

Digenean life cycle truncation has enabled the opportunistic exploitation of herbivorous fishes

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Abstract

New, well-known and predicted life cycles for trematodes of the Haploporoidea (Haploporidae and Emprostiotrematidae) and three families of the Lepocreadioidea (Enenteridae, Gorgocephalidae, Gyliauchenidae) involve encystment of the metacercaria in the open (usually on vegetation) followed by ingestion by a range of herbivorous or detritivorous fishes. These life cycles appear among relatively highly derived plagiorchiidan trematodes in which three-host life cycles incorporating an animal second intermediate host are dominant. We hypothesise that the two-host life cycles in the Haploporoidea and Lepocreadioidea arose by secondary truncation of a three-host cycle; the second intermediate host was lost in favour of encystment in the open. Modification of a three-host life cycle effective for the infection of carnivores is consistent with the understanding that fishes arose as carnivores and that multiple lineages have secondarily become detritivores and herbivores. Four of the five trematode families involved infect fishes relating to multiple orders, suggesting a complex history of host-switching. In contrast, the Gorgocephalidae, the smallest of the families, has been found only in a single family, Kyphosidae. The timing of the evolutionary events leading to this putative life cycle truncation is yet to be deduced, but the rich developing understanding of the history of the fishes creates a strong template for future analysis.

Introduction

The Digenea have a vast array of forms of life cycles, including variation in the number of sequential hosts ranging from just one (rarely, for example, Jamieson 1966) to at least four (e.g., Louvard *et al.* 2024). Inference of the evolutionary history of the derivation of these differences is partly enabled by consideration of their distribution on the phylogeny of the Trematoda (Cribb *et al.* 2003). In this context, the sister group to the Digenea, the Aspidogastrea, is arguably not reliably informative. Unlike digeneans, aspidogastreans lack asexual reproduction, and their juveniles are typically unencysted forms essentially on the external surfaces of their intermediate hosts. Within the Digenea, a basal dichotomy is recognised between the two orders, the Diplostomida and the Plagiorchiida. The Diplostomida are enigmatic in intermediate host usage in that more basal taxa typically have three-host life cycles, whereas the blood fluke (Schistosomatoidea), which have two-host-cycles (except for the Clinostomidae), are relatively derived. If ancestral diplostomidans had two-host life cycles, there is now no direct evidence of them. In contrast, the Plagiorchiida has many taxa with two-host cycles including the two most basal, the Bivesiculoidea and the Transverstromatoidea. It seems logical that two-host life cycles preceded three-host life cycles in the evolution of the Digenea, and that view was supported by the interpretation of the topology of the plagiorchiidan phylogeny by Cribb *et al.* (2003).

One of the possibly plesiomorphic digenean two-host life cycles involves the cercaria emerging from the molluscan first intermediate host to be eaten directly by the definitive host (Cribb *et al.* 2003). This cycle, and easily envisaged adaptations thereupon, can be seen in basal lineages of the order Plagiorchiida, such as for at least some of the Bivesiculoidea, Azygioidea, and Gymnophalloidea (Figure 1). Pearson (1972) argued that the next important life cycle innovation may have been external encystment of the cercaria. The benefits of a two-host life cycle in which metacercariae encyst externally in the environment, as a simple extension of the plesiomorphic condition that enhances longevity of infective stages outside the first intermediate host, seems reasonably straightforward (Pearson 1972). Such life cycles are used universally by species of the relatively basal superfamilies Haplospinoidea, Paramphistomoidea, and Pronocephaloidea (see Cribb *et al.* 2020; Huston *et al.* 2018; Jones 2005). External encystment in these lineages was made possible by the acquisition of cystogenous glands, which secrete the material which forms the metacercarial cyst wall (Galaktionov and Dobrovolskij 2003). Cystogenous glands are not known from species of the basal Plagiorchiida superfamilies Azygioidea, Hemiuroidea, and Heronimoidea (Cribb *et al.* 2003) and appear to have been acquired first by the ancestor of the remaining lineages of the Plagiorchiida (Figure 1). These glands are well developed in the

