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DIGENEA, PLAGIORCHIIDA

Haplosplanchnata (Suborder): Two Hosts with Half the Guts

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Phylum Platyhelminthes
  Class Trematoda
    Subclass Digenea
      Order Plagiorchiida
        Suborder Haplosplanchnata

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Chapter 39

Haplosplanchnata Olson et al., 2003 (Suborder): Two Hosts with Half the Guts

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Introduction

The suborder Haplosplanchnata Olson et al., 2003 represents a small, but distinct lineage within the Plagiorchiida. The suborder includes a single superfamily and family, the Haplosplanchnoidea Poche, 1925 and Haplosplanchnidae Poche, 1926, which encompass 9 genera and 59 species (Cribb, 2010).

Haplosplanchnids are intestinal parasites, mostly of marine herbivorous (grazing, scraping, and excavating) fishes, although a few species occur in predatory fishes (Nahhas, 1997; Huston et al., 2017; 2018a). As with most trematodes of wildlife, haplosplanchnids are not considered of medical, veterinary, or economic importance. For those interested in the evolution of the Digenea, however, haplosplanchnids present some intriguing morphological and life cycle adaptations. Some of these, such as a derived 2-host life cycle, add support to emerging evolutionary paradigms. Others, such as the specialized suckers possessed by some species, present new questions.

Identifying Haplosplanchnata

Haplosplanchnids gained their name from the type genus *Haplosplanchnus* Looss, 1902. The name means single-gut and is derived from Ancient Greek **haplo** (= single) and **splanch** (= intestine). The presence of a single intestinal cecum is the major feature uniting haplosplanchnids. All but 2 of the species currently recognized lack a cirrus sac and possess only a single testis. Species of 2 monotypic genera are problematic: *Prohaplosplanchnus diorchis* Tang & Lin, 1978 possesses 2 testes and *Parahaplosplanchnus cirrusaci* (Lü, 1995) possesses a cirrus sac. Neither has been evaluated with molecular data and it is likely that they will be found to belong elsewhere in the digenean phylogeny when such data become available. If these 2 species are ignored, haplosplanchnids can be recognized readily by the single intestinal cecum, lack of a cirrus sac, and a single testis. Other than in these features, haplosplanchnids have a typical digenean body plan with an oral sucker, ventral sucker, and a single ovary. In some groups the oral or ventral suckers may be specialized. Specialized glands are often visible in the ventral portion of the oral sucker, the so-called salivary glands. The vitelline follicles are highly restricted in some species, although in many they are profusely developed and often obscure the internal anatomy. Eggs are unembryonated in most species, but embryonated in utero in some.

Haplosplanchnid genera are readily differentiated morphologically (for example, Figure 1, and see the key in Huston et al., 2018a). Conversely, species-level identifications are far more difficult because of the simplified internal anatomy of most species. Thus, molecular data have become increasingly important for the taxonomy of the group (Huston et al., 2017; 2018a).

Haplosplanchnata in Relation to Other Organisms

Two haplosplanchnid life cycles have been elucidated, that of *Schikhobalotrema acutum* (Linton, 1910) and *Haplosplanchnus pachysomus* (Eysenhardt, 1829) (Cable, 1954; Fares and Maillard, 1975). In both, cercariae emerge from the intermediate gastropod host (families Cerithiidae and Hydrobiidae for *S. acutum* and *H. pachysomus*, respectively) and encyst as metacercariae on vegetation. In light of the derived position of the haplosplanchnids in the overall phylogeny of the Digenea (Olson et al., 2003; Littlewood et al., 2015), this form of metacercarial encystment suggests there was no second intermediate host in the evolution of the haplosplanchnid lineage (Cribb et al., 2003). External encystment has been demonstrated in multiple digenean lineages which exploit herbivorous fishes as definitive hosts, for example, the Atractotrematidae, Gorgocephalidae, Gyliauchenidae, and Microscaphidiidae (Al-Jahdali and Hassanine, 2012; Hassanine et al., 2016; Huston et al., 2016; 2018b).

Some species of the genus *Schikhobalotrema* infect predatory needlefishes (Beloniformes: Belonidae) (Nahhas et al., 1997; Huston et al., 2017). Although this might suggest that some haplosplanchnids have 3-host life cycles, a 2-host life cycle seems more likely, and can be inferred from the evolutionary relationships of their beloniform hosts. Some species of *Schikhobalotrema* are also known from the related halfbeaks (Beloniformes: Hyporhamphidae) (Nahhas et al., 1997). Halfbeaks are surface feeding omnivores which incorporate large amount of plant matter in their diet, thus representing a typical host group for haplosplanchnids. Cable (1954) elucidated the life cycle of *S. acutum* and found adults

