

Life history constraints on the evolution of abbreviated life cycles in parasitic trematodes

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Abstract

Abbreviations of the complex life cycle of trematodes, from three to two hosts, have occurred repeatedly and independently among trematode lineages. This is usually facultative and achieved via progenesis: following encystment in the second intermediate host, the metacercaria develops precociously into an egg-producing adult, bypassing the need to reach a definitive host. Given that it provides relatively cheap insurance against a shortage of definitive hosts, it is not clear why facultative progenesis has only evolved in a few taxa. Here a comparative approach is used to test whether progenetic trematodes are characterized by larger body size and egg volumes, two traits that correlate with other key life history features, than other trematodes. These traits may constrain the evolution of progenesis, because precocious maturation might be impossible when the size difference between the metacercaria and a reproductive adult is too large. First, trematode species belonging to genera in which progenesis has been documented were found not to differ significantly from other trematode species. Second, using within-genus paired comparisons across 19 genera in which progenesis has been reported, progenetic species did not differ, with respect to body size or egg size, from their non-progenetic congeners. Third, using intraspecific paired comparisons in species where progenesis is facultative, no difference was observed in the sizes of eggs produced by worms in both the intermediate and definitive host, suggesting that opting for progenesis does not influence the size of a worm's eggs. Overall, the lack of obvious differences in body or egg size between trematodes with truncated life cycles and those with the normal three-host cycle indicates that basic life history characteristics are not acting as constraints on the evolution of progenesis; trematodes of all sizes can do it. Why facultative progenesis is not more widespread remains a mystery.

Introduction

Many animals have life cycles characterized by a succession of morphologically-distinct developmental stages each using a different habitat. This is a hallmark of many taxa of parasites, in which various developmental stages must go through a sequence of different

host species to complete the life cycle. Current hypotheses about the evolution of complex life cycles in parasites invoke adaptive adjustments following historical events, such as the appearance of new predators feeding on the original host or on the parasite's dispersal stages (Poulin, 1998; Combes, 2001). In particular, recent models have highlighted how adding hosts to a parasite life cycle can result in increased transmission efficiency, reduced larval mortality, and/or higher adult fecundity (Morand *et al.*, 1995; Brown *et al.*, 2001; Choisy *et al.*, 2003; Parker *et al.*, 2003). Empirical tests of most of the predictions generated

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by these models are difficult, however, because increases in the complexity of parasite life cycles occurred on just a few occasions over evolutionary time. For instance, the two-host life cycles of all extant acanthocephalans are descended from a single evolutionary event, offering no scope for comparative analyses between species with simple and complex life cycles. A similar situation prevails in other groups of parasitic helminths. In contrast, simplifications or abbreviations of complex life cycles have occurred repeatedly and independently in parasitic trematodes (Poulin & Cribb, 2002), allowing sister-lineage comparisons between taxa with different life cycles.

The life cycle of a typical digenean trematode involves three transmission events. First, eggs released from adult worms in the definitive host (usually a vertebrate) hatch into larvae that must find a suitable mollusc first intermediate host. Second, the free-swimming, but short-lived, cercariae emerging from the first intermediate host must invade 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. There are variations on this theme, but this life cycle is the basic pattern for most trematodes (Kearn, 1998). However, in some species belonging to higher taxa characterized by this three-host cycle, the life cycle is truncated to two hosts (Grabda-Kazubska, 1976; Poulin & Cribb, 2002). The most frequent way in which trematodes truncate their life cycle is by adopting a progenetic development: following encystment as a metacercaria in the second intermediate host, the worm develops precociously into an adult. Eggs are produced by self-fertilization (most trematodes are hermaphroditic), bypassing the need for the worm to mature in a definitive host. An extreme form of this type of life cycle truncation is seen in all blood flukes (families Sanguinicolidae, Schistosomatidae and Spirorchidae), in which cercariae penetrate a vertebrate host and develop into adults directly. Progenesis in most other trematodes is usually facultative (i.e. only shown by some individuals in a species). In at least one species, the opoecolid *Coitocaecum parvum*, it has been shown that progenesis can be triggered by external cues associated with a low probability of transmission to the definitive host (Poulin, 2003). Excluding blood flukes, progenetic development has been reported from numerous species scattered across the phylogenetic tree of trematodes; its occurrence in at least 15 families suggests multiple independent origins (Poulin & Cribb, 2002). Typically, progenesis has only arisen within some species within a genus, i.e. the macroderoidid genus *Alloglossidium* (Carney & Brooks, 1991; Smythe & Font, 2001; Brooks, 2003), a situation that allows independent comparisons between species with progenesis and congeneric species with the normal three-host cycle.

