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Trematode life cycles: short is sweet?

Robert Poulin and Thomas H. Cribb

Complex life cycles are a hallmark of parasitic trematodes. In several trematode taxa, however, the life cycle is truncated: fewer hosts are used than in a typical three-host cycle, with fewer transmission events. Eliminating one host from the life cycle can be achieved in at least three different ways. Some trematodes show even more extreme forms of life cycle abbreviations, using only a mollusc to complete their cycle, with or without sexual reproduction. The occurrence of these phenomena among trematode families are reviewed here and show that life cycle truncation has evolved independently many times in the phylogeny of trematodes. The hypotheses proposed to account for life-cycle truncation, in addition to the factors preventing the adoption of shorter cycles by all trematodes are also discussed. The study of shorter life cycles offers an opportunity to understand the forces shaping the evolution of life cycles in general.

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From simple beginnings, the life cycles of parasitic helminths have evolved into complex sequences of improbable events. Both adaptive scenarios and evolutionary contingencies are often invoked to explain the complexity of their life cycles [1–3]. For example, if a new type of predator evolves, the parasite of the prey might add a developmental stage to their life cycle inside the predator. Alternatively, transmission from prey host to predator host could serve to concentrate conspecific parasites and facilitate cross-fertilization [3]. Whatever the origin of complex life cycles, they have imposed new selective pressures on parasites by being so difficult to complete.

The life cycle of a typical digenean trematode offers a good example of a complex cycle, involving three transmission challenges. First, eggs released from adult worms in the DEFINITIVE HOST (see Glossary) hatch into MIRACIDIA, which must find a suitable mollusc as the FIRST INTERMEDIATE HOST. Second, the free-living, but short-lived, CERCARIAE that emerge from the first intermediate host must locate a suitable SECOND INTERMEDIATE HOST. Third, METACERCARIAE must be ingested, along with the second intermediate host, by an appropriate definitive host for the life cycle to be completed. Natural selection has favored various adaptations in trematodes to counteract the odds stacked against the completion of the cycle. Examples include high adult-fecundity, asexual multiplication within the molluscan first intermediate host, efficient host-finding mechanisms in miracidia and cercariae, and parasite-mediated increases in the susceptibility of the second intermediate host to predation [2,4].

In some species, however, evolution has taken a drastic approach, resulting in the typical three-host life cycle being truncated to two hosts or even to one host [1,2]. The corresponding decrease in the number

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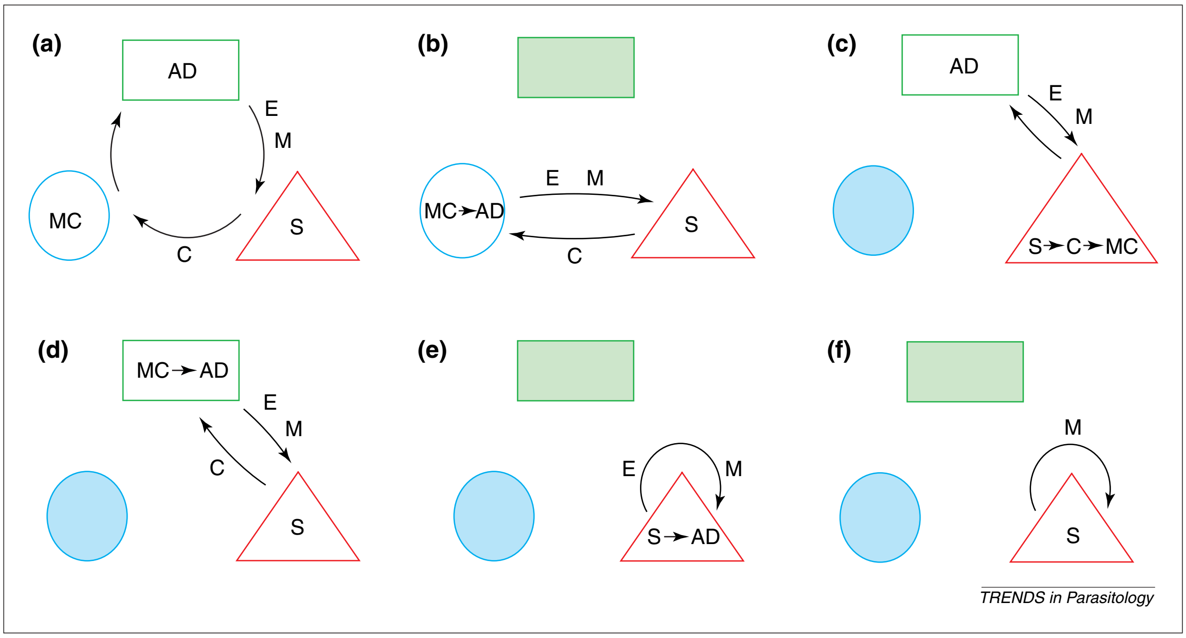