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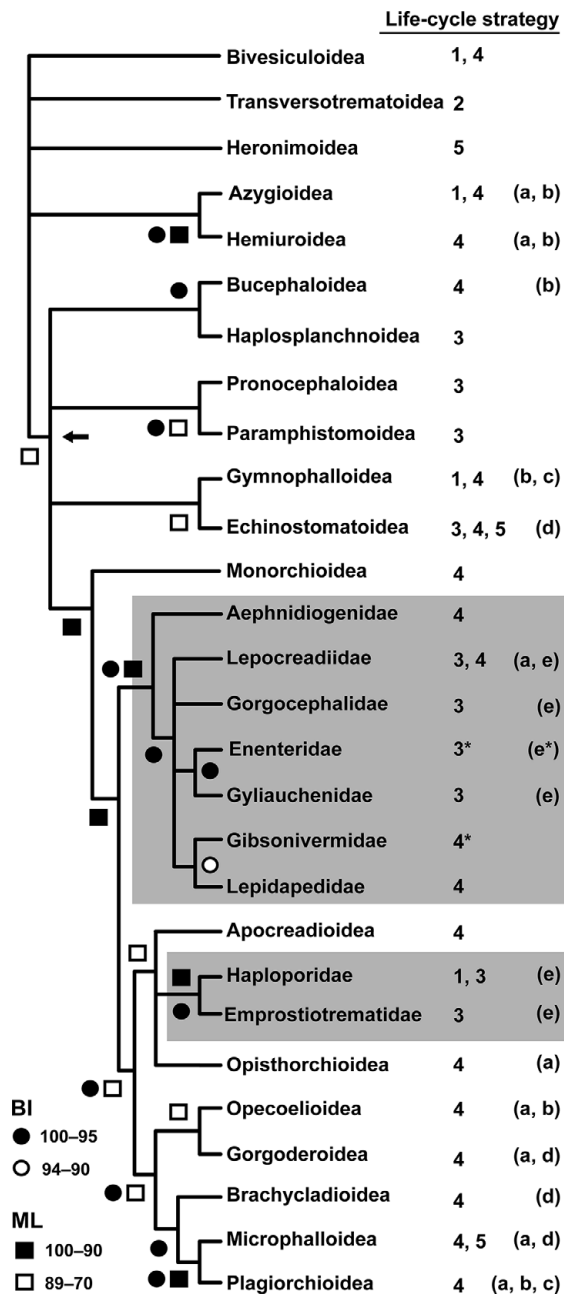


Figure 1. Generalized phylogeny and life-strategies in the Plagiorchiida. Overall phylogeny follows the tree based on the large subunit ribosomal gene (28S rDNA) from Perez-Ponce de Leon and Hernandez-Mena (2019). Expanded section for the Lepocreadiidae follows Bray *et al.* (2023). Bayesian inference (BI) posterior probabilities (pp) for nodes represented by circles, maximum likelihood (ML) bootstrap support (bs) represented by squares. Support values less than 0.90 (pp) and 70 (bs) not shown. The superfamilies Haploporoidea and Lepocreadiidae have been expanded to family level and are highlighted in grey. The arrow indicates the probable origin of cystogenous glands in the Plagiorchiida. Common life cycle strategies for each lineage (numbers) and truncation patterns (letters in parentheses) follow Cribb *et al.* (2003) and Poulin and Cribb (2002), respectively, but have been simplified and are updated with life cycle data elucidated subsequently to those studies. Life cycle strategy numbering: 1, cercaria eaten by definitive host; 2, cercariae attaches directly to definitive host; 3, cercariae encysts as metacercaria in the environment; 4, cercaria forms metacercaria within second intermediate host; 5, cercaria remains in first intermediate host. Truncation pattern lettering: a, progenesis in second intermediate host; b, sexual adult develops in first intermediate host; c, second intermediate host used as definitive host; d, first intermediate host used as second intermediate host. e, second intermediate host dropped due to relaxed selection. An asterisk (*) indicates a presumed pattern for select taxa for which a life cycle has yet to be elucidated.

externally encysting Haplospalchnoidea, Paramphistomoidea, and Pronoccephaloidea, and are also present in the Bucephaloidea (Cribb *et al.* 2003; Galaktionov and Dobrovolskij 2003). Although cystogenous glands are often reduced or absent in lineages of the Plagiorchiida which utilize second intermediate hosts, they are still present in at least some representatives of each remaining superfamily (with the notable exception of the Gymnophalloidea) including highly derived lineages such as the Gorgoderoidae and Plagiorchioidea (Cribb *et al.* 2003; Galaktionov and Dobrovolskij 2003).

The transition from a two-host life cycle to a three-host life cycle occurs when cercariae infect (and often but not always encyst on or in) a second intermediate host in which they form a metacercaria. Such three-host cycles appear within the Hemiurioidea, Bucephaloidea, Echinostomatoidea, Gymnophalloidea, and most more derived taxa. [A grey area of life cycle classification is noticeable for some pronoccephaloids for which metacercariae encyst on the outside of prey animals (especially gastropods) but with no evident host specialisation. Whether this should be considered a two- or a three-host cycle is moot and is considered further below.]

