

REVIEW ARTICLE

Progenesis in digenean trematodes: a taxonomic and synthetic overview of species reproducing in their second intermediate hosts

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SUMMARY

Precocious egg production, i.e. progenesis, has been documented for a number of species in scattered reports throughout the trematode literature. The last 2 extensive studies on the subject date from Buttner in the early 1950s (in French) and from Tang in the early 1980s (in Chinese). Overall, 43 species were then known for their ability to produce eggs at the metacercarial stage while still in the second intermediate host. Here, we update the list, and document the existence of progenesis in a total of 79 digenean trematode species, for which we provide information on the taxonomy of the hosts, the facultative or obligate character of progenesis, relevant references, as well as some other pertinent biological information. We then review the subject by asking 7 questions of fundamental evolutionary importance. These include: What favours progenetic development? What are the associated costs and benefits? How are progenetic eggs released from the host? While exposing the various opinions of previous authors, we attempt to give a synthetic overview and stress on the importance of the metacercarial cyst wall (whether it is present, and if so its thickness) in the evolution and the adoption of a progenetic life-cycle.

Key words: Digenea, life-cycle, metacercariae, reproductive strategies, self-fertilization, egg production.

INTRODUCTION

Precocious egg production in parasites has been known since the report by von Siebold (1835), 'Helminthologische Beiträge', on eggs released from metacercariae found in the crayfish *Astacus astacus*. The term 'progénèse', i.e. progenesis later in English, was originally proposed by Giard (1887) for sexual maturity of animals that have not yet attained the adult stage. Dollfus (1924) first applied the term to trematodes when he observed egg production by the metacercariae of *Pleurogenoides medians* (Pleurogenidae). Now, the concept of progenesis is widely employed in palaeontology and botany, and quite commonly reported in many animal taxa (Anura, Urodela, Polychaeta).

At present, the accepted definition is the formal one proposed by Gould (1977): any heterochronic development in which first reproduction occurs at an earlier age, i.e. sexual maturation in an organism still in a morphologically juvenile stage. It is often confused with the term neoteny, but differs from it in

that, in neotenic organisms, first reproduction occurs at the same age as in normal organisms, via the retardation of somatic development. Both these processes are thus characterized by the retention of juvenile characters by adult stages (paedomorphic phenotypes; see for example Reilly, Wiley & Meinhardt, 1997). So, basically, progenesis is wrongly applied to trematodes, in which precocious worms are morphologically similar to the adults found in the definitive host. However, the term progenesis is now so widely used in the parasitological literature that it would be pointless and confusing to introduce a more specific term. We must simply use the term keeping in mind that it refers to the attainment of both sexual and somatic development in the non-definitive host. In our view, the most relevant definition for progenesis in trematodes is the production of viable eggs in individuals inhabiting an organism that would normally be considered an intermediate host.

Progenesis in trematodes thus encompasses all cases where a larval stage, a metacercaria or even a cercaria, attains such a degree of maturity that it can produce viable eggs. As a result, the life-cycle may be completed in 2 hosts or even in a single host. Progenesis may manifest itself in various degrees,

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from sporadic cases of egg production (1st stage of progenesis, according to Buttner, 1955) up to the obligate progenetic life-cycle (4th stage of progenesis). In such extreme cases, progenetic metacercariae are functionally and morphologically similar to adult forms in the definitive host, and are sometimes referred to as adults. However, we agree with Grabda-Kazubska (1976), that it is less confusing to keep calling them progenetic metacercariae or progenetic forms rather than adults, specifically when dealing with the evolution of life-cycles. Similarly, it seems to us important and useful to use the term historical host (see Maillard, 1973) to refer to the functional host in the ancestral 3-host life-cycle (e.g. the historical definitive host).