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Fig. 1. Typical and abbreviated trematode life cycles. (a) In a typical cycle, adult worms (AD) living inside definitive hosts (open green rectangle) release eggs (E) into the environment. The miracidia (M) hatched from these eggs infect a molluscan first intermediate host (open red triangle). Following asexual amplification of larval stages inside sporocysts (S) (sometimes in rediae), cercariae (C) leave the mollusc to encyst as metacercariae (MC) inside the second intermediate host (open blue circle). The cycle is completed when this second intermediate host is ingested by the definitive host. Five different types of life cycle truncation are: (b) progenesis in the second intermediate host; (c) first intermediate host used as second intermediate host; (d) second intermediate host also used as definitive host (sequentially); (e) sexual adult develops in first intermediate host; and (f) sporocysts in the first intermediate host produce miracidia directly. Shaded shapes indicate absence of particular host in trunctuated life cycle.

of transmission events appears to be the main benefit of this truncation, with a simpler life cycle being easier to complete. There are many evolutionary paths towards an abbreviated life cycle, which have been followed by several trematode lineages independently.

The truth about truncation

There are many ways in which trematodes can achieve a simpler life cycle. Some need profound changes to developmental schedules and others require only minor adjustments to the ancestral life cycle. To help discussion, the shorter life cycles have been grouped into five basic types (Fig. 1), with examples given in Table 1.

The first way to abbreviate the life cycle is to adopt progenetic development: following encystment as a metacercaria in the second intermediate host, the worm develops precociously into an adult. Eggs are produced within the metacercarial cyst by self-insemination, bypassing the need for the worm to mature in a definitive host. In other words, the last transmission event in the cycle (i.e. ingestion of the second intermediate host by the definitive host) is eliminated. Examples of this type of life cycle truncation include several species of the genus *Alloglossidium* (Macroderoididae), in which all worms produce eggs in their second and final hosts (crustaceans or leeches, depending on the species) [5] and some individuals of *Coitocaecum parvum* (Opecoelidae) that produce eggs at the metacercarial stage in amphipod hosts as opposed to their conspecifics who mature only in the fish definitive host [6]. The apparent end point of adopting this kind of abbreviation is seen in the blood flukes (Sanguinicolidae, Schistosomatidae and Spirorchidae), in which cercariae penetrate a vertebrate host and develop into adult worms directly. Overall, deletion of the definitive host (either facultatively or permanently) is probably the most common way in which life cycles are abbreviated (Table 1).

A second type of life cycle truncation consists of using the molluscan first intermediate host also as the second intermediate host. Cercariae do not emerge from the molluscan host; instead,

Glossary

Cercariae: A larval stage of trematodes, produced asexually by sporocysts or rediae, and released from the first intermediate host.
Definitive host: The host (usually a vertebrate) in which adult trematodes reproduce sexually.
First intermediate host: The host (usually a mollusc) in which trematode larvae multiply asexually to produce cercariae.
Metacercariae: The final larval stage in the life cycle of trematodes, which are usually encysted and quiescent in the second intermediate host.
Miracidia: The first larval stage of a trematode, hatched from an egg, ciliated and often free-swimming.
Progenesis: Precocious development of the reproductive system, leading to early sexual maturity in juvenile stages.
Rediae: An asexual stage of development in some trematodes, which are usually produced by sporocysts.
Second intermediate host: The host infected by trematode cercariae and in which the metacercariae develop, often within a cyst.
Sporocysts: An asexual stage of development in trematodes, found in the first intermediate host.