The independent evolutionary appearance of three-host cycles can arguably be recognised within at least the Azygioidea, the Gymnophalloidea, and the Echinostomatoidea, all of which have both two- and three-host life cycles (Pearson 1972; Tkach *et al.* 2016). The advantages of a metacercarial stage within a second intermediate host are illustrated by the fact that this strategy has been inferred to have been adopted independently by multiple digenean lineages (Cribb *et al.* 2003) and that second intermediate hosts, and cercariae which feature specialised penetration structures, are relatively ubiquitous in the more derived lineages of the Plagiorchiida (Figure 1). However, despite the apparent advantages of a three-host life cycle, two-host life cycles appear sporadically in derived parts of the Plagiorchiida, principally in the Haploporoidea and the Lepocreadiidae, where three-host life cycles should be expected based on the phylogenetic topology of the order. Such examples are here interpreted as having arisen by a process known as life cycle truncation, where a host from an original multi-host life cycle is omitted.

Life cycle truncation

The landmark review by Poulin and Cribb (2002) identified five forms of truncated life cycles. In brief, these are

- 1) elimination of the definitive host through adoption of proge-netic development in the second intermediate host;
- 2) elimination of the second intermediate host by the cercariae not leaving the molluscan first intermediate host so that the digenean uses this host as both the first and second intermedi-ate host;
- 3) elimination of the second intermediate host by the same vertebrate acting as both the second intermediate and definit-ive host;
- 4) elimination of the definitive host (and possibly second inter-mediate host) by adult worms maturing within the intramol-luscan stages; and
- 5) **partial** elimination of the definitive host by sporocysts pro-ducting miracidia directly.

Poulin and Cribb (2002) detailed five hypotheses to explain how truncated life cycles may have been derived.

- The ‘environmental instability hypothesis’ proposes that, for digeneans occurring in ephemeral habitats, such as streams which may dry during summers, larvae may become isolated in small pools without access to definitive hosts, and thus, there will be selective pressure for facultative progenesis.
- The ‘rare or missing host hypothesis’ also centres around periodic unavailability of the vertebrate definitive host, such as digenean species which utilize migratory shore birds. In such cases, there would be selective pressure to complete a life cycle without these hosts.
- The ‘developmental time hypothesis’ suggests that some digenean species may have a genetic clock which prompts them to develop to maturity if they have not encountered an appropriate definitive host after a certain period. This would again be related to a lack of a definitive host, but the trigger would be temporal.
- The ‘cannibalism hypothesis’ seeks primarily to explain how truncated life cycles of some digeneans which infect amphibians were derived; the metacercariae of some digenean species encyst in the skin of frogs which are then eaten when the frog later sheds its skin and consumes it. As many frogs are cannibalistic and consume tadpoles, the hypothesis proposes that the need for a predation event was dropped in the truncated version of these digenean life cycles.
- Lastly, the ‘latitudinal gradient hypothesis’ proposes that shorter life cycles allow some digenean species to move into colder waters at higher latitudes, reducing dependence on certain kinds of hosts. Some support for this hypothesis can be found in species of digeneans occurring in polar regions which appear to mostly lack free-swimming cercarial stages, probably as a response to seasonal freezing of coastal waters.

Poulin and Cribb (2002) summarised reports of life cycle truncation for representatives of 32 digenean families. Overwhelmingly, these related to relatively small numbers of taxa from families that typically have more hosts in their life cycles. The metacercaria of the aepnidiogenid *Stegodexame anguillae* is progenetic (Herrmann and Poulin 2012), whereas that of *S. callista* is not (Watson 1984); the metacercaria of bucephalid *Rhipidocotyle johnstonei* is progenetic (Pulsford and Matthews 1984), whereas those of *R. transversale* and *R. lintoni* are not (Stunkard 1976). Thus, these truncated life cycles can be interpreted as having arisen as relatively isolated and recent phenomena that have not been associated with major radiations. In contrast, the Cyclocoelidae, Eucotyidae, and three blood fluke families were interpreted as having truncated life cycles for the entire family. In the case of the Cyclocoelidae and Eucotyidae, the truncation is in the form of cercariae forming metacercariae within the first gastropod intermediate host which is then eaten by the definitive host, eliminating the second intermediate host (Assis *et al.* 2021; Assis and Pinto 2023; Kingston 1965; Timon-David 1955). For the blood fluke families, the life cycle was interpreted as representing progenesis in the second intermediate host. That interpretation is open to challenge (see Cribb *et al.* 2003); it is possible that the cycle is plesiomorphically two-host. However, that issue does not impinge on the hypothesis proposed here which is that further substantial taxon-wide life cycle truncation in the Digenea is presently not recognised as such.