Progenesis and abbreviated life-cycles have been considered previously in the context of life-cycle evolution in trematodes, but usually as a marginal phenomenon (Ginetsinskaya, 1988; Galaktionov & Dobrovolskij, 2003). Truncated life-cycles have evolved independently many times in the phylogeny of trematodes (Poulin & Cribb, 2002). Progenesis is, in fact, only one of many ways in which trematodes can abbreviate their complex life-cycle (Grabda-Kazubska, 1976; Poulin & Cribb, 2002). Basically, in addition to progenesis, elimination of 1 or 2 hosts from the life-cycle can be achieved by (i) using the mollusc first intermediate host as the second intermediate host (no historical second host, metacercariae encyst in the mollusc and are ingested by a vertebrate definitive host), or by (ii) using the mollusc first intermediate host as second intermediate as well as definitive hosts (no historical second intermediate and vertebrate hosts, sporocysts directly produce either sexual adults or miracidia). However, progenesis is by far the most common way to shorten the life-cycle and 1-host life-cycles are very rare (Poulin & Cribb, 2002). In this review, we focused only on the possible elimination of the historical vertebrate host (i.e. egg production by the metacercariae in the historical second intermediate host). We thus restricted our synthesis to trematodes for which a cercarial stage penetrates, then matures into a metacercarial stage and produces eggs in a second intermediate host. We only investigated the subclass Digenea, with no regard to the small sister group Aspidogastrea. Moreover, it must be pointed out that we did not consider in our taxonomic review the species belonging to families for which all members are progenetic, i.e. the blood flukes Sanguinicolidae, Spirorchidae, and Schistosomatidae. They represent an ancestral life-cycle truncation inherited by all species in the clade, and are therefore much more specialized for a 2-host cycle than other taxa. Accounts of the biology and epidemiology of these 3 families and other relevant information can be found elsewhere in the literature. Nonetheless, because they represent a major transition in trematode evolution, we consider blood flukes in our synthetic

overview of progenesis, if only for comparative purposes. Here, we first provide an up-to-date compilation of progenetic trematode species, prior to addressing a range of important questions about the evolution of progenesis.

TAXONOMIC REVIEW: UPDATING THE LIST

Based on 2 previous works (Wu, 1938; Dawes, 1946), Yeh & Wu in 1950 compiled a list of 12 trematode species for which progenesis had been recorded. The first extensive review, however, was completed by Buttner in 4 consecutive papers published in French (Buttner, 1950*a*; 1951*a, b, c*). This author investigated the biological significance of progenesis and discussed in detail 30 progenetic trematode species. A second species list was later published in Chinese by Tang in 1980. The author, mainly referring to the Asian literature, compiled a list of 23 progenetic trematode species. So, at the time of this last review, leaving out duplicates, somewhere around 43 progenetic trematodes were known (i.e. taxa identified to species level).

Since then, a significant number of species needs to be added to the list for different reasons: (i) oversight of progenetic species in the previous lists, (ii) new evidence of progenetic development among previously described species, (iii) description of new species exhibiting progenetic development, (iv) revision of the trematode taxonomy.

Excluding blood flukes, we list here 79 trematode species for which egg production has been documented at the metacercarial stage (see Table 1). They belong to 50 genera and 24 families. Some of these families appear over-represented in the list; 5 out of the approximately 100 trematode families currently recognized (see Gibson, Jones & Bray, 2002) account for more than 50% of the total number of progenetic species listed here (Allocreadiidae $N=9$; Hemiuridae $N=6$; Macroderoididae $N=11$; Microphallidae $N=6$; Opecoelidae $N=9$). Among these families, the genus *Alloglossidium* (Macroderoididae) is particularly remarkable with a total of 11 progenetic species. Aquatic invertebrates are the historical second hosts of most progenetic trematodes (crustaceans $N=47$; insects $N=14$; leeches $N=8$; molluscs $N=7$; polychaetes $N=1$), though vertebrates are not rare (fish $N=14$; amphibians $N=8$). Concerning the definitive hosts, most of them are fish in case of facultative progenesis (fish $N=45$; amphibians $N=7$; mammals $N=6$; reptiles $N=5$; birds $N=4$). Overall, obligate progenetic species (i.e. with no demonstrated definitive host) represent 26% of progenetic species for which we have information on this aspect (obligate progenetic species: $N=17$; facultative progenetic species: $N=48$).

BIOLOGICAL REVIEW: QUESTIONS AND ANSWERS

Throughout the last century, many evolutionary aspects of progenesis in trematodes have been the subjects of fruitful debates. Some authors have greatly contributed to our understanding of the phenomenon: Dollfus (1924, 1927, 1929, 1938, 1954, 1958), Buttner (1950*a,b*, 1951*a,b,c*, 1953, 1955), Stunkard (1959, 1976), Stunkard & Uzmann (1959), Grabda-Kazubska (1969, 1975, 1976), Font (1980, 1994), Font & Corkum (1975, 1976). However, most have focused on particular taxa (e.g. Grabda-Kazubska on Leptophallidae, Font on Macroderoididae), in such a way that there have hitherto been few surveys covering progenesis in trematodes as a whole (see Poulin & Cribb, 2002, for an exception). Here, we attempt to present the various opinions found in the literature and draw up a synthetic overview by tackling 7 questions of major evolutionary interest.