There are certain costs associated with progenetic development. For instance, because they self-inseminate, progenetic worms have offspring with lower genetic heterogeneity (Font, 1980; Poulin & Cribb, 2002). Also, because the worms are encysted in the second intermediate host, there may be constraints on the quantity of eggs that can be produced, and getting these eggs out of the host may be difficult (Poulin & Cribb, 2002). In spite of

these drawbacks, there are clear advantages: progenesis in the second intermediate host eliminates the need for one transmission event in the life cycle (Buttner, 1955). Indeed, the many hypotheses (reviewed by Poulin & Cribb, 2002) for the evolution of progenesis have one recurring theme: truncated life cycles should be favoured when trematodes experience low rates of transmission to the definitive host, for one reason or another. Some of the disadvantages mentioned above are not even prohibitive: if eventually ingested by a suitable definitive host, a progenetic worm could mate with other worms and achieve greater fecundity. Thus progenesis might be an insurance against shortages of definitive hosts. The question is then: why has facultative progenesis not evolved in all trematodes?

Here, the hypothesis that certain life history features are pre-conditions for the evolution of progenesis in trematodes is tested. Specifically, the prediction is that trematode species capable of progenetic development in a second intermediate host are characterized by relatively larger sizes at all developmental stages than other trematodes. Data on adult body size and egg size are readily available for most trematode species; because adult body size and egg size generally correlate positively with sizes of other developmental stages such as cercariae and metacercariae (Loker, 1983; Poulin & Latham, 2003), they can be used to determine whether progenetic species are relatively large and/or produce relatively large eggs. Related trematode species without these features may be constrained from maturing precociously, because the size difference between the larval stages and a reproductive adult is too large. First, we determine whether trematode species belonging to genera in which progenesis has been documented differ from other trematode species. In other words, are taxa in which progenesis has been documented characterized by larger bodies or larger eggs than other trematode taxa? Second, using within-genus paired comparisons, we contrast congeneric species that differ with respect to their ability to develop progenetically as a way to assess whether they differ in body size or egg size while controlling for phylogenetic influences. Third, using intraspecific paired comparisons in species where progenesis is facultative, the sizes of eggs produced by worms in both the intermediate and definitive host are compared, to determine whether opting for progenesis influences the size of a worm's eggs.

Methods

Data were obtained from life cycle studies and new species descriptions found in an electronic search of the Zoological Record database (years 1979 to 2004), as well as in the references cited in those articles. Morphometric data were gathered on both progenetic and non-progenetic species from the genera identified by Poulin & Cribb (2002) as including progenetic species, as well as from a few other genera identified during the search. Most described trematode species are known only from some, and not all, of their developmental stages, and thus data were rarely available on the sizes of cercariae or metacercariae; therefore only data on adult body size and egg size were used. Only life history data for parasites

collected from naturally-infected host species were included, and not from experimental infections of laboratory hosts. This is important because commonly used laboratory hosts are often immunosuppressed and thus provide unnatural growing conditions for trematodes.

Data on 201 trematode species belonging to 116 genera in which progenesis has never been recorded were obtained from the dataset of Thomas & Poulin (2003), for comparisons with trematode genera in which progenesis occurs.

When available, the dimensions (length and width) of eggs, progenetic adults in intermediate hosts, and 'normal' adults in definitive hosts were recorded. Methods used for the preparation and fixation of trematode specimens vary from study to study, and they can affect the accuracy of measurements of worm length or width. However, there is no reason to expect that this would affect the direction of any difference observed between trematode taxa. Measurements recorded from the literature were either means or the mid-points of ranges based on the examination of several individuals. Given that the worms are more or less flat, the best measure of their body size is their surface area. This was obtained separately (if applicable) for both progenetic and normal adult worms using the formula for the surface area of an ellipse, $\pi(L/2)(W/2)$, where L and W are, respectively, the length and width of the worms. Similarly, the volume of the eggs was calculated as the volume of an ellipsoid, $(\pi LW^2)/6$, with L and W being the length and width of the egg. Areas and volumes were \log_{10} -transformed for all analyses described below.