Table 1. Examples of trematode taxa in which truncated life cycles have been observed

Family	Genus[a]	Facultative[b]	Type of life cycle truncation[c]				Refs
			Progenesis in second IH	Use first IH as second IH	Use second IH as DH	Use snail host only	
Allocreadiidae	*Allocreadium*	No	Yes				[32]
Azygiidae	*Proterometra*	No	Yes			Yes	[33,34]
Brachycoeliidae	*Brachycoelium*	Yes	Yes				[12]
Bucephalidae	*Bucephaloides*	Yes	Yes				[35]
Bunocotylidae	*Bunocotyle*	No				Yes	[36]
Cephalogonimidae	*Cephalogonimus*	Yes			Yes		[12]
Cryptogonimidae	*Aphalloides*	No	Yes				[37]
Cyathocotylidae	*Mesostephanus*	Yes				Yes	[14]
Cyclocoeliidae	All genera	No		Yes			[38]
Derogenidae	*Genarchella*	Yes				Yes	[39]
Diplostomidae	*Alaria*	Yes			Yes		[12]
Echinostomatidae	*Echinostoma*	No		Yes			[38]
Eucotylidae	All genera	No		Yes			[38]
Eumegacetidae	*Orthetrotrema*	Yes	Yes				[40]
Fellodistomidae	*Proctoeces*	Yes		Yes		Yes	[9,41]
Gorgoderidae	*Phyllodistomum*	Yes	Yes	Yes			[42,43]
Gymnophallidae	*Gymnophallus*	Yes		Yes			[10]
	Parvatrema	No		Yes			[11]
Hasstilesiidae	*Hasstilesia*	No		Yes			[44]
Hemiuridae	*Parahemiurus*	No				Yes	[45]
Lecithodendriidae	*Pleurogenes*	Yes	Yes				[46]
	Pleurogenoides	Yes	Yes				[12]
	Prosotocus	Yes	Yes				[12]
Lepocreadiidae	*Stegodexamene*	Yes	Yes				[47]
Leucochloridiidae	*Leucochloridium*	No		Yes			[48]
Lissorchiidae	*Asymphylodera*	Yes	Yes	Yes			[8,49]
Macroderoididae	*Alloglossidium*	No	Yes				[5,16]
	Glypthelmins	No			Yes		[12]
	Haplometra	No			Yes		[12]
Microphallidae	*Microphallus*	No		Yes			[7]
	Maritrema	No		Yes			[7]
Opecoelidae	*Coitocaecum*	Yes	Yes				[6,27]
	Plagioporus	Yes				Yes	[15]
Opisthorchiidae	*Ratzia*	Yes	Yes				[46]
Plagiorchiidae	*Opisthioglyphe*	Yes			Yes		[12]
	Paralepoderma	No	Yes			Yes	[12]
Sanguinicolidae	All genera	No	Yes				[38]
Schistosomatidae	All genera	No	Yes				[1]
Spirorchidae	All genera	No	Yes				[38]
Zoogonidae	*Deretrema*	Yes	Yes				[17]

[a] Truncated life cycle do not necessarily occur in all species within a genus.

[b] Facultative truncation of life cycle is only shown by some individuals within a species.

[c] Abbreviations: DH, definitive host; IH, intermediate host.

they lose their tail and form metacercariae within the same mollusc and await ingestion by the definitive host. This sort of life cycle abbreviation avoids host-finding by free-swimming cercariae. It is shown by some species of Microphallidae [7], Lissorchiidae [8], Fellodistomidae [9] and Gymnophallidae [10,11]. In some species, such as *Gymnophallus choledochus*, this truncation of the life cycle occurs on a seasonal basis [10]: the parasite follows its normal three-host cycle in summer and switches to the simpler two-host cycle during winter months. In addition to the use of a first intermediate host by some species in the aforementioned families, formation of the metacercaria in this host (and the loss of the second intermediate host) is apparently fixed as a permanent character in the Cyclocoeliidae, Eucotylidae, Hasstilesiidae and Leucochloridiidae.