(1) Is progenesis a relict or a novelty?

In the traditional interpretation, progenesis of the metacercariae takes place in what is considered an historical second intermediate host (Cable, 1965; Pearson, 1972; Grabda-Kazubska, 1976; Font, 1980). In this view, the progenetic species we observe today are secondarily derived from an ancestral 3-host life-cycle; this is the novelty hypothesis. Some other authors, in contrast, have regarded progenesis of the metacercariae as a reminiscence of an ancestral 2-host cycle, i.e. what it is referred to as the relict hypothesis (Stunkard, 1959; Riggs & Ulmer, 1983). In this last scenario, all trematodes were primitively reproducing in their second invertebrate hosts (historical definitive host for a time) and, as vertebrates evolved they displaced the higher-order invertebrate consumers from their positions at the top of the food chains. The progenetic species we observe today would thus correspond to the ones that did not incorporate a vertebrate host in their life-cycle.

The issue of the debate about the relictual or the novel character of progenesis inevitably raises the more general question, early pointed out by MacIntosh (1935), regarding the priority of the invertebrates or the vertebrates as definitive hosts in the evolution of trematodes (respectively in favour of the relictual and the novel hypotheses). Today, phylogenetic reconstructions all agree on a primitive cycle involving a mollusc as first host and a predatory vertebrate as definitive host. Much later, trematodes adjusted their developmental schedule to incorporate a second intermediate host as a trophic link to increase transmission toward the vertebrate host (Rohde, 1994; Ewald, 1995; Cribb *et al.* 2003). It is then on the basis of an ancestral 3-host cycle that abbreviation appeared independently in various

lineages. Recent investigations using analysis of character convergence strongly support the idea that the 2-host life-cycle derived from a more ancient 3-host life-cycle (Carney & Brooks, 1991; Smythe & Font, 2001). Therefore, it appears that progenesis must be considered as a novelty in the evolution of trematode life-cycles.

(2) What favours the evolution of progenesis?

This question needs to be investigated at 2 taxonomic levels: at the inter-specific level (between species) and at the intra-specific level (within species).

At the inter-specific level, we observe species that reproduce progenetically and others that do not, and this ability has evolved independently among unrelated trematode families (Grabda-Kazubska, 1976; Poulin & Cribb, 2002). In a recent study, we used a comparative approach to test whether progenetic species share common morphological or biological patterns that may explain the adoption of this alternative method of reproduction. We failed to detect any significant life-history differences between progenetic and non-progenetic taxa that could drive the evolution to progenesis (Lefebvre & Poulin, 2005*a*). However, although we could not test this, we suspect along with other authors that the presence and/or the thickness of the metacercarial cyst wall are of great significance. Indeed, while encystment in a relatively thick cyst wall is the rule in most trematodes (Lackie, 1975; Johnston & Halton, 1981), for the 51 progenetic species for which we possess information, 10% ($N=5$) are characterized by a thin cyst (transparent 1-layered envelope) and 43% by the absence of any cyst (i.e. free metacercariae; $N=22$).

Interestingly, in the progenetic *Proisorhynchoides gracilescens* (Bucephalidae), autoradiographic experiments measuring the level of incorporation of trace-labelled substrates suggested that the full development of encysted metacercariae is related to the thickness and permeability of the cyst wall (Halton & Johnston, 1982). So, it could be that acquisition of resources from the second intermediate host, which must be necessary for accelerated growth and egg production, is not possible in all trematodes because of the presence of an impermeable and thick metacercarial cyst. In contrast, the absence of a cyst wall would allow unrestricted feeding on host tissues (Matthews, 1973). It is worth noting that encystment in some Microphallidae is delayed and occurs only after the onset of sexual maturity (Sogandares-Bernal, 1962 in *Sogandaritrema progeneticus*; Caveny & Etges, 1971 in *Microphallus opacus*). In those situations when progenesis is the sole way of development for a given species, intrinsic or genetic factors are suspected to be involved in the determinism (Buttner, 1951*c*, 1953; Grabda-Kazubska, 1976).

