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DIGENEA, PLAGIORCHIIDA

Monorchiata (Suborder): Two Families Separated by Salinity

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Phylum Platyhelminthes
  Class Trematoda
    Subclass Digenea
      Order Plagiorchiida
        Suborder Monorchiata

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Chapter 41

Monorchiata Olson et al., 2003 (Suborder): Two Families Separated by Salinity

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Introduction

The Monorchiata Olson et al., 2003 is a speciose suborder of digenean trematodes parasitizing fishes as adults. It contains only 1 superfamily, the Monorchioidea Odhner, 1911, which comprises the families Monorchiidae Odhner, 1911 and Lissorchiidae Magath, 1917. Most species from the 2 groups have a single testis, which separates them from many other trematode groups, and they also generally have a spinous tegument and restricted vitellaria. The Monorchiidae was established for *Monorchis monorchis* (Stossich, 1890) and presently comprises 258 species in 48 genera (Gibson and Cribb, 2010). Magath (1917) proposed the subfamily Lissorchiinae for *Lissorchis fairporti* Magath, 1917, under the family Plagiorchiidae Lühe, 1901. Poche (1926) subsequently elevated the group to family status. The Lissorchiidae comprises only 43 species in 8 genera (Bray, 2008).

Monorchiids and lissorchiids are differentiated by 6 key traits: 1) Infection of marine versus freshwater fishes; 2) oculate (with eye spots) versus non-oculate cercariae; 3) infection of bivalve versus gastropod first intermediate hosts; 4) cercariae development in sporocysts versus rediae; 5) having a median versus lateral genital pore; and 6) having a complex metraterm with a specialized terminal organ versus simple metraterm (Shimazu, 1992). Although phylogenetic analyses clearly indicate that they are sister taxa, the 2 families are so distinct that they are dealt with separately here.

Family Monorchiidae

Monorchiids infect marine bony fishes from over 70 families. They normally have a spinous tegument, complex and spined male (cirrus sac) and female (terminal organ) terminal genitalia, and restricted fields of vitelline follicles (Madhavi, 2008) (Figure 1). In many monorchiids, the female terminal organ is bipartite, comprising an unspined posterior chamber and a spined anterior tubular section. The posterior chamber usually contains a fibrous mass that has been suggested to be remnants of prostatic secretions (Dove and Cribb, 1998). The genus *Cableia* Sogandares-Bernal, 1959, is exceptional; species of this group lack the major morphological characters of the family and it may be a basal monorchiid genus. Despite the name of the family referring to a single testis, monorchiids can also have 2 or 8 testes.