A new hypothesis for life cycle truncation

In the years since the study of Poulin and Cribb (2002), refinements to the digenean phylogeny (e.g., Littlewood *et al.* 2015; Olson *et al.*

2003; Pérez-Ponce de León and Hernández-Mena 2019) and the elucidation of new digenean life cycles (Al-Jahdali and Hassanine 2012; Huston *et al.* 2016, 2018) permit the proposal of an additional hypothesis by which digenean life cycles became truncated. We hypothesise the following:

Life cycles in multiple digenean lineages have been truncated (in evolutionary terms) through the loss of an ancestral second intermediate host as the definitive hosts became herbivores and detritivores.

In essence, we argue that as multiple lineages of fishes adopted plants and detritus as their diet, digeneans with three-host life cycles involving encystment of metacercariae in a second intermediate host discarded the second intermediate host in favour of encystment directly on the (usually plant) food of the definitive host.

This hypothesis differs from previously proposed mechanisms which centre around a lack or limitation of available hosts, leading to selective pressure for life cycle strategies effective in the absence of these hosts. The new mechanism of life cycle truncation acts differently and can be interpreted as a response to a new opportunity. Although all hosts are present, the selective pressure (or advantage) for a digenean to use a second intermediate host for trophic transmission is ‘relaxed’ (or disappears). Because herbivorous hosts will consume infective digenean metacercariae attached to food incidentally during grazing and are no longer actively seeking prey, there is no need (or value) for the digenean to use predation to reach the definitive host. Predation will be increasingly ineffectual for transmission as herbivorous or detritivorous diets becomes increasingly obligate. Our hypothesis shares the omission of a predation event for trophic transmission with the ‘cannibalism hypothesis’; herbivorous hosts incidentally consume infective digenean metacercariae attached to food during grazing. Our new hypothesis differs from the ‘cannibalism hypothesis’ in that the latter still includes encystment of metacercariae within tissue; the new hypothesis postulates a reversal from a derived three-host life cycle to a two-host life cycle in which metacercariae encyst outside a host.

We propose this hypothesis based primarily on our understanding of the life cycles of digeneans occurring in the gastrointestinal tracts of marine Indo-west Pacific herbivorous and detritivorous fishes. Herbivorous fishes in this system comprise a multi-taxon guild (especially of Acanthuridae, Kyphosidae, Mugilidae, scarine Labridae, and Siganidae), divided into multiple functional types which feed on one or more algal reef elements – for example, macroalgae, epilithic algal turfs, algal mats, detritus, and associated micro- and macro-organisms (Green and Bellwood 2009). Browsers feed primarily on macroalgae, and grazers feed on epilithic algae and algal mats, as well as detrital aggregates. Scrapers closely crop algae growing on hard reef substratum, whereas excavators remove and consume large chunks of hard reef substrate (Green and Bellwood 2009). We see clear evidence for life cycle truncation in two superfamilies, the Haploporoidea and the Lepocreadioidea, which are nested within the more derived lineages of the Plagiorchiida. Species from these superfamilies occur in multiple herbivorous fish families across all the functional feeding types.

Evidence from phylogeny

Our hypothesis depends on the accuracy of the phylogenetic hypotheses for the Digenea presented by the most recent and comprehensive study, that of Pérez-Ponce de León and Hernández-Mena (2019). We also rely on more focussed studies of the

Lepocreadioidea by Bray *et al.* (2023). We are cognisant that future phylogenomic studies (incorporating more taxa or improved data) may alter the positions of some of the taxa considered here, and thus, conceivably, our inferences may have less support or be invalidated.