Table 1. Updated list of digenean trematode species known to exhibit progenesis at the metacercarial stage

(Species are listed alphabetically according to their genus and species names, with authorities and dates of original descriptions. The taxonomy of the hosts is given by order (with full genus and species names in parentheses in cases of second intermediate hosts). The column F/O indicates whether progenesis is obligate or facultative. The column Sperm indicates whether sperm was observed in the reproductive system of the metacercariae. The column Cyst provides information about the presence/absence or thickness of the metacercarial cyst at the time of egg production. The column Viability provides information on tests of viability of progenetic generations (+ : hatching miracidia from egg; ++ : infection of the mollusc; +++ : infection up to the second intermediate host). Throughout the table, empty cells indicate that no corresponding information was found in the literature. To keep the references as succinct and informative as possible, priority was given to the latest issues of easily accessible international journals. Initials in parentheses indicate whether the species was already reported in the previous lists (B: Buttner, 1950a; Y&W: Yeh & Wu, 1950; T: Tang, 1980)).

Family	Species name	Second intermediate host	F/O	Definitive host	Sperm	Cyst	Viability	References
Allocreadiidae	<i>Allocreadium lobatum</i> Wallin, 1909	Amphipoda (<i>Gammarus pseudolimnaeus</i> , <i>Crangonyx gracilis</i>), Isopoda (<i>Caecidotea communis</i> , <i>C. intermedius</i>)	F	Fish Cypriniformes		No		DeGiusti, 1962; Camp, 1989
Allocreadiidae	<i>Allocreadium neotenicum</i> Peters, 1957	Coleoptera (<i>Acilius semisulcatus</i> , <i>Dytiscus</i> sp., <i>Agabus</i> sp.), Isopoda (<i>Caecidotea forbesi</i>)	O	No		No		Peters, 1957; Camp, 1992 (T)
Allocreadiidae	<i>Allocreadium tumidulum</i> (Rudolphi, 1819)	Ephemeroptera (<i>Hexagenia variabilis</i>)						Stafford, 1932 (B)
Macroderoididae	<i>Alloglossidium anomophagis</i> Poinar <i>et al.</i> 1995	Anomopoda (<i>Daphnia obtusa</i>)	O	No		Yes, thin		Poinar, Schwartz & Cameron, 1995
Macroderoididae	<i>Alloglossidium cardiacola</i> (Corkum & Turner, 1977)	Decapoda (<i>Procambarus acutus</i>)	O	No		No		Corkum & Turner, 1977; Turner, 1999
Macroderoididae	<i>Alloglossidium greeri</i> Font, 1994	Decapoda (<i>Cambarellus schufeldti</i>)	O	No	Yes	No		Font, 1994
Macroderoididae	<i>Alloglossidium hamrumi</i> Neumann & Vande Vusse, 1976	Leeches Gnathobdellida (<i>Haemopsis plumbea</i> , <i>Macrobdeella decora</i>)	O	No		No		Neumann & Vande Vusse, 1976; Font, 1980
Macroderoididae	<i>Alloglossidium hirudicola</i> Schmidt & Chaloupka, 1969	Leeches Arhynchobdellida (<i>Macrobdeella decora</i> , <i>M. ditetra</i>), Gnathobdellida (<i>Haemopsis grandis</i> , <i>H. lateromaculata</i> , <i>H. marmorata</i> , <i>H. plumbea</i>)	O	No		No		Schmidt & Chaloupka, 1969; Taft & Kordiyak, 1973
Macroderoididae	<i>Alloglossidium macrobdellensis</i> Beckerdite & Corkum, 1974	Leeches Arhynchobdellida (<i>Macrobdeella decora</i> , <i>M. ditetra</i>)	O	No		No		Corkum & Beckerdite, 1975; Font, 1980
Macroderoididae	<i>Alloglossidium progeneticum</i> (Sullivan & Heard, 1969)	Decapoda (<i>Procambarus spiculifer</i>)	F	Fish Siluriformes		Yes		Sullivan & Heard, 1969; Font & Corkum, 1975
Macroderoididae	<i>Alloglossidium renale</i> Font & Corkum, 1975	Decapoda (<i>Palaemonetes kadiakensis</i> , <i>P. paludosus</i>)	O	No		No		Font & Corkum, 1975; Font & Corkum, 1976