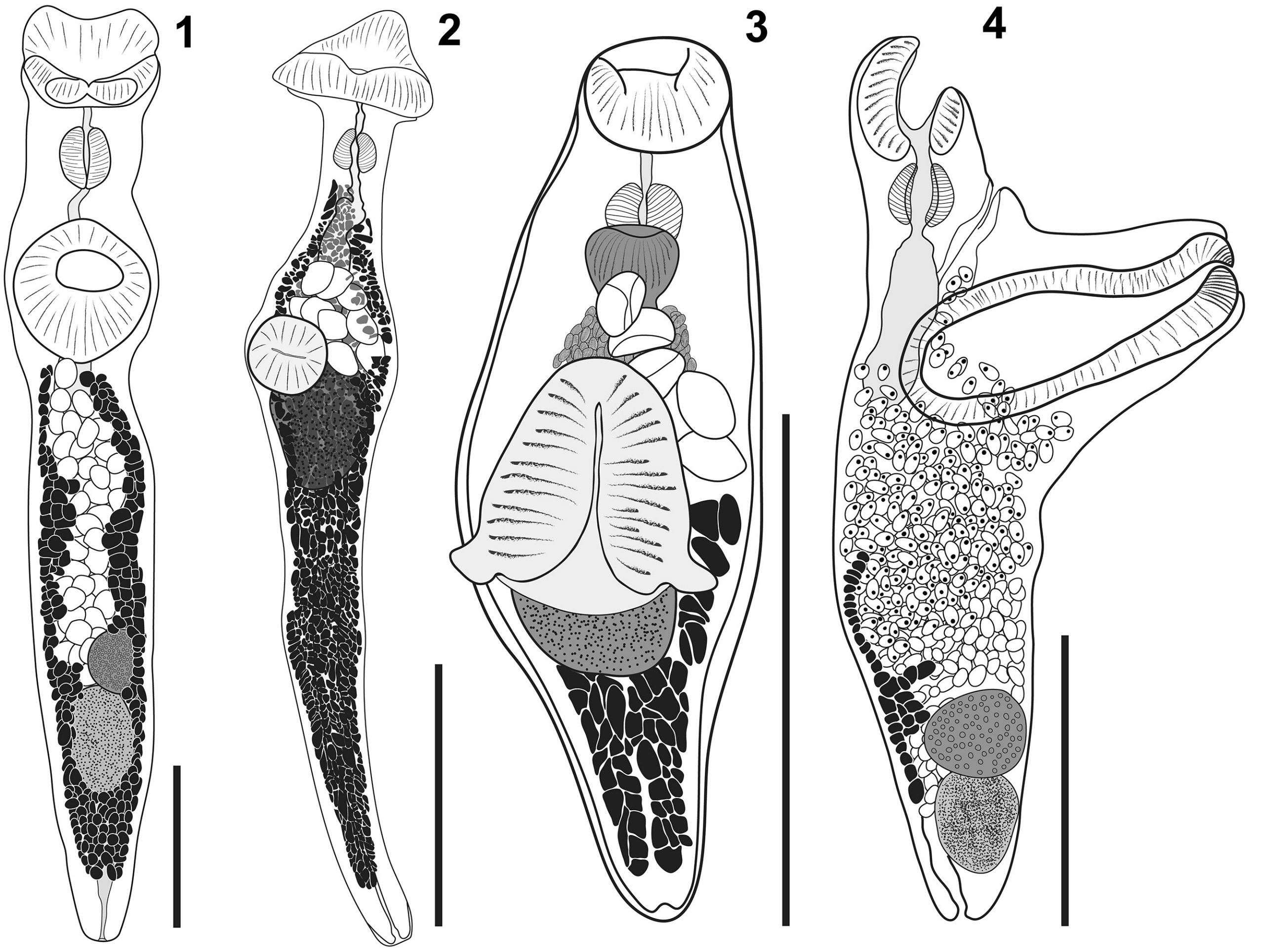

Figure 1. Representative species of the Haplosplanchnata. 1*) Hymenocotta mulli*. 2) *Trigonocephalotrema hipparchi*. 3) *Schikhobalotrema huffmani*. 4) *Haplosplanchnus pachysomus*. The single caecum is obscured in all except for *H. pachysomus*; this is frequently the case because of the densely packed vitellarium. Scale bars = 500 µm. Source: D. C. Huston. License: CC BY-NC-SA 4.0.

in both halfbeaks and needlefishes. Perhaps the haplosplanchnid species which have colonized belonids were parasites of halfbeaks which host-switched into the related belonids. Belonids likely consume metacercariae on vegetation incidentally when hunting, or perhaps *S. acutum* cercariae encyst on hard-bodied invertebrates on which the belonids feed. In either case, it seems likely that these species of *Schikhobalotrema* have 2-host life cycles, as do typical haplosplanchnids.