The third way to achieve an abbreviation of the life cycle involves using the second intermediate host as a definitive host as well. As in the case of progenetic metacercariae, this eliminates the need for transmission to the definitive host through predation on a second intermediate host. One possible version of this type of truncation involves the retention of the metacercarial stage, which is common in parasitic trematodes of amphibians. For example, cercariae of *Opisthioglyphe ranae* (Plagiorchiidae) encyst in the superficial epithelium of the skin of their frog host; when this epithelium is shed, it is swallowed together with the encysted metacercariae by the frog, and then the metacercariae excyst and develop into adults inside the frog [12]. Similarly, cercariae of *Haplometra cylindracea* (Macroderoididae) penetrate the buccal cavity of their frog host where they encyst as metacercariae on the buccal mucosa; after a few days, the cysts burst and the worms migrate to the frog's lungs where they mature into adults. In this species, however, the metacercarial stage is sometimes bypassed altogether [12].

The fourth and fifth types of life cycle truncation consist of one-host life cycles derived from a three-host cycle. In the fourth type, sexually mature adult worms develop inside REDIAE or SPOROCYSTS within the mollusc and produce eggs, which hatch into miracidia (see examples in Table 1). In these cases, there could be a single transmission event in the life of the trematode, involving infection of the mollusc by miracidia.

The fifth and most surprising form of life cycle abbreviation occurs only in certain cyathocotylids. In *Mesostephanus haliasturis*, for example, sporocysts inside the first intermediate host (snail) can produce miracidia directly, which exit the snail by an unknown route [13,14]. It is presumed, but not demonstrated, that these miracidia infect new snails. The sporocysts in these infections also produce daughter sporocysts and cercariae; hence, the typical three-host life cycle is also maintained in these species.

It must be emphasized that shorter life cycles are, in some cases, adopted by all members of a species (or even all species within a family), and that, in other cases, they appear to be a facultative developmental strategy, only seen in certain individuals of a species. Detailed morphological examination of co-occurring individuals exhibiting typical and shorter life cycles have confirmed that they belong to the same species [6,14,15], although genetic evidence would be welcome. Why are the three-host cycle and the abbreviated cycle both displayed by conspecific worms? There are at least three possible explanations. First, some trematode species showing both types of life cycles could be cases of evolutionary transitions between the ancestral life cycle and a newly derived, simpler cycle. This seems unlikely or we are extremely fortunate to be able to witness so many simultaneous evolutionary changes in trematode life cycles. Second, the three-host and the shorter life cycles might represent alternative reproductive strategies that yield roughly equal fitness payoffs, such that they coexist in the same population with only minor fluctuations in their relative frequencies. Third, shorter life cycles could be conditional life history strategies, adopted only under certain environmental conditions. In this case, larval trematodes would adjust their developmental schedules in response to extrinsic cues, such as resource availability inside the host or external temperature: under certain conditions, the normal cycle is preferable but, under unfavorable conditions, a switch to the abbreviated life cycle is favored. Distinguishing between these alternative explanations could be achieved experimentally in some of the species concerned.