Macroderoididae	<i>Alloglossidium richardsoni</i> (Fish & Vande Vusse, 1976)	Leeches Arhynchobdellida (<i>Macrobdella decora</i>), Gnathobdellida (<i>Haemopsis</i> spp.)			No			Fish & Vande Vusse, 1976; Smythe & Font, 2001
Macroderoididae	<i>Alloglossidium schmidti</i> Timmers, 1979	Leech Gnathobdellida (<i>Haemopsis grandis</i>)	O	No				Timmers, 1979; Vande Vusse, 1980
Macroderoididae	<i>Alloglossidium turnbulli</i> Neumann & Vande Vusse, 1976	Leeches Gnathobdellida (<i>Haemopsis grandis</i> , <i>H. plumbea</i>)	O	No		No		Neumann & Vande Vusse, 1976; Carney & Brooks, 1991
Cryptogonimidae	<i>Aphalloides coelomicola</i> Dollfus <i>et al.</i> 1957	Fish Perciformes (<i>Potamoschistus microps</i>)	O	No	Yes	No		Dollfus, Chabaud & Golvan, 1957; Maillard, 1973
Heterophyidae	<i>Ascocotyle angrense</i> (Travassos, 1916)	Fish Cypriniformes (<i>Phalloceros caudimaculatus</i>)	F	Birds Ciconiiformes, Mammals Carnivora				Travassos, 1931; Buttner, 1950a (B)
Allocreadiidae	<i>Astacotrema cirrigerum</i> (Baer, 1827)	Decapoda (<i>Astacus astacus</i>)					Yes	Buttner, 1951c (B, Y&W)
Allocreadiidae	<i>Astacotrema tuberculatum</i> (Zawadowsky, 1926)	Decapoda						In Yeh & Wu, 1950 (Y&W)
Monorchidae	<i>Asymphyldora demeli</i> Markowski, 1935	Polychaeta (<i>Nereis diversicolor</i>)	F	Fish Cypriniformes, Perciformes		No		Reimer, 1973; Vaes, 1974
Brachycoeliidae	<i>Brachycoelium salamandrae</i> (Frölich, 1789)	Anura (<i>Rana esculenta</i>), Urodela (<i>Triturus</i> <i>marmoratus</i> , <i>T. palmatus</i>)	F			Yes		Buttner, 1951c (B)
Hemiuridae	<i>Bunocotyle meridionalis</i> Chabaud & Buttner, 1959	Copepoda (<i>Poppella guernei</i>)	F	Fish Perciformes	Yes			Chabaud & Biguet, 1954
Hemiuridae	<i>Bunocotyle progenetica</i> (Markowski, 1936)	Mollusc Monotocardia (<i>Hydrobia ventrosa</i>)						Markowski, 1936; Buttner, 1950a (B)
Opecoelidae	<i>Coitocaecum angusticolle</i> (Hausmann, 1896)	Amphipoda (<i>Echinogammarus</i> <i>berilloni</i> , <i>Gammarus pulex</i>)	F	Fish Anguilliformes, Scorpaeniformes	Yes	Yes		Dollfus, 1938; Buttner, 1950a (B)
Opecoelidae	<i>Coitocaecum parvum</i> Crowcroft, 1945	Amphipoda (<i>Anaspides</i> <i>tasmaniae</i> , <i>Paracalliope</i> <i>fluviatilis</i>), Mysidacea (<i>Tenagomysis chiltoni</i>)	F	Fish Anguilliformes, Osmeriformes, Perciformes, Salmoniformes	Yes	Yes, thin	++	Holton, 1984b; Lefebvre & Poulin, 2005b (B, Y&W, T)
Opecoelidae	<i>Coitocaecum testiobliquum</i> Wisniewski, 1932	Amphipoda (<i>Pontogammarus</i> <i>bosniacus</i> , <i>Rivulogammarus</i> <i>spinicaudatus</i>)	F	Fish Salmoniformes		Yes		Wisniewski, 1932; Buttner, 1950a (B, T)
Allocreadiidae	<i>Crepidostomum cornutum</i> (Osborn, 1903)	Decapoda (<i>Cambarus nais</i> , <i>C. propinquus</i> , <i>C. virilis</i>)	F	Fish Siluriformes	Yes	Yes		Buttner, 1950a; Cheng, 1957 (B)
Proterodiplostomidae	<i>Crocodicicola pseudostoma</i> (Willemoes-Suhm, 1870)	Fish Siluriformes (<i>Hemisorubim platyrhynchos</i> , <i>Rhamdia guatemalensis</i>)	F	Reptiles Crocodylia				Pérez-Ponce de León, Osorio-Sarabia & García-Prieto, 1992; Guidelli, Isaac & Takemoto, 2003

Table 1. (Cont.)