The superfamily Haploporoidea is comprised of just two families, the Emprostiometridae and Haploporidae, species of which have radiated primarily in herbivorous fishes (Huston *et al.* 2024; Overstreet and Curran 2005a, b). The relatively derived position of the Haploporoidea in the Plagiorchiida (Figure 1), and the three-host cycles known for closely related lineages (especially Apocreadioidea and Opisthorchioidea), suggest that the ancestry of the haploporoids involved a life cycle with three hosts. [The alternative interpretation requires repeated, non-parsimonious adoption of three-host cycles in derived digeneans.] Numerous life cycles are known for the family Haploporidae (Cable 1962; Cable and Isseroff 1969; Ditrich *et al.* 1997; Fares and Maillard 1974; Graefe 1970; Martin 1973; Martorelli 1986; Shameem and Madhavi 1991; Szidat 1970; Szidat 1973; Tang and Lin 1979), and just one is known for its much smaller sister family, the Emprostiometridae (Huston *et al.* 2018). In all known haploporid life cycles, cercariae encyst in the environment, although Martorelli (1986) also reported direct ingestion of cercariae. The single life cycle known for the Emprostiometridae also has cercariae which encyst in the environment. These life cycles are consistent with the inference that a two-host life cycle, where cercariae encyst in the environment as metacercariae, is universal for the superfamily. Thus, we infer that the ancestral haploporoid modified a three-host life cycle to one with two-hosts in which cercariae encysted on algae and/or other substrates in the environment. The life cycles of Haploporidae and Emprostiometridae make sense in the context that their hosts (species of Acanthuridae, Blenniidae, Chanidae, Cichlidae, Kyphosidae, Labridae (subfamily) Scarinae, Mugilidae, Scatophagidae, and Siganidae) are overwhelmingly heavily or partly herbivorous or detritivorous.

The superfamily Lepocreadioidea is represented by seven families (Aepnidiogenidae, Enenteridae, Gibsonivermidae, Gorgocephalidae, Gyliuchenidae, Lepidapedidae, and Lepocreadiidae) and resolves in a relatively derived position in the plagiorchiidan phylogeny, nested among superfamilies that overwhelmingly have three-host life cycles (Figure 1). Of the seven families, the Aepnidiogenidae, Lepocreadiidae, and Lepidapedidae have three-host life cycles involving a wide range of invertebrate and occasional vertebrate second intermediate hosts (Bartoli and Prévôt 1978; Køie 1975; Køie 1985; Macfarlane 1951; Martorelli 1991; Stunkard 1969; Stunkard 1980; Watson 1984). There is no life cycle information available for the monotypic Gibsonivermidae which infects carnivorous sillaginid fishes. The Aepnidiogenidae, Gibsonivermidae, Lepidapedidae, and Lepocreadiidae (excluding a few genera noted below) have radiated widely in carnivorous fishes (Bray and Cribb 2012; Bray *et al.* 2018a, b). The dominant families in terms of numbers of records are the Balistidae, Carangidae, Gadidae, non-scarine Labridae, Macrouridae, Monacanthidae, Nototheniidae, Scombridae, Sparidae, and Tetraodontidae. The Enenteridae, Gorgocephalidae, and Gyliuchenidae differ dramatically from the other four families in both life cycles and hosts infected. Probably all have two-host cycles. Cercariae in the one known life cycle for the Gyliuchenidae (Al-Jahdali and Hassanine 2012) and the several known for the Gorgocephalidae (Huston *et al.* 2016; Huston *et al.* 2021) all encyst on algae. Although no life cycle is yet known for the Enenteridae, given its position as sister to the Gyliuchenidae (Bray and Cribb 2012; Bray *et al.* 2023; Pérez-Ponce de León

and Hernández-Mena 2019) and that species of the Enenteridae occur in the same herbivorous hosts as those of the Gorgocephalidae, we predict that enenterid cercariae also encyst on algae. The Gyliuchenidae, Gorgocephalidae, and Enenteridae have radiated in close association with marine herbivorous fishes, principally the Acanthuridae, Kyphosidae, Siganidae, and scarine Labridae (Huston *et al.* 2019b; Huston *et al.* 2019a; Huston *et al.* 2021; Huston *et al.* 2022). In addition to these three families, the lepecreadiid *Diploproctodaeum arothroni* has been reported to have cercariae which encyst on algae (Hassanine 2006). The host of *D. arothroni* is the pufferfish *Arothron hispidus*, which feeds on algae, detritus, sponges, and other benthic invertebrates (Meyers 1991). *Diploproctodaeum* falls in a strongly supported clade with several other genera (*Bianium*, *Diplocreadium*, *Lobatocreadium*) with species concentrated in tetradontiform fishes (Bray *et al.* 1996, 2009). Although no life cycles are yet known for any other species in this clade, many other tetradontiform fishes feed on algae, detritus, and benthic invertebrates, suggesting externally encysting metacercariae may be common in this clade. Lastly, two genera of lepecreadiids, *Preptetos*, and *Neopreptetos* have radiated in herbivorous fishes (Bray and Cribb 1996; Bray *et al.* 2022). Although no life cycles are yet known for species of these genera, their almost complete restriction to herbivorous fishes suggests that they likely also have metacercariae associated with algae.