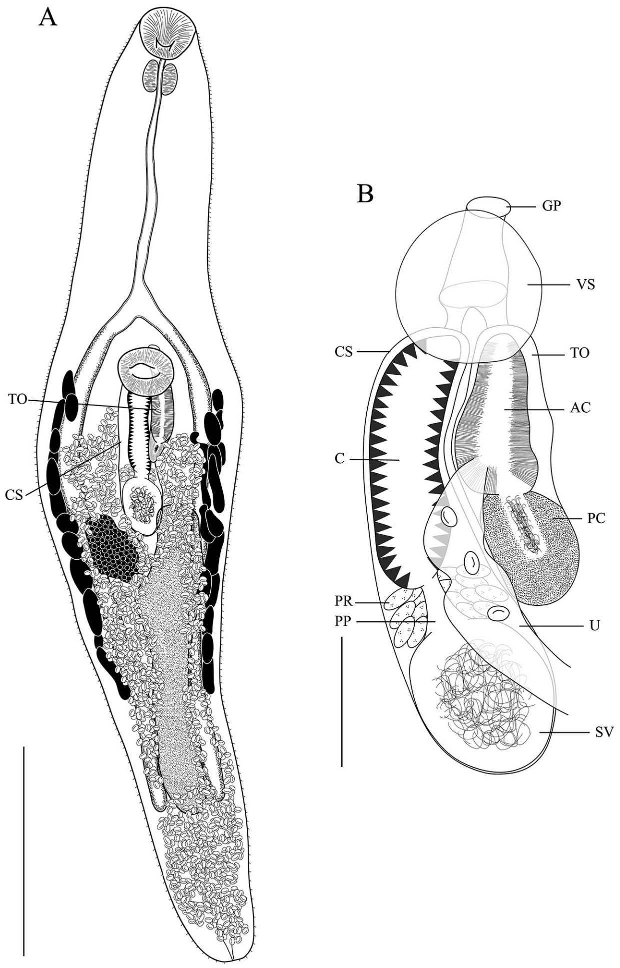

Figure 1. A typical monorchiid, *Parachrisomon delicatus* (Manter & Pritchard, 1964) Madhavi, 2008. A) Whole worm, ventral view; B) Terminal genitalia, ventral view. Abbreviations: AC: Anterior chamber; C: Cirrus; CS: Cirrus sac; GP: Genital pore; PC: Posterior chamber; PP: Pars prostatica; PR: Prostatic cells; SV: Seminal vesicle; TO: Terminal organ; U: Uterus; VS: Ventral sucker. Scale bars: A) 500 µm; B) 100 µm. Source: N. Q.-X. Wee. License: CC BY-NC-SA 4.0.

Systematics and Taxonomy

Uncertainty about which morphological features are useful in differentiating monorchiid taxa has led to issues with the systematics of the family. The composition of some large genera, such as *Lasiotocus* Looss, 1907 and *Genolopa* Linton, 1910, is doubtful, given the broad morphological variation in features such as body shape and the shape of the oral sucker among species. The need for revision of such genera and has been demonstrated by recent phylogenetic analyses (Cribb et al., 2018; Wee et al., 2018), showing that sequenced species of *Lasiotocus* are not monophyletic. Phylogenetic analyses also demonstrate the need to revise the subfamilial characterization of the family. Sequenced representatives of *Helicometroides* Yamaguti, 1934, *Hurleytrematoides* Yamaguti, 1953 and *Provitellus* Dove & Cribb, 1998, which are united in having filamented eggs (eggs with filaments on the polar parts of the egg) and as such putatively belong to the subfamily Hurleytrematinae Yamaguti, 1958, according to Madhavi (2008), are only distantly related to each other.

Life Cycles

Most monorchiids have 3-host life cycles (Figure 2). As presently known, complete monorchiid life cycles incorporate bivalves (specifically, pelecypod molluscs) as the first intermediate hosts (Cremonte et al., 2001). Mother sporocysts develop in the visceral mass of the bivalve as simple sacs. They produce daughter sporocysts, which in turn produce cercariae. The cercariae usually leave the first intermediate host in search of the second intermediate host (Gilardoni et al., 2013). Monorchiid cercariae all have a spinous tegument but otherwise are highly varied, with 4 distinct forms: 1) Fusiform body, short tail; 2) elongate body, short, bifurcated tail; 3) fusiform to elongate body, long tail; and 4) elongate body, minute tail (Figure 3). Cercariae with long tails swim in search of a second intermediate host, whereas cercariae with short tails, especially those with minute tails, crawl on the substrate or adhere to a particle, to be picked up by the next intermediate host (Stunkard, 1981a; 1981b).