Family	Species name	Second intermediate host	F/O	Definitive host	Sperm	Cyst	Viability	References
Derogenidae	<i>Derogenes varicus</i> (Müller, 1784)	Chaetognaths Aphragmophora (<i>Sagitta bipunctata</i> , <i>S. elegans</i> , <i>S. setosa</i>), Decapoda (<i>Pagurus</i> <i>pubescens</i>), Copepoda, Cephalopoda	F	Fish Anguilliformes, Gadiformes, Salmoniformes				Dollfus, 1954; Øresland, 1986 (B, Y&W, T)
Hemiuridae	<i>Dimurus tornatus</i> (Rudolphi, 1819)	Decapoda (<i>Cerataspis</i> <i>monstrosa</i>)	F	Fish Perciformes		No		Dollfus, 1927; Buttner, 1950a (B, T)
Allocreadiidae	<i>Distoma agamos</i> Linstow, 1872	Amphipoda (<i>Gammarus pulex</i>), Isopoda (<i>Asellus aquaticus</i>)			Yes	Yes		Buttner, 1950a (B)
Allocreadiidae	<i>Distoma reinhardi</i> (Baer)	Decapoda (<i>Astacus</i> <i>leptodactylus</i>)				No		Buttner, 1950a (B)
Bucephalidae	<i>Dollfustrema echinatum</i> Komiya & Tajimi, 1941	Fish Cypriniformes (<i>Pseudorasbora parva</i>)						Komiya & Tajimi, 1941 (T)
Bucephalidae	<i>Dollfustrema foochowensis</i> Tang & Tang, 1963	Fish Perciformes (<i>Boleophthalmus chinensis</i>)						In Tang, 1980 (T)
Hemiuridae	<i>Ectenurus lepidus</i> Looss, 1907	Chaetognath Aphragmophora (<i>Sagitta bedoti</i>)	F	Fish Perciformes				Jarling & Kapp, 1985; Shimazu, 1991
Derogenidae	<i>Genarchella genarchella</i> Travassos <i>et al.</i> 1928	Fish Cypriniformes, Molluscs Neotaenioglossa (<i>Littoridina</i> <i>australis</i> , <i>L. parachappei</i>)	F	Fish Characiformes, Siluriformes				Martorelli, 1989; Scholtz, Vargas-Vasquez & Salgado- Maldonado, 1995 (T)
Derogenidae	<i>Genarchopsis shanghaiensis</i> Yeh & Wu, 1955	Decapoda (<i>Macrobrachium</i> <i>nipponensis</i>)						Yeh & Wu, 1955 (T)
Microphallidae	<i>Gynaecotyla adunca</i> Linton, 1905	Amphipoda (<i>Corophium</i> <i>volutator</i>)	F	Birds Charadriiformes		No		Hunter & Vernberg, 1953
Microphallidae	<i>Gynaecotyla longiintestinata</i> Leonov, 1958	Decapoda (<i>Carcinus</i> <i>mediterraneus</i>)	F	Birds Charadriiformes		No		Prévot, 1974
Haematoloechidae	<i>Haematoloechus similis</i> (Looss, 1899)	Odonata (<i>Calopteryx virgo</i>)				No		Buttner, 1950a (B)
Derogenidae	<i>Halipegus mehransis</i> Srivastava, 1933	Odonata (<i>Brachythemis</i> <i>contaminata</i>)	F	Anura	Yes			Nath & Pande, 1970
Hemiuridae	<i>Hemiurus levinseni</i> Odhner, 1905	Chaetognath Aphragmophora (<i>Sagitta elegans</i>), Mysidacea (<i>Mysis stenolepis</i> , <i>Neomysis</i> <i>americana</i>)	F	Fish Gadiformes, Pleuronectiformes				Myers, 1956; Jackson, Marcogliese & Burt, 1997
Hemiuridae	<i>Lecithochirium rufoviride</i> (Rudolphi, 1819)	Fish Perciformes (Blennius pholis)	F	Fish Anguilliformes, Lophiiformes		Yes		Buttner, 1950a (B)
Zoogonidae	<i>Limnoderetrema minutum</i> (Manter, 1954)	Mysidacea (<i>Tenagomysis</i> <i>chiltoni</i>)	F	Fish Anguilliformes, Osmeriformes		Yes		Manter, 1954; Holton, 1983