The phylogeny of shorter life cycles

Shorter life cycles are observed in members of >32 trematode families (Table 1). The survey of the literature presented here is not exhaustive. In addition, few trematode life cycles have been elucidated, considering the thousands of species currently known; no doubt many other shorter life cycles are yet to be uncovered. Nevertheless, it is safe to say that some sort of life cycle truncation has appeared on >20 independent occasions during the evolutionary history of the trematodes (Fig. 2). With the exception of the blood flukes and the four other families in which all species have a similar two-host life cycle, abbreviations of the typical three-host life cycle are only known from few genera or species per family. This suggests that life cycle truncation is a derived feature, evolved recently from the more complex ancestral life cycle. Phylogenetic reconstructions have demonstrated this in the macroderoidid genus *Alloglossidium* [5,16], and the same thing has happened independently in several other trematode lineages. It is likely that shorter life cycles have arisen independently on more than one occasion within several different families, and the above minimum estimate of 20 evolutionary events is a conservative number. The five lineages boxed in Fig. 2 all have two-host life cycles in which there is no involvement of a second intermediate host. Because the most basal lineage of digeneans includes three-host life cycles, it is not clear at which point(s) two-host life cycles could have expanded to three-host cycles. The high positions of some of the lineages that have two-host life cycles might suggest that for at least some, the life cycle represents a truncation of a three-host cycle. At present, the phylogeny of the Digenea and the evolution of their life cycle are not sufficiently well known to enable this interpretation with confidence. Clearly, however, the basic life cycle of trematodes is flexible, given the number of times it has been modified by natural selection.

Why short is sweet

With so many independent origins, powerful and ubiquitous selective forces must drive the evolution of shorter life cycles. What factors promote the truncation of trematode life cycle? It is unlikely that there is a single, universal explanation accounting for all observed cases. A few hypotheses have been proposed. These are not mutually exclusive and none of them are backed by strong empirical evidence: for each hypothesis, there do exist trematode taxa in which truncation would be expected but is not observed.

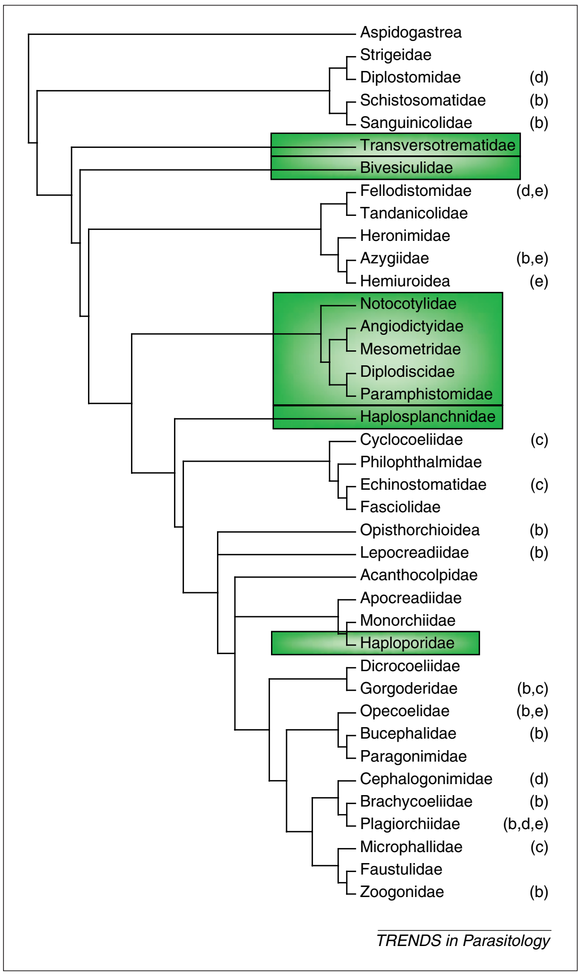

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Fig. 2. Abbreviated life cycles mapped onto a partial phylogeny of the Digenea; (b) progenesis in second intermediate host; (c) first intermediate host used as second intermediate host; (d) second intermediate host also used as definitive host (sequentially); (e) sexual adult develops in first intermediate host, as in Fig. 1. Phylogeny is proposed by Cribb *et al.* [31]; the tree excludes several taxa whose position has not yet been determined and families for which no life cycles are known. Families within the Hemiuroidea and Opisthorchioidea are reduced to the superfamilies. Taxa within green boxes (five separate lineages) have two-host life cycles, in which the cercaria either attaches directly to the definitive host (Transversotrematidae), is eaten by the definitive host (Bivesiculidae) or encysts in the open to be eaten by the definitive host. These taxa have no second intermediate hosts and are not capable of having their life cycles abbreviated by method (b). For some families, the life cycles are either not known or only partially resolved.