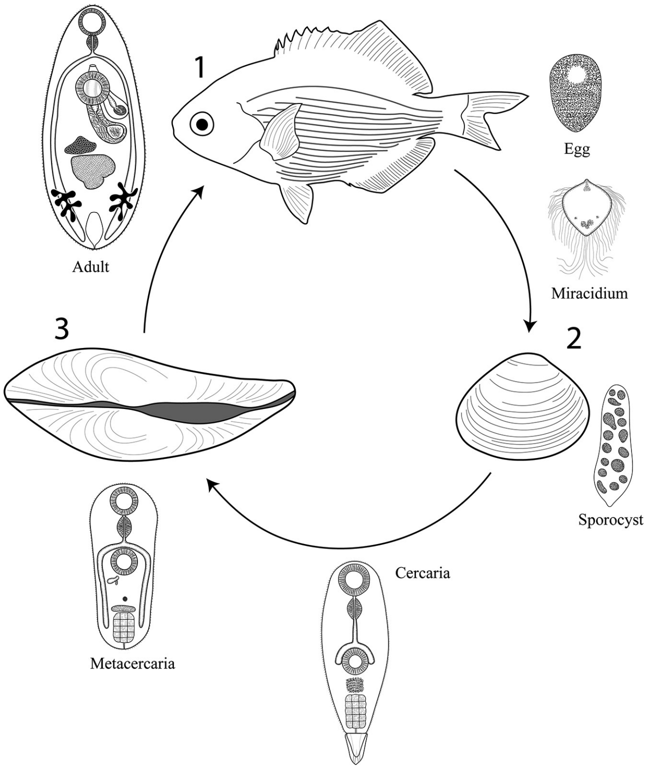

Figure 2. Life cycle of *Telolecithus pugetensis* Lloyd & Guberlet, 1932 (Monorchiidae). Source: modified from DeMartini and Pratt, 1964. License: CC BY-NC-SA 4.0.

All known second intermediate hosts are also bivalves. Once in contact with an exposed part (such as a foot, or mantle) of a bivalve, the cercariae adhere via their tails, penetrate, shed their tail, encyst in the host tissue, and await ingestion by the definitive fish host.

Although all known second intermediate hosts are bivalves, the broad range of diets of fishes that harbor monorchiids, suggesting that other groups might also be exploited. For example, species of *Hurleytrematoides* mainly infect chaetodontids (butterflyfishes), which rarely consume bivalves. Instead, chaetodontids eat a broad range of organisms such as copepods, sponges, polychaetes, and corals (Sado, 1989). Thus, their metacercariae probably infect 1 of these organisms as second intermediate hosts.

It has also been suggested and shown experimentally shown that some monorchiids might use a carnivorous invertebrate as the second intermediate host (Stunkard, 1981a; Gilardoni et al., 2013). Stunkard (1981a; 1981b) described the metacercariae of some monorchiid species as being embedded in a thick-walled cyst or jelly-like matrix that can be shed into the environment. The cyst is then suspended and floats in seawater or sinks to the bottom, awaiting ingestion by the second intermediate host.

Some monorchiids have abbreviated life cycles that include only 2 hosts. For these species, cercariae encyst and develop into metacercariae inside the sporocyst within the first intermediate host (Stunkard, 1981b; 1981a; Cremonte et al., 2001; Gilardoni et al., 2013; Bagnato et al., 2016). It has been suggested that environmental stresses drive the evolution of an abbreviated life cycle that ensures that transmission of the parasite (Poulin and Cribb, 2002; Bagnato et al., 2016).

Biogeography

The biogeographical patterns of monorchiids are poorly understood. Only 1 study (McNamara et al., 2012) has explored monorchiid distributions in detail, examining 18 species of *Hurleytrematoides* infecting 45 species of chaetodontid fishes from 6 sites across the tropical Indo-West Pacific. Seven of these species were found at just 1 locality, 11 were