Microphallidae	<i>Microphallus minus</i> Ouchi, 1928	Decapoda (<i>Palaemon asperulus</i> , <i>P. nipponensis</i>)	F	Mammals Carnivora, Primates, Rodentia	Yes	Yes		Yeh & Wu, 1950 (Y&W, T)
Microphallidae	<i>Microphallus opacus</i> (Ward, 1894)	Decapoda (<i>Cambarus propinquus</i>)	F	Fish, Mammals, Reptiles	Yes	Yes		Sogandares-Bernal, 1965; Caveny & Etges, 1971 In Tang, 1980 (T)
Echinostomatidae	<i>Neoacanthoparyphium petrowi</i> (Nevostrueva, 1953)	Anura (<i>Rana temporaria</i>)	F	Birds? Mammals?				
Lecithodendriidae	<i>Neoprosthodendrium progeneticum</i> Hall, 1960	Odonata (<i>Hetaerina americana</i>)				No		Hall, 1960 (T)
Opecoelidae	<i>Nicolla gallica</i> (Dollfus, 1941)	Amphipoda (<i>Echinogammarus berilloni</i> , <i>Gammarus pulex</i>)	F	Fish Anguilliformes, Scorpaeniformes	Yes	Yes		Dollfus, 1958
Opecoelidae	<i>Opecoeloides manteri</i> (Hunninen & Cable, 1940)	Amphipoda (<i>Amphitoe longimana</i> , <i>Carinogammarus mucronatus</i>)	F	Fish Syngnathiformes		Yes		Hunninen & Cable, 1941; Buttner, 1950a (B, Y&W, T)
Eumegacetidae	<i>Orthetrotrema monostomum</i> Macy & Basch, 1972	Odonata (<i>Orthetrum sabina</i> , <i>Tramea limbata</i>)	O	No	Yes	No	+	Macy & Basch, 1972; Madhavi & Swarnakumari, 1995
Leptophallidae	<i>Paralepoderma acervocalciferum</i> (Gastaldi, 1854)	Anura (<i>Rana esculenta</i>)	F	Reptiles Squamata				Buttner, 1950a (B)
Leptophallidae	<i>Paralepoderma brumpti</i> (Buttner, 1950)	Anura (<i>Alytes obstetricans</i> , <i>Rana ridibunda</i>), Urodela (<i>Triturus palmatus</i>)	O	No		Yes	+++	Buttner, 1950b, 1955 (B, T)
Leptophallidae	<i>Paralepoderma progeneticum</i> (Buttner, 1950)	Amphipoda (<i>Gammarus</i> sp.), Mollusc Basommatophora (<i>Planorbis planorbis</i>)	O	No		No	+++	Buttner, 1951c; Grabda- Kazubaska, 1975 (B, T)
Gorgoderidae	<i>Phyllodistomum lesteri</i> Wu, 1938	Decapoda (<i>Palaemon asperulus</i> , <i>P. nipponensis</i>)	F	Fish	Yes	Yes		Wu, 1938; Buttner, 1950a (B, Y&W, T)
Gorgoderidae	<i>Phyllodistomum nocomis</i> Fischthal, 1942		F					Wanson & Larson, 1972
Opecoelidae	<i>Plagioporus cooperi</i> Hunter & Bangham, 1932	Ephemeroptera (<i>Blasturus cupidus</i>)	F	Fish Cypriniformes, Cyprinodontiformes				Cooper, 1915; Buttner, 1950a (B)
Opecoelidae	<i>Plagioporus siliculus</i> Sinitsin, 1931	Decapoda (<i>Astacus</i> sp.)				Yes		Sinitsin, 1931; Buttner, 1950a (B)
Pleurogenidae	<i>Pleurogenoides japonicus</i> (Yamaguti, 1936)	Decapoda (<i>Macrobrachium nipponensis</i> , <i>Neocaridinia denticulata</i>)	F	Anura		Yes		Okabe & Shibue, 1951; in Tang, 1980 (T)

Table 1. (Cont.)