The environmental instability hypothesis

Holton [17] noted that three of the four trematode species, which have resolved life cycles and mature in New Zealand freshwater fish, exhibit facultative PROGENESIS at the metacercarial stage. He observed that conditions in New Zealand streams are unpredictable, with stream-beds often completely dry in summer months and liable to heavy floods during other parts of the year. Under such conditions, intermediate hosts can become stranded in marginal pools where no definitive hosts are available for the completion of the life cycle. Other progenetic trematodes have also been found exclusively in ephemeral habitats [18]. Facultative progenesis would then be an option for metacercariae in intermediate hosts, and it should be selected in any unstable or temporary habitat [17].

The rare or missing host hypothesis

In many systems, one host in the life cycle, often the vertebrate definitive host, will be unavailable periodically. In these cases, alternative ways of completing the life cycle, such as skipping the missing host, would be favored by selection. This hypothesis has been proposed to explain shorter cycles in which the definitive host undergoes seasonal migrations or fluctuations in abundance [17]. It could explain the marked seasonality in the occurrence of shorter life cycles in some trematodes parasitic in shore birds [10,19]. It could also account for systems where predatory definitive hosts are present, but predation rates are so low that the predator might as well be absent to a metacercaria waiting inside a second intermediate host [20]. The metacercarial stage is generally seen as a late addition in the evolution of trematode life cycles, prolonging the infective life of the cercaria and enhancing its chances of ingestion by the definitive host [21]. It should be advantageous to the parasite when this ingestion is a rare event. Pushed to its extreme, the rare host hypothesis can even explain the two-host life cycle of the schistosomes–spirorchids–sanguinicolids clade. Their cercariae penetrate large vertebrates that are often without predators (i.e. hosts that are a dead end when used as second intermediate hosts). Thus, because a predatory definitive host was missing, evolution might have favored the present two-host life cycle seen in schistosomes [1].

The developmental time hypothesis

If a trematode has been encysted as a metacercaria for a relatively long time, until it becomes infective to the definitive host, it is possible that some internal developmental clock will cause it to mature inside the second intermediate host and start producing eggs [12]. This would only indirectly result from low predation rates or an absent definitive host: the real cause would be ageing of the parasite inside the second intermediate host (i.e. a developmental schedule that cannot be delayed beyond a certain time). Subsequent ingestion of a precocious metacercaria by a definitive host would simply put the life cycle back on track but would not be necessary. In this context, it is also interesting that accelerated trematode development, in addition to developmental anomalies, are often more common in ageing snail hosts [12]. Thus the end of the parasite's life or that of its host could trigger developmental attempts to abbreviate the life cycle. This hypothesis could explain several cases in which progenesis is facultative or even sporadic in a trematode species using a second intermediate host that can outlive the metacercaria.

Box 1. Egg release in progenetic trematodes

Progenetic metacercariae, developing in the tissues or body cavity of what should normally be an intermediate host, face one major challenge: getting their eggs to the external environment from an infection site with no exit. Certain species have come up with innovative solutions. The lepocreadiid *Stegodexamene anguillae*, for example, uses small freshwater fish as second intermediate hosts and New Zealand eels as definitive hosts. In the small fish, normal metacercariae are found in the muscles or in the body cavity, but progenetic metacercariae occur mainly in the gonads of the fish [a]. These precocious worms self-fertilize and release their eggs within the metacercarial cyst. During dissections of gravid female fish (families Galaxiidae and Eleotridae), it is almost impossible to distinguish between fish eggs and metacercarial cysts filled with parasite eggs: they are of similar dimensions and color (R. Poulin, unpublished). When the fish spawns, it expels its eggs and those of the trematode!