Although the monophyly of the Lepocreadioidea is well-supported, the relationships between lepecreadioid families remained unresolved (Figure 1). In the most recent molecular phylogeny of the Lepocreadioidea (Bray *et al.* 2023), the seven constituent families formed a five-way polytomy of sister clades: the Aepnidiogenidae, Lepocreadiidae, Gibsonivermidae + Lepidapedidae, Gorgocephalidae, and Gyliuchenidae + Enenteridae. Notably, the three herbivore-infecting families did not form a monophyletic clade. The lack of resolution in this study, and in the previous phylogenetic analyses of the Lepocreadioidea (Bray *et al.* 2009; Bray and Cribb 2012; Bray *et al.* 2018a), limits inference about the life cycle of the ancestral lineage for the group. The overall digenean topology suggests that the Lepocreadioidea arose from among taxa with 3-host life cycles. However, we cannot presently distinguish between the possibilities that either the most recent common ancestor of the superfamily was two-host (implying at least one secondary evolution of three-host cycles) or three-host (implying multiple secondary abbreviations to two-host cycles within the superfamily). This issue may be resolved by resolution of the relationships within the Lepocreadioidea.

Possible mechanisms for herbivore-derived life cycle truncation

Although the herbivorous host hypothesis describes the most parsimonious explanation of life cycle truncation in the digenean lineages discussed above, how would the actual transition from using a second intermediate host to encysting in the environment occur? We hypothesise that the transition occurred as a reversal of the way a three-host life cycle is thought to have arisen from a two-host life cycle: external association leading to progressively more intimate association and subsequent penetration (Cribb *et al.* 2003). In this scenario, a two-host life cycle would be derived from a three-host cycle in the opposite direction; gradually less intimate association, leading to a transition from internal to external encystment, and ultimate abandonment of the second intermediate host. Such modification would be favoured if there was greater

transmission opportunity through external encystment and if the physiological benefits of encystment within a host, such increased longevity and continued development (Galaktionov and Dobrovolskij 2003), were offset by the increased transmission rate.

Life cycle truncation or a host switch?

In discussions following the presentation of this work at *Trematodes 2024*, a colleague argued that the system may represent a host-switch rather than life cycle truncation. They argued that the algae on which the metacercariae encyst should be considered the new second intermediate host. The debate is largely one of semantics, perhaps centred around the definition of 'host'. Many definitions for 'host' are available, but all broadly agree that a host is a living organism; algae certainly meets that criterion. In the context of parasitism, however, we expect some level of interaction and dependence between host and parasite. From the perspective of the 'host' algae, the only possible significance could be increased or decreased browsing as a result of the presence of metacercariae. Both outcomes seem exceptionally unlikely. Algae bearing metacercariae are hardly 'parasitised'. From the perspective of the parasite, the use of algae as a substrate is more nuanced. Among the Haploporoidea, cercariae from species of both families and multiple genera will encyst on nearly any substrate encountered, be it algae, the surface film of water, rocks, or the sides of the glass or plastic containers in which they are observed (Cable 1962; Díaz *et al.* 2009; Huston *et al.* 2018; Shameem and Madhavi 1991). Such lack of 'host specificity' suggests that the algae should be thought of as no more than a 'substrate' rather than as a host, although the available studies are perhaps insufficiently detailed to distinguish cercarial preferences. In contrast, the cercariae of the lepecreadioid *Gorgocephalus yaaji* were found to encyst as metacercariae on algae within 24 hours, but not on the sides of the plastic container in which they were held (Huston *et al.* 2016). Morley (2015) summarised a significant literature showing that paramphistome and fasciolid cercariae are often preferentially attracted to green or yellow light with the implication that this phototaxis leads to encystment on plants and subsequently transmission to the definitive host. Thus, there is limited evidence of some site-specificity in externally encysting cercariae. Such specificity clearly confers potential improvement in chances of transmission. In our view, none of the available evidence suggests that the algae on which metacercariae often encyst is better considered a host than a substrate. Morley (2015) interprets the role as 'plant transport hosts', a terminology which captures the nature of the role without implying any sophistication of interaction.