Haplosplanchnata in Relation to Others in Their Group

The evolutionary relationships between the haplosplanchnids and other lineages of the Plagiorchiida is still somewhat unclear. The family Haplosplanchnidae has been placed at times in either the Echinostomatoidae or Haploporoidea (see Madhavi, 2005). The molecular phylogenetic study of Olson et al. (2003) did not fully resolve the placement of the haplosplanchnids, but did demonstrate the lineage as distinct, warranting the erection of the Haplosplanchnata. Based on Olson et al. (2003) and other molecular phylogenies of the Digenea (for example, Littlewood et al., 2015), the haplosplanchnid lineage has the greatest affinity with the Paramphistomoidea Fischoeder, 1901, Pronocephaloidea Looss, 1899, and Echinostomatoidea Looss, 1902. It is significant that, like for the haplosplanchnids, cercariae of the Pronocephaloidea and Paramphistomoidea reach their definitive hosts by encysting on vegetation as metacercariae.

Most Important Groups

The most important haplosplanchnid genera are probably *Haplosplanchnus* and *Schikhobalotrema*, though important insights are to be gained from some of the smaller groups. Species of *Haplosplanchnus* are globally distributed and their definitive hosts are freshwater, brackish, and marine mullet (Mugilidae). Species of *Haplosplanchnus* have robust ventral suckers (often exceptionally so), which may be cannulated (for example, Figure 1.4). The function of such suckers

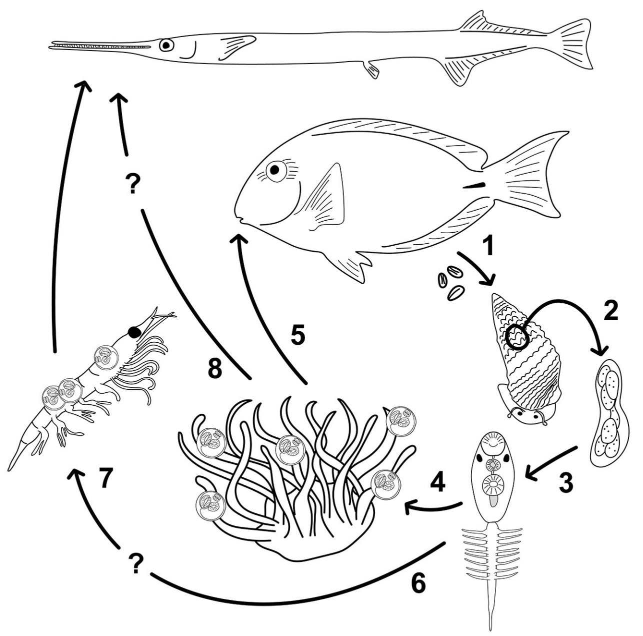

Figure 2. The haplosplanchnid life cycle. 1) Adult trematodes lay eggs, which pass into the environment with the host's waste. 2) Miracidium hatches from egg, infects snail intermediate host. Miracidium transforms to mother sporocyst; mother sporocyst produces daughter sporocysts. 3). Sporocysts produce cercariae; cercariae emerge from snail. 4) Cercariae encyst on vegetation as metacercariae. 5) Vegetation with metacercariae consumed by definitive host; metacercariae mature into adults. 6) It is not known how metacercariae reach predatory needlefish hosts, it is possible that cercariae 7) Encyst on the exterior of hard-bodied prey, or 8) Needlefishes consume plant matter incidentally, or purposefully. Source: D. C. Huston. License: CC BY-NC-SA 4.0.

is unclear. The eggs embryonate to miracidia with prominent eye spots *in utero*. The adaptive value of *in utero* embryonation is not known. The embryonated eggs in species of *Haplosplanchnus* form part of an unexplained pattern where multiple unrelated trematode lineages have embryonated eggs in species that parasitize mullets, and unembryonated eggs in species parasitizing other fish hosts.

Schikhobalotrema is the most species-rich genus in the Haplosplanchnidae. The most common host groups are the parrotfishes (Scaridae), surgeonfishes (Acanthuridae), and mullets (Mugilidae). Species parasitizing these fishes have unspecialized oral and ventral suckers. The species that parasitize predatory belonids, however (as discussed above), have unusual lateral lobes extending from the posterior part of their ventral sucker, and the ventral sucker has a longitudinal slit aperture. The function of this strange ventral sucker is unknown, but perhaps it is an adaptation for life in the very short gut of the belonid host.

Species of the genera *Discocephalotrema* Machida, 1993, *Hymenocotta* Manter, 1961, and *Trigonocephalotrema* Huston, Cutmore & Cribb, 2018 are all interesting with respect to their oral suckers. In species of these 3 genera the ventral suckers are unspecialized, but the oral suckers form specialized lobed or flattened plates, with small oral openings. Again, the adaptive significance of these specializations is not known. Although molecular data are not available for *Discocephalotrema*, molecular phylogenetic analyses of the Haplosplanchnidae (Huston et al., 2017; 2018a), support *Hymenocotta* as basal, and *Trigonocephalotrema* as sister to *Schikhobalotrema* + *Haplosplanchnus*. Thus, specialized and unspecialized suckers are distributed throughout the haplosplanchnid phylogeny. The molecular data available for the Haplosplanchnata are not yet comprehensive enough to make deep evolutionary inferences into the origin of sucker specialization in this group. However, it seems that the standard sucker template has been modified repeatedly, allowing for the exploitation of a wide variety of hosts and niches.

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