The cryptogonimid *Aphalloides coelomicola* provides another good example. After penetrating the skin of gobiid fish, the cercariae of this trematode all go through a metacercarial stage before maturing into progenetic adults within the body cavity of the fish [b]. The eggs produced by these worms can only reach the outside environment following the death and disintegration of the fish host. There is evidence that *A. coelomicola* has a higher level of virulence than that in related trematodes, and it can accelerate the death of its fish host [c,d]. In addition, the trematode is usually associated with a myxozoan parasite (*Kudoa* sp.) which can rapidly liquefy the host's muscles following its death (C. Pampoulie *et al.*, pers. commun.), thus speeding up the disintegration of the fish host and the liberation of the trematode's eggs.

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The cannibalism hypothesis

In some trematodes, metacercariae encysted in a host species are transmitted to other members of the same host species by intraspecific predation – cannibalism. This is common among trematodes parasitizing amphibians, where adult frogs regularly feed on conspecific tadpoles. From the perspective of the parasite, the second intermediate and definitive hosts are the same, and transmission by predation does not take the parasite to a different host. Predation could easily be dropped from the life cycle. It is possible that the trematodes that have shorter life cycles, with adults developing in the same amphibian host in which they were encysted as metacercariae, are legacies of cannibalistic tendencies in the ancestral host [12].

The latitudinal gradient hypothesis

In trematode species with facultatively truncated life cycles, it has been suggested that shorter life cycles might be favored at higher latitudes [22,23]. This would allow a species to expand its range into colder waters by reducing its dependence on the usual hosts. The only proper test of this hypothesis has provided no support in its favor [23]. However, support for it comes from the observation that, in the Barents Sea, trematode species with free-swimming cercariae are almost absent in polar regions, where they are replaced by species with shorter cycles [24]. In polar habitats, where coastal waters freeze for most of the year, there is only a brief, annual, window of opportunity for transmission by free-swimming stages, and selection could favor shorter cycles in these conditions.

Why short might not be sweet

A common theme runs through most of the above hypotheses: shorter life cycles will be favored by selection whenever trematodes experience, on a permanent or regular basis, low or highly variable probabilities of transmission at one or more stages during their complex life cycle. A simplified life cycle requiring fewer host species provides an insurance against local extinction when host-to-host transmission is temporarily or permanently interrupted. This all makes sense, but it could be argued that low probabilities of transmission characterize the life cycle of all trematodes. Thus, the important question might not be why have shorter life cycles evolved in several trematode lineages, but why have they not evolved in all trematodes? Surely there must be constraints preventing these simpler life cycles from appearing in more trematode taxa. For example, there is evidence that minor morphological adaptations could be necessary in cercariae of progenetic trematodes [25]. More importantly, the developmental schedules of trematodes are so closely linked with the living conditions provided by the host that dropping a particular host from the life cycle might just be a big evolutionary step for many taxa. Even when development can be achieved in fewer hosts, say two instead of the usual three, there are still obstacles that could prevent the completion of the cycle. For example, most adult trematodes simply release their eggs into the lumen of their definitive host gut; the eggs reach the external environment in the host's feces. When metacercariae mature precociously by progenesis and start producing eggs, they are typically located inside the body cavity of the second intermediate host: there is no easy way out for their eggs. Some progenetic trematodes have come up with creative solutions to this problem (Box 1), but in other trematodes this might represent an insurmountable obstacle.

There might also be fitness costs associated with shorter life cycles; if these are not compensated in some way by the increased likelihood of completing a shorter life cycle, then truncation will not be favored. Two obvious costs are associated with offspring quality and quantity.

(1) Certain types of life cycle truncation can lead to the production of offspring with low genetic heterogeneity with potentially reduced viability [26]. This is the case in progenetic metacercariae enclosed