Herbivorous and detritivorous diets

A key component of considerations of the nature of the exploitation of herbivores and detritivores by trematodes is the origin of these diets. Vertebrates, as fishes, arose principally as carnivores (Helfman *et al.* 1997). Chondrichthyans remain carnivores exclusively. Among teleost fishes, however, herbivorous and detritivorous diets have arisen repeatedly and in a wide variety of forms, although they remain far less common than carnivory. A key indication of the secondary adoption of herbivory in both fishes and tetrapods is the widespread dependence of herbivores on microorganism to at least partially digest their plant-based food (Clements and Choat 1995, 1997; Fidopiastis *et al.* 2006; Mountfort *et al.* 2002; Theodorou and France 2005).

For the Gorgocephalidae, Gyliachenidae, Haploporidae, Emprostiometridae, and Enenteridae, 18 families of fishes account for approximately 83% of published records of trematode species / fish family combinations (Table 1). Numerous features of the distribution of records are noteworthy. The 18 families include all the most important fish host families for all five trematode families, but another 41 fish families have low numbers of reports. The richest 18 families relate to nine orders of fishes of which the Acanthuriformes is represented by six families, the Characiformes by four, and the 'Eupercaria incertae sedis' by two. Of the orders with only one infected family, the Centrarchiformes (Kypnosidae) and Mugiliformes (Mugilidae) are amongst the most heavily infected. Notes on the diet of these fish families compiled from FishBase (Froese and Pauly 2025) show that, for the most frequently infected families, there is a strong tendency towards herbivory and or detritus feeding. The breadth of host range differs dramatically between the five trematode families with just one fish-host family (Kypnosidae) for the Gorgocephalidae (the smallest of the five trematode families) to 36 for the Haploporidae (the largest). Species richness in the five trematode families is strongly correlated with the number of host families from which each is reported. The Haploporidae (over 60% of all the species) has been reported from all but one of the 18 richest families (and another 19 in addition). No fish family has been reported with representatives of all five families, but the Kypnosidae has all but emprostiometrids and four families harbour three of the trematode families.

Taken together, the patterns described above show a strong correlation between an herbivorous or detritivorous diet for fishes and infection with species of five families of trematodes with externally encysting cercariae. Rare infections in fish families that are not notably herbivorous or detritivorous suggest cases of host or parasite specialisation and, probably, some cases of errors in identification. The key host fishes are drawn from multiple lineages, consistent with the idea that herbivorous and detritivorous diets have arisen repeatedly in fishes and that consequent advantage has been taken of these diets repeatedly. Species of Emprostiometridae, Enenteridae, Gyliachenidae, and Haploporidae all infect fish families relating to multiple orders suggesting histories of significant host-switching. Without doubt, the richest component of all these host/parasite combinations is the Haploporidae in the Mugilidae where richness of over 100 trematode species well exceeds the richness of the Mugilidae itself. The details of the evolution of these systems remain to be inferred. We note a rich developing understanding of the phylogenetic history and diets of the fishes involved which should support such analysis (Lobato *et al.* 2014; Streelman *et al.* 2002; Tebbett *et al.* 2022).

We consider it clear that trematodes have shown remarkable flexibility in their exploitation of herbivorous and detritivorous fishes. A sharp illustration of evolutionary flexibility of trematodes to exploit dietary opportunity is evident from sparid fishes. Sparids occur globally and typically have broad carnivorous diets that lead to infections with a wide range of trematode families (over 30) of which many have abundant records (Acanthocolpidae, Aephiidiogenidae, Cryptogonimidae, Derogenidae, Faustulidae, Fellodistomidae, Gyliachenidae, Hemiuroidae, Lecithasteridae, Lepocreadiidae, Mesometridae, Monorchidae, Opecoelidae, and Zoogonidae). Of these, the four known species of Gyliachenidae from sparids are reported from only two sparid species, *Boops boops* and *Sarpa salpa* (Bartoli 1987; Perez-del-Olmo *et al.* 2007). Both *B. boops* and *S. salpa* are exceptional among sparids in being heavy consumers of algae (Escalas *et al.* 2021). It seems a non-controversial conclusion that it is their secondarily adopted

Table 1. Richness of five families of haploporoid and lepecreadioid fish trematodes in the 18 most heavily infected fish families. Numbers represent counts of parasite species / host family combinations.