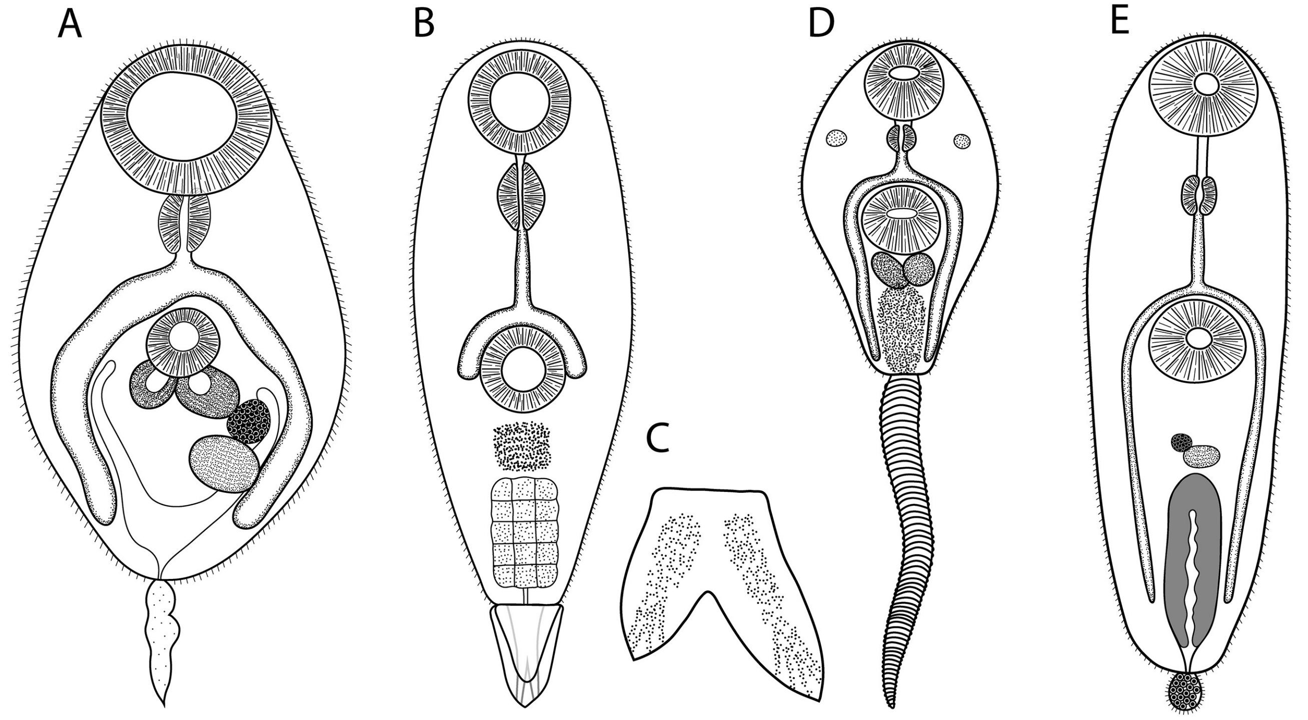

Figure 3. Monorchiid cercariae showing different body forms. A) *Monorchis parvus* Looss, 1902; B) *Telolecithus pugetensis* Lloyd & Guberlet, 1932; C) Bifurcated tail of *T. pugetensis* cercariae; D) *Paratimonia gobii* Prévot & Bartoli, 1967; E) *Proctotrema bartolii* Carballo, Laurenti & Cremonte, 2011. Source: Adapted from Bartoli et al., 2000; DeMartini and Pratt, 1964; Maillard, 1975; Gilardoni et al., 2013. License: CC BY-NC-SA 4.0.

found at multiple locations, and just 1 was found at all 6 sites. They suggested that species of monorchiids were not as widespread as their hosts due to their limited dispersal capabilities. Adult monorchiids parasitize adult fishes, which are site-attached to reefs but have long-lived pelagic larvae that enable widespread distribution. In contrast, the larval stages of monorchiids are unable to survive for an extended period outside their hosts. This discrepancy in dispersal ability probably plays a role in the unequal distribution of these parasites and their hosts.

Family Lissorchiidae

Species of Lissorchiidae infect freshwater fishes, most of which are cypriniforms (carp, loaches, minnows, and relatives). They are known from the Nearctic, Palaearctic, India, and Southeast Asia. Lissorchiids resemble monorchiids in having a spinous tegument, a spined ejaculatory duct, and restricted fields of vitelline follicles. However, lissorchiids have a laterally orientated genital pore and have a simple spined or unspined metraterm, but they lack a complex terminal organ (Bray, 2008) (Figure 4).

Systematics and Taxonomy

Magath (1917) proposed the subfamily Lissorchiinae for *Lissorchis*, stating that the group either belonged in the Plagiorchiidae Lühe, 1901, or that it required full family status. Subsequently, Poche (1926) found evidence that the Lissorchiinae does not belong to the Plagiorchiidae and raised it to the family level.