Box 2. Truncation and the loss of sexual reproduction

Of all the trematode taxa listed in Table 1 in the main text, the cyathocotylid *Mesostephanus haliasturis* is the only one in which abbreviating the life cycle can mean going without sexual reproduction [a]. In this parasite, sporocysts within the snail first intermediate host produce miracidia directly and asexually, without having to go through the adult stage where sexual reproduction takes place. The main advantage of sex is believed to be the genetic diversity maintained generation after generation, an asset for organisms in a changing world [b,c]. Abstaining from sex in every generation would presumably be disadvantageous, but abstaining from it sometimes has clear advantages [d,e]. *Mesostephanus haliasturis* lives in a nearly unchanging world: its hosts are snails of the family Thiaridae, which reproduce asexually [f]. The selective pressure on the trematode to adjust to an evolving host is thus reduced in this system: the snail host shows the same limited genetic heterogeneity as the parasite from one generation to the next. This feature of its host, in addition to other ecological factors, could have helped the evolution of this extreme form of life cycle abbreviation in *M. haliasturis*.

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within their cyst that can only self-fertilize, or in trematodes with one-host life cycles in which miracidia are produced asexually by sporocysts. A one-host life cycle scenario might not always be disadvantageous (Box 2), but generally only the forms of abbreviation that do not interfere with sexual reproduction have become the dominant paradigm within families. Therefore, blood flukes, which are able to cross-fertilize, represent a major radiation. Similarly, encystment of metacercariae within the first intermediate host does not interfere with sex, and ancestors with this shorter life cycle have produced significant radiations in the Cyclocoeliidae and Eucotylidae. There has been no radiation of a taxon where cross-fertilization is impeded by abbreviation.

(2) Fecundity could also be reduced in the abbreviated life cycles. The egg production of progenetic worms inside a small, short-lived, invertebrate host could be much less than that achieved normally inside a vertebrate definitive host. For example, progenetic metacercariae of *Coitocaecum parvum* can produce a maximum of ~200 eggs in their amphipod host [20,27]; the lifetime fecundity of their normal conspecifics inside their fish definitive host is unknown, but is probably much higher. Of course, in species where progenetic metacercariae often end up in the definitive host, the head-start achieved in the second intermediate host can be advantageous [28], but this applies only to taxa in which the shorter life cycle is facultative. Similarly, the number of cercariae that can be produced in an infection where the cercariae remain in (and fill) the mollusc first intermediate host might be considerably lower than could be produced if the cercariae leave the snail.

The above arguments point towards a key condition for the evolution of shorter life cycles: the higher probability of producing offspring (which could be fewer in quantity or of lower quality) must lead to a net fitness greater than that resulting from the low probability of reaching a definitive host in which high fecundity can be achieved. This trade-off has presumably been a major barrier to the spread of abbreviated life cycles in many trematode taxa.

The long and the short of it

Complex life cycles are a hallmark of most parasitic helminths, and yet little is known about how they evolved [1–3,29,30]. It is known in which evolutionary sequence hosts were added to the life cycle, but the ecological conditions that promoted the lengthening of the cycle can only be estimated. Shorter life cycles in trematodes offer a unique opportunity to investigate the opposite phenomenon (i.e. the shortening of the cycle). In particular, species in which both typical and shorter cycles occur allow the examination of factors favoring shorter cycles using experimental approaches, and to test some of the aforementioned ideas and hypotheses. For example, the genetic basis of shorter life cycles could be determined by quantifying the proportion of individuals adopting shorter vs typical cycles in the first and subsequent generations issued from parent stocks showing one or the other type of cycle. If frequencies of individuals opting for a shorter life cycle do not differ between the offspring of trematodes with typical and shorter cycles then this would suggest that truncation is a conditional strategy. Further experiments could be designed to identify the cues that trigger a switch to an abbreviated cycle; possible cues include temperature, size or age of the intermediate host, its nutritional status and the number of other parasites the host harbors. Comparisons between the viability and infectivity of miracidia produced the usual way or after some sort of life cycle truncation are also needed and are easy to achieve. Given the relatively short generation time of many trematodes showing facultative life cycle truncation, selection experiments could also be a possibility in some cases; these would provide invaluable information on the forces favoring shorter life cycles and on the rate at which they can select for them. In summary, trematodes and their diverse life histories provide an ideal opportunity to address one of the most fundamental question concerning parasitic helminths, the evolution of their complex life cycle, by studying under what circumstances they can become simpler.

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