A one-way ANOVA was used to compare morphometric data from trematode species belonging to three groups: those from genera not known to use progenesis, those not known to use progenesis but belonging to genera in which progenesis is known to occur, and those capable of progenesis (facultative or not). The phylogenetic position of all these taxa is currently not fully resolved (Cribb *et al.*, 2003). This analysis therefore does not account for phylogenetic effects, and serves only to identify general differences in body size or egg size between different types of trematodes. For these analyses, the values used for egg sizes of facultatively progenetic species are those of eggs produced when the worms are in their normal definitive hosts, to allow a more relevant comparison with other trematodes. To correct for the influence of adult trematode body size on egg volume, egg volume was regressed against adult worm size, and the residuals were used as corrected measures in the ANOVA; the same applies to subsequent analyses, when adequate.

Second, to control for potential phylogenetic influences, we computed a single contrast between progenetic and non-progenetic species within each genus, so that each species and each genus contributed to no more than one data point in the analyses (Harvey & Pagel, 1991). If there were more than one species of each type per genus, these values were averaged. Comparisons between progenetic trematodes and their non-progenetic congeners were computed across all genera using paired two-tailed t -tests.

Finally, intraspecific comparisons were performed using facultatively progenetic species. Specifically, the

volumes of eggs produced precociously in the intermediate host were compared with those produced in the normal definitive host. Comparisons between progenetic and non-progenetic conspecifics were computed across all species using paired two-tailed t -tests.

Results

In all, data were obtained for 19 trematode genera in which progenesis has been documented but for which also there are non-progenetic species (104 species in total, 34 progenetic and 70 non-progenetic; see table 1); the full data set, including the complete list of literature sources, is available upon request from the authors (or freely at <http://www.otago.ac.nz/zoology/downloads/poulin/progenesis.xls>). These 19 genera represent 63% (19 out of 30) of all genera known to include progenetic species found during the survey; quantitative data for both progenetic and non-progenetic species could not be obtained for the other genera. Data on all variables were not available for all of the 19 genera, so sample sizes for various tests are different. In the majority of taxa in the present data set, progenesis is facultative, i.e. only a fraction of the worms mature precociously in intermediate hosts, the rest pursue their normal development in the definitive host.

Our first comparison aimed at finding general differences between progenetic and non-progenetic species in those 19 genera, and trematode species from a more or less random sample of other genera. No difference was found between these three groups of trematodes with respect to either adult body size ($F_{2,299} = 0.355$, $P = 0.701$) or egg volume ($F_{2,259} = 1.551$, $P = 0.214$), although non-progenetic species belonging to genera capable of progenesis were marginally larger than other trematodes (fig. 1). There was a significant positive relationship between adult body size and egg volume across all trematode species ($r^2 = 0.242$, $N = 261$, $P = 0.0001$), and egg volumes had to be corrected for worm size. Using residual egg volumes (see Methods), again no difference was found among the three groups of trematodes ($F_{2,259} = 2.026$, $P = 0.134$), although species belonging to genera capable of progenesis had marginally smaller eggs for their body size than other trematodes (fig. 1).

In the second analysis, non-progenetic and progenetic species were paired from the same genus for comparison. There was no difference between progenetic and non-progenetic congeners with respect to either body size (paired t -test: $t = 0.324$, $df = 15$, $P = 0.750$; fig. 2) or egg volume, whether comparisons were used of eggs produced by progenetic worms in their intermediate host ($t = 0.408$, $df = 17$, $P = 0.688$) or definitive host ($t = 0.037$, $df = 11$, $P = 0.971$; fig. 3). Therefore, progenetic species are not consistently different in terms of body size or egg size from their non-progenetic congeners (figs 2, 3). There was no correlation between worm body size and egg volume, either across progenetic species only, non-progenetic species only, or all species (all $P \geq 0.17$).

Finally, in intraspecific comparisons between non-progenetic and progenetic conspecifics, no difference in volume was found between eggs produced by progenetic

Table 1. Summary of the trematode genera (with number of species included), and their life cycle characteristics, that were used in the analyses.

