, *Helicometra fasciata* (Rudolphi, 1819) and *Trilobovarium parvvatis* Martin et al., 2017, are reliably known from fishes belonging to more than a single family (Miller et al., 2011; Martin et al., 2017a). Compelling cases for lower specificity are more frequent among taxa exploiting freshwater, deep sea or polar fishes.

## Phylogenetics

Determination of phylogenetic affinities among opecoelid genera and the identification of major lineages within the family is an area of active study for the Opecoelidae. Since the early 1980s the organization of the Opecoelidae has been dominated by a 4-subfamily classification hypothesis established by Gibson and Bray (1982; 1984). This hypothesis is based principally on the presence versus absence of 2 features of the adult worm, a well-developed cirrus sac and a canalicular seminal receptacle. However, with increasing availability of phylogenetically informative rDNA sequence data, recent analyses have demonstrated that this classification does not adequately reflect the evolutionary history of the group (Bray et al., 2016; Fayton and Andres, 2016). Consequently, the classification of the Opecoelidae is rapidly being revised; it presently comprises 9 subfamilies (Bathycreadiinae, Helicometrinae, Opecoelinae, Opecoelininae, Opistholebetinae, Plagioporinae, Podocotylinae, Polypipapiliotrematinae, and Stenakrinae), although analyses of currently available sequence data, both published and unpublished, suggest that at about 14 subfamilies might be required.

These analyses do not suggest that the morphological characters used by Gibson and Bray (1982; 1984) are not informative at the subfamily level, but rather that these characters, as well as others of adult worms, together with consideration for the ecological and phylogenetic groups of hosts exploited must all be considered (Martin et al., 2018d). In particular, it appears that radiation of some major lineages within the family occurred following switches of the second intermediate hosts exploited. Thus, the Opecoelinae, Helicometrinae, and Podocotylinae appear to exploit only crustacean second intermediate hosts, whereas the Plagioporinae, a freshwater group, use aquatic insects and annelids, the Opistholebetinae are only known to use hard-bodied invertebrates, namely gastropods (snails) and echinoids (urchins), the Polypipapiliotrematinae are the only known trematodes to exploit scleractinian anthozoans (corals), and species of an as yet unnamed clade appear to specialize in using small fishes (Martin et al., 2018b; 2018d; 2018f). This diversity in second intermediate host groups exploited has almost certainly been an important driver for the huge richness and success of the family. However, it must be appreciated that these patterns are based on few known life cycles, especially when considered against the enormous richness of the family. Therefore, the elucidation of further life cycles will most likely prove crucial for understanding the phylogenetic organization of the Opecoelidae and interpreting the evolutionary history of lineages within the group.

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