Classification within the family has been primarily based on morphology. Some species previously thought to be lissorchiids now belong to other families; for instance, species of *Anarchichotrema* Shimazu, 1973 and *Neolissorchis* Machida, 1985 are now considered to belong to the Zoogonidae. Additionally, some lissorchiid genera, such as *Asymphylodora* Looss, 1899 and *Palaeorchis* Szidat, 1943, generally resemble monorchiids, which hindered their recognition as lissorchiids. Finally, the validity of some lissorchiid species such as *Tigrotrema gwailiorense* Bhadauria & Dandotia, 1984 are doubtful as their morphological characters are not typical for the family (Bray, 2008). It appears that molecular sequencing will be necessary to resolve the classification within the family. However, few sequences are currently available.

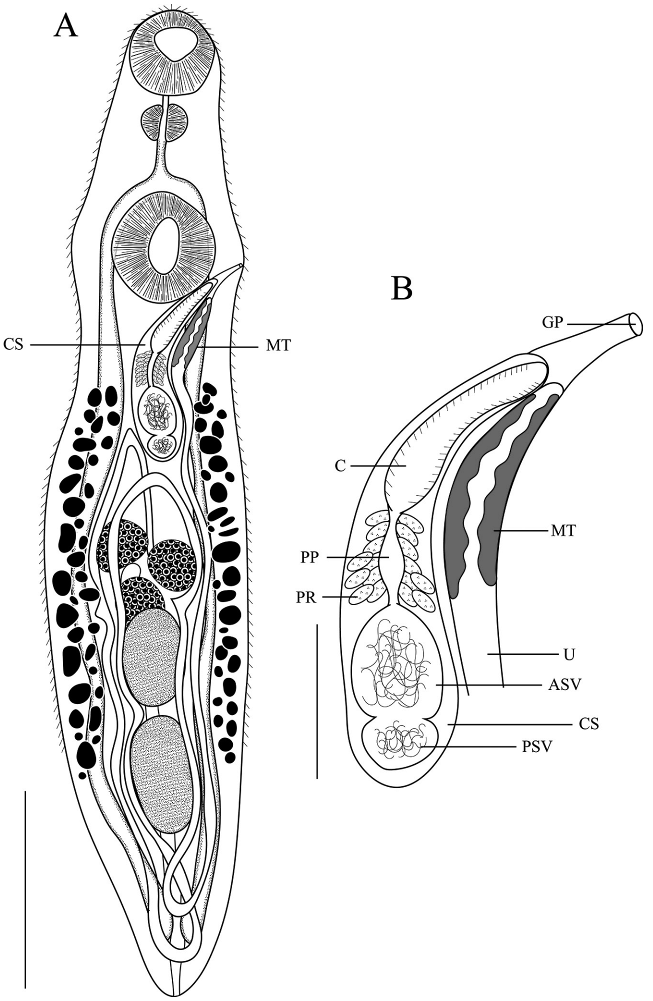

Figure 4. A typical lissorchiid, *Lissorchis hypentelii* (Fischthal, 1942). A) Whole worm, ventral view; B) Terminal genitalia, ventral view. Abbreviations: ASV: Anterior seminal vesicle; C: Cirrus; CS: Cirrus sac; GP: Genital pore; MT: Metraterm; PP: Pars prostatica; PR: Prostatic cells; PSV: Posterior seminal vesicle; U: Uterus. Scale bars: A) 400 µm; B) 200 µm. Source: Adapted from Fischthal, 1942. License: CC BY-NC-SA 4.0.

Life Cycles

Lissorchiids have a 3-host life cycle (Figure 5). To date, in 6 studies complete life cycles have been elucidated, all of which report gastropods as the first intermediate hosts (Wallace, 1941; Stunkard, 1959; Schell, 1973; Macy and English, 1975; Našincová and Scholz, 1994; Besprozvannykh et al., 2012).