| Genus | Number of non-progenetic species | Number of progenetic species | Second intermediate host | Definitive host (if any) |
|------------------------|----------------------------------|------------------------------|--------------------------|--------------------------|
| <i>Allocreadium*</i> | 13 | 3 | Insects | Fish |
| <i>Alloglossidium</i> | 3 | 7 | Crustaceans, leeches | Fish |
| <i>Asymphyiodora*</i> | 3 | 2 | Snails, polychaetes | Fish |
| <i>Brachycoelium*</i> | 2 | 1 | Amphibians | Amphibians |
| <i>Bucephaloides</i> | 2 | 1 | Fish | Fish |
| <i>Coitocaecum*</i> | 10 | 3 | Crustaceans | Fish |
| <i>Deretrema*</i> | 6 | 1 | Crustaceans | Fish |
| <i>Halipegus</i> | 2 | 1 | Insects | Amphibians |
| <i>Hemiurus*</i> | 3 | 1 | Crustaceans | Fish |
| <i>Lecithodendrium</i> | 2 | 1 | Insects | Mammals |
| <i>Microphallus*</i> | 1 | 3 | Crustaceans | Mammals, birds |
| <i>Nicolla*</i> | 1 | 1 | Crustaceans | Fish |
| <i>Paralepoderma</i> | 2 | 1 | Amphibians | Reptiles |
| <i>Phyllodistomum</i> | 4 | 1 | Crustaceans | Fish, amphibians |
| <i>Pleurogenes*</i> | 4 | 2 | Insects | Fish, amphibians |
| <i>Pleurogenoides*</i> | 5 | 2 | Insects, crustaceans | Amphibians |
| <i>Prosotocus*</i> | 4 | 1 | Insects | Amphibians |
| <i>Psilostomum</i> | 1 | 1 | Crustaceans | Birds |
| <i>Stegodexamene*</i> | 2 | 1 | Fish | Fish |

*Genus in which progenesis is facultative within species using this strategy.

worms in intermediate hosts and those produced by normal adult worms in definitive hosts ($t = 0.811$, $df = 11$, $P = 0.435$; fig. 4).

Discussion

The life cycle of trematodes can be viewed as a sequence of unlikely events. Natural selection has favoured a range of adaptations to overcome the obstacles faced by trematodes on their way to completing their life cycles. Examples include asexual multiplication within the molluscan first intermediate host, efficient host-finding mechanisms in cercariae, parasite-induced increases in the susceptibility of the second intermediate host to predation by the definitive host, and high adult fecundity (Combes, 1991; Combes *et al.*, 1994; Poulin, 1998). In some lineages, a more drastic approach has been to truncate the life cycle from three to two hosts, and thus simply eliminate a transmission event (Buttner, 1955; Poulin & Cribb, 2002; Brooks, 2003). The results of our comparative analyses suggest that there are no obvious differences in body size or egg size between trematode taxa with truncated life cycles and those with the normal three-host cycle. Body size in animals is a fundamental determinant or covariate of all major life history and ecological characteristics (Peters, 1983; Calder, 1996), and the similarity in body size between progenetic and non-progenetic taxa suggests that they also share many other traits.

In a comparative analysis such as the present one, it is difficult to determine the direction of causality. Certain life history traits of progenetic species may be pre-adaptations for progenesis, i.e. traits that the species possessed before and that pre-disposed it for an abbreviated cycle. In contrast, they could be traits evolved following the adoption of progenesis because

they were favoured by the new, shorter life cycle. Distinguishing between cause and consequence is not an issue here: there was no significant divergence in body size or egg size between progenetic species and their close relatives not known to use progenesis (figs 2, 3). This is particularly evident for egg sizes, which tend to be very similar within genus whether the species are progenetic or not, and within species whether the eggs are produced by progenetic worms or normal adults. The results also indicate that progenesis has appeared in taxa that differ widely (by almost two orders of magnitude; figs 2, 3) with respect to both body size and egg size. Progenesis is thus an option opened to small and large trematodes alike.

The present results are unlikely to have been affected by confounding variables, such as the fact that progenetic and non-progenetic species have different host species. Adult worm body size, egg volume, and relative growth rate of trematodes are not influenced by the taxonomic affinities or body mass of the definitive host (Poulin, 1997; Poulin & Latham, 2003). Also, egg volume and its variability are not linked with host characteristics or the likelihood of ending up in an inhospitable external environment (Poulin & Hamilton, 2000). No information is available on the sizes of the second intermediate hosts used by progenetic and non-progenetic species. However, in a given trematode genus, progenetic and non-progenetic species generally used the same type of second intermediate host, often within the same taxon, and there is therefore no reason to believe that the identity of this host has any bearing on whether progenesis is used or not.