| Orders | Row Labels | No. of Fish Species | Emprostiostomatidae | Enenteridae | Gorgocephalidae | Gyliauchenidae | Haploporidae | Grand Total | Diet |
|---------------------------|---------------------|---------------------|---------------------|-------------|-----------------|----------------|--------------|-------------|---|
| Acanthuriformes | Scatophagidae | 4 | 2 | | | | 6 | 8 | Algae and faeces |
| | Siganidae | 29 | 4 | | | 17 | 1 | 22 | Benthic algae |
| | Acanthuridae | 84 | | | | 12 | 8 | 20 | Benthic algae, zooplankton, detritus |
| | Pomacanthidae | 91 | | 1 | | 5 | 3 | 9 | Algae, zooplankton, invertebrates, algae, fish eggs |
| | Lutjanidae | 113 | | 1 | | | 4 | 5 | Mainly crustaceans and fishes, plankton |
| | Chaetodontidae | 136 | | | | 3 | | 3 | Cnidarians, invertebrates, filamentous algae, plankton |
| Beloniformes | Hemiramphidae | 61 | | 1 | | | 3 | 4 | Algae, zooplankton, fishes |
| Blenniiformes | Blenniidae | 402 | | | | 1 | 2 | 3 | Algae, benthic invertebrates, plankton, skin of larger fishes |
| Cantrarchiformes | Kyphosidae | 16 | | 23 | 5 | 1 | 16 | 45 | Mainly algae |
| Characiformes | Prochilodontidae | 21 | | | | | 6 | 6 | Detritus and periphyton |
| | Anostomidae | 162 | | | | | 6 | 6 | Mostly herbivores or detritivores. |
| | Curimatidae | 107 | | | | | 3 | 3 | Organic matter, detritus, vegetation, and filamentous algae |
| | Characidae | 1,183 | | | | | 4 | 4 | Diverse, carnivorous to herbivorous |
| Cichliiformes | Cichlidae | 1,786 | | | | | 7 | 7 | Carnivores, herbivores, omnivores, planktivores, detritivores |
| Eupercaria incertae sedis | Labridae (Scarinae) | 100 | 1 | | | 5 | 3 | 9 | Mainly epilithic algae |
| | Sparidae | 162 | | 1 | | 5 | 2 | 8 | Hard-shelled benthic invertebrates + rare herbivores |
| Gonorynchiformes | Chanidae | 1 | 4 | | | | 1 | 5 | Benthic algae and invertebrates |
| Mugiliformes | Mugilidae | 78 | 1 | | | | 121 | 122 | Fine algae, diatoms and detritus |

herbivory that has led these fishes to be susceptible to infection with these trematodes.

Haplospilchnoidea, Pronocephaloidea, and Paramphistomoidea

The infection of herbivores and associated two-host life cycles is not restricted to haploporoids and certain lepecreadioids. Three major lineages, the Haplospilchnoidea (parasites of fishes only), Paramphistomoidea (parasites of fishes and tetrapods), and Pronocephaloidea (principally parasites of tetrapods, rarely fishes) are highly comparable. Notably, Mesometridae, Microscaphidiidae and Cladorchiidae (all Paramphistomoidea), and Haplospilchnidae infect some of the same herbivorous fishes as harbour haploporoids and lepecreadioids. Almost everything that we have discussed above about the haploporoids and lepecreadioids also applies to these three superfamilies – specifically, heavy concentration in multiple taxa of herbivorous animals and associated two-host life cycles involving external encystment. Only one biological distinction seems important. For pronocephaloids, metacercariae often form on the shells of gastropods, presumably enhancing their transmission, and extending their host range from herbivores to, especially at least, partly carnivorous turtles (Chodkowski *et al.* 2016; Horsfall 1935; Hunter 1967). We have not discussed these three superfamilies in parallel with the haploporoids and lepecreadioids because their far more basal position in the phylogeny of the Plagiorchiida means that it is possible, perhaps likely, that their life cycles are plesiomorphically two-host. If that is the case, it could be inferred that these two-host life cycles have been arisen by two entirely different pathways. Distinctions between the two possibilities will require a greater depth of phylogenetic understanding together with an improved understanding of the timing of cladogenetic events with the Digenea.

Concluding remarks

Perhaps the key feature of the evolution and diversification of the Digenea has been in the flexibility, or opportunism, in the exploitation of aspects of host biology that has enabled infection of a huge range of animals. Here we see evidence of a distinct category of this opportunism in what we interpret as the secondary truncation of three-host life cycles to two-host forms that have enabled the infection of lineages of fishes that have themselves pursued ‘new ecological opportunities’ by the adoption of herbivory. The present phylogenetic evidence suggests that this kind of truncation has occurred in at least two distinct and major lineages. We infer that this form of truncation has been limited by the underlying metacercarial biology of digenean taxa. That is, we suspect that only those taxa that incorporate relatively unspecialised metacercariae have been capable of undergoing this form of life cycle truncation. Digenean families with large and highly developed metacercariae have not recognisably been able to make the switch.

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