Mother sporocysts in the first intermediate host produce rediae in which cercariae develop. Gastropods, insect larvae, planarians, oligochaetes, and fishes have all been reported as second intermediate hosts. The cercariae penetrate the second intermediate host and encyst in thin-walled membranes. Similar to the Monorchiidae, lissorchiid cercariae have a spinous

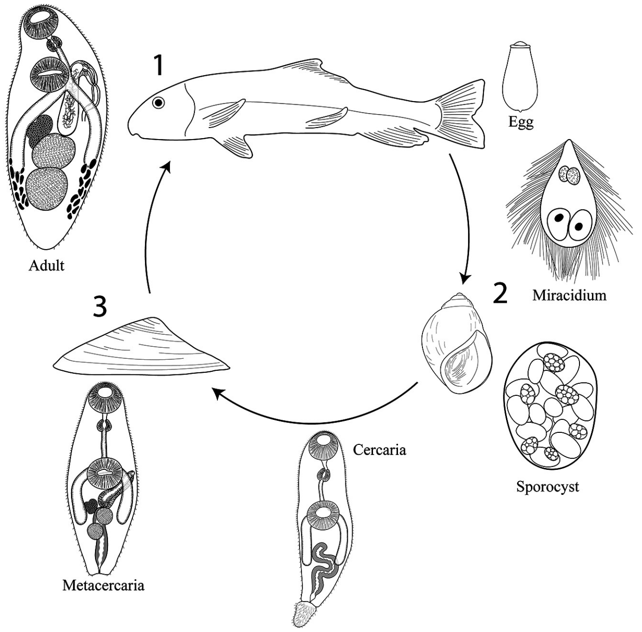

Figure 5. Life cycle of *Neopaleorchis catostomi* Schell, 1973 (Lissorchiidae). Source: Adapted from Schell, 1973. License: CC BY-NC-SA 4.0.

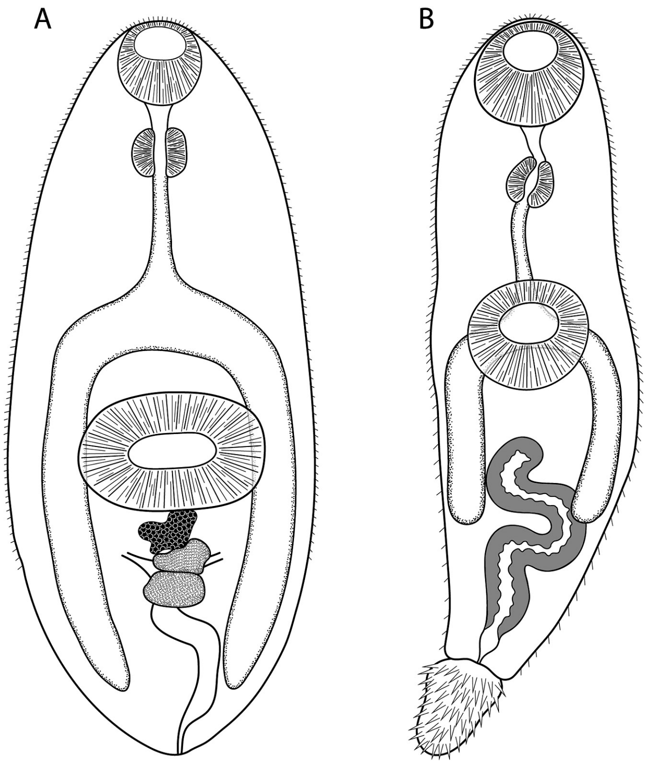

Figure 6. Lissorchiid cercariae showing different body shapes. A) *Lissorchis mutabile* (Cort, 1918); B) *Neopaleorchis catostomi* Schell, 1973. Source: Adapted from Wallace, 1941; Schell, 1973. License: CC BY-NC-SA 4.0.

tegument and also exhibit variation in overall tail morphology; some lack a tail completely, whereas others have a short, spined and knobbed tail (Figure 6).

Some lissorchiids have a truncated life cycle. *Palaeorchis problematicus* (Macy and Berntzen, 1970) and *Asymphylodora tincae* (Modeer, 1970) have a 2-host life cycle, infecting only a freshwater snail and a cyprinid (Macy and English, 1975; Našincová and Scholz, 1994). Experimental infections of *A. tincae* showed that cercariae harbored by gastropods that were fed to fishes developed into adults without a metacercarial stage (Našincová and Scholz, 1994).

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