Most hypotheses attempting to explain the occurrence of progenesis in trematodes invoke low rates of transmission to the definitive host: in situations where transmission is unlikely, either permanently or periodically, progenesis should be favoured (Grabda-Kazubska,

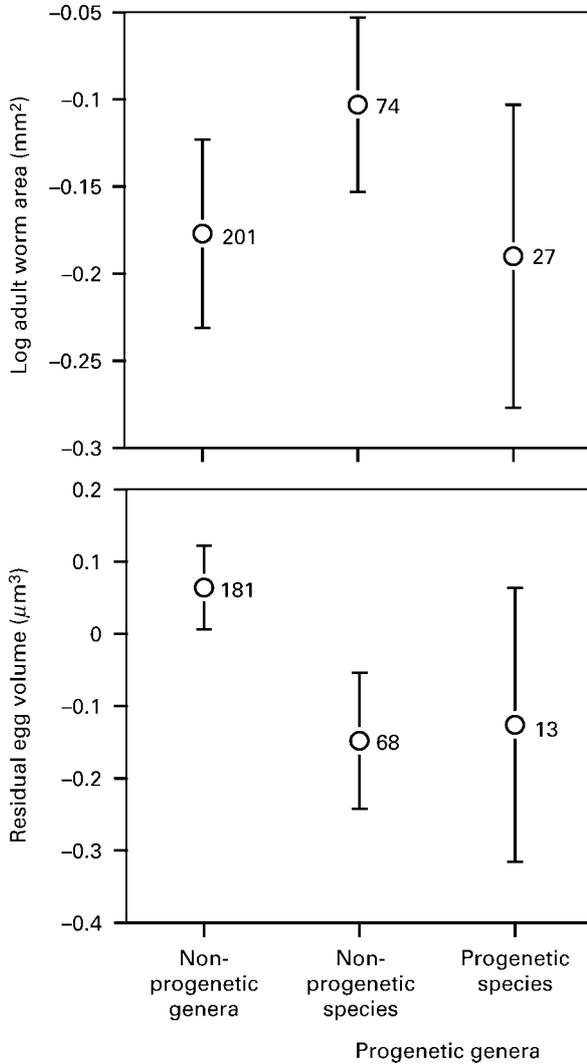


Fig. 1. Mean (\pm SE) adult worm surface area and egg volume for trematode species belonging to three categories: those in genera not known to use progenesis, those not known to use progenesis but belonging to genera in which it occurs, and those known to be progenetic. Egg volumes are expressed as the residuals of the regression of \log_{10} egg volume against \log_{10} worm surface area, across all species in the analysis. Numbers indicate the number of species in each category.

1976; Poulin & Cribb, 2002). What these hypotheses fail to explain is why, under conditions of low transmission rates to the definitive host, only certain trematode species adopt progenesis and a truncated life cycle. Progenesis can be viewed as a relatively cheap insurance against shortages of definitive hosts. Thus, if basic life history features such as body size are not preventing progenesis, what is? Perhaps other features are important. For instance, progenesis and egg production within a second intermediate host must require uptake of nutrients from this host. As metacercariae are generally encysted within the second intermediate host, the permeability of the cyst may determine whether or not

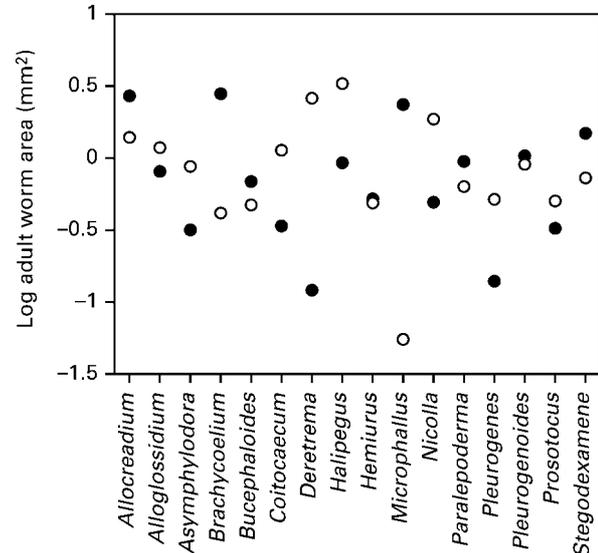


Fig. 2. Adult worm area of trematode species in 16 genera containing both progenetic (●) and non-progenetic (○) species. Some points represent the average value for several congeneric species sharing the same life cycle (see table 1).

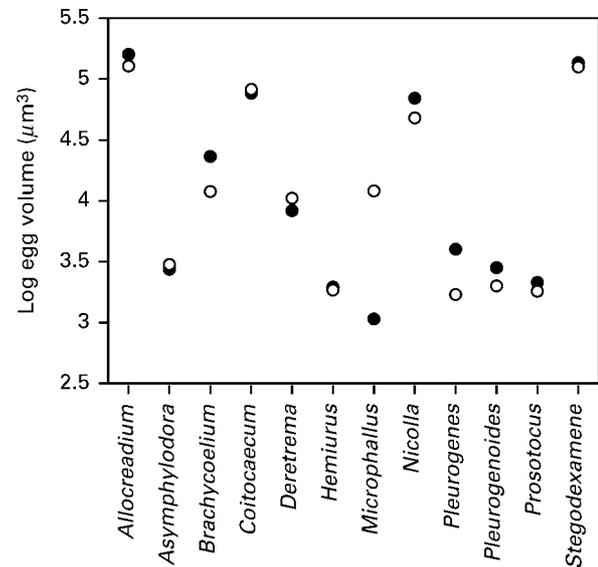


Fig. 3. Egg volume of trematode species in 12 genera containing both progenetic (●) and non-progenetic (○) species. Some points represent the average value for several congeneric species sharing the same life cycle (see table 1).

development and egg production are possible in the second intermediate host. Also, the benefits of progenesis and a truncated life cycle may be reduced in trematode species with low host specificity, i.e. species capable of exploiting a range of different definitive hosts. Information on cyst permeability or true host specificity is not available for the trematodes in our analysis or for trematodes in general, and these possibilities could not be examined in this study.

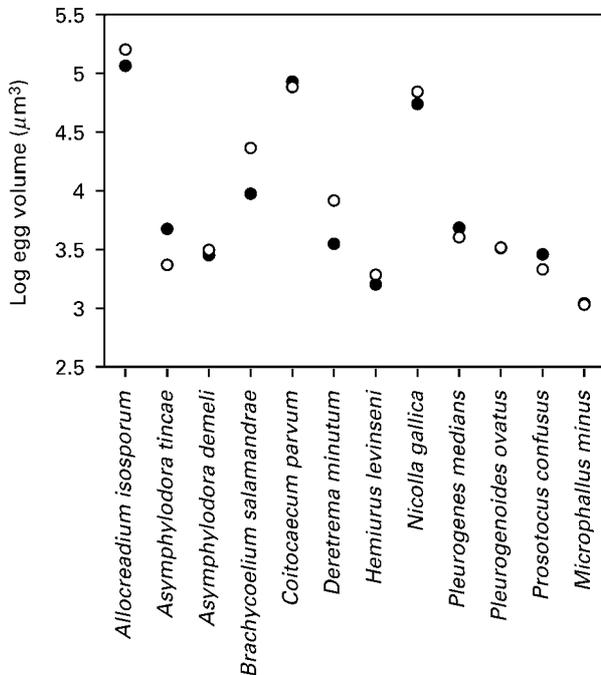


Fig. 4. Volume of eggs produced by both pro-genetic metacercariae in intermediate hosts (●) and non-pro-genetic, normal adults in definitive hosts (○) in 12 trematode species in which both development routes are observed. (Note: both points are stacked for *Pleurogenoides ovatus*.)

Although our analyses have not uncovered any basic life history difference between pro-genetic and non-pro-genetic trematodes, they have revealed one thing: the evolution of progenesis is not constrained by size-related traits. Truncation of the life cycle involving processes other than progenesis has also been documented in trematodes (Poulin & Cribb, 2002), including more drastic abbreviations from three hosts down to a single one (Barker & Cribb, 1993; Barger & Esch, 2000). Progenesis and life cycle abbreviations of other types are also known from other groups of parasites, such as nematodes (Jackson *et al.*, 1997; Levsen & Jakobsen, 2002). Perhaps the ability to truncate the life cycle is an intrinsic property of most trematodes and parasites with complex life cycles in general, and we have simply failed to notice it in most species. This is unlikely, however, given the large number of species that have been well studied. There must therefore exist some fundamental differences between species capable of life cycle truncation and those not capable of it. The recent emergence of many wildlife diseases shows how parasites can adjust to environmental changes that modify the conditions under which they are transmitted among hosts (Daszak *et al.*, 2000; Patz *et al.*, 2000; Harvell *et al.*, 2002). Progenesis and life cycle truncation provide many trematodes with the flexible transmission and developmental pathways necessary to adjust to environmental changes. Understanding the evolution of progenesis in trematodes is thus an important challenge for evolutionary biologists and parasitologists.

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