Family	Species name	Second intermediate host	F/O	Definitive host	Sperm	Cyst	Viability	References
Pleurogenidae	<i>Pleurogenoides medians</i> (Olsson, 1876)	Amphipoda (<i>Gammarus pulex</i> , <i>Echinogammarus berilloni</i>), Coleoptera (<i>Dytiscus</i> <i>marginalis</i>), Diptera (<i>Chironomus</i> sp.), Ephemeroptera (<i>Ephemerides</i> sp.), Neuroptera (<i>Sialis</i> <i>lutaria</i>), Odonata (<i>Aeschna</i> sp., <i>Libellula</i> sp.)	F	Anura, Urodela	Yes	Yes, thin		Dollfus, 1924; Buttner, 1951 b (B, Y&W, T)
Pleurogenidae	<i>Pleurogenoides ovatus</i> Rao, 1977	Decapoda (<i>Paratelphusa</i> <i>hydrodromous</i>)	F	Anura		Yes		Rao, 1977; Janardanan, Ramanandan & Usha, 1987
Pleurogenidae	<i>Pleurogenoides sitapurii</i> (Srivastava, 1934)	Decapoda (<i>Paratelphusa</i> <i>ceylonensis</i>)	F	Anura				Dissanaike & Fernando, 1960 (T)
Opecoelidae	<i>Podocotyle atomon</i> (Rudolphi, 1802)	Amphipoda (<i>Amphitoe</i> <i>longimana</i> , <i>Carinogammarus</i> <i>mucronatus</i> , <i>Gammarus</i> sp.)	F	Fish Anguilliformes, Gadiformes, Gasterosteiformes, Perciformes, Pleuronectiformes, Scorpaeniformes, Syngnathiformes				Hunninen & Cable, 1943; Køie, 1981 (B)
Fellodistomidae	<i>Proctoeces lintoni</i> Siddiqi & Cable, 1960	Limpets Gastropoda (<i>Fissurella</i> spp.)	F	Fish Gobiesociformes, Perciformes				Oliva & Huaquin, 2000
Fellodistomidae	<i>Proctoeces maculatus</i> (Looss, 1901)	Molluscs Bivalvia (<i>Mytilus</i> spp., <i>Scrobicularia plana</i>), Gastropoda (<i>Buccinum</i> <i>undatum</i> , <i>Nucella lapillus</i>)	F	Fish Perciformes	Yes			Stunkard & Uzman, 1959; Bray & Gibson, 1980 (T)
Derogenidae	<i>Progonus mülleri</i> (Levinsen, 1881)	Amphipoda (<i>Caprella</i> <i>septentrionalis</i>)						Uspenskaya, 1960
Bucephalidae	<i>Prosorhynchoides gracilescens</i> (Rudolphi, 1819)	Fish Gadiformes (<i>Ciliata</i> <i>mustela</i> , <i>Gadus aeglefinus</i> , <i>G. callarias</i> , <i>G. merlangus</i> , <i>G. minutus</i> , <i>G. pollachius</i> , <i>G. virens</i> , <i>Merluccius</i> <i>merluccius</i> , <i>Molva molva</i> , <i>Urophycis blenoides</i>)	F	Fish Lophiiformes	Yes	Yes, thin, sometimes free		Matthews, 1974; Erwin & Halton, 1983
Bucephalidae	<i>Prosorhynchus squamatus</i> Odhner, 1905	Fish	F	Fish Gadiformes, Pleuronectiformes, Scorpaeniformes, Anguilliformes				Chubrik, 1952

Pleurogenidae	<i>Prosotocus confusus</i> (Looss, 1894)	Odonata (<i>Aeschna cyanea</i> , <i>A. grandis</i> , <i>A. juncea</i> , <i>Anax</i> <i>imperator</i>)	F	Anura, Reptiles Squamata	Yes		++	Bayanov, 1975
Lecithodendriidae	<i>Prosthodendrium chilostomum</i> (Mehlis, 1831)	Trichoptera (<i>Phryganea</i> <i>grandis</i> , <i>Phryganea</i> sp.)	F	Mammals Chiroptera	Yes	Yes		Skrjabin, 1915; Brown, 1933 (B, Y&W)
Allocreadiidae	<i>Pseudoalloeceadium</i> <i>alloneotenicum</i> (Wootton, 1957)	Trichoptera (<i>Limnephilus</i> sp.)	O	No			++	Wootton, 1957; Caira & Scudder, 1985
Opecoelidae	<i>Pseudopecoelus japonicus</i> (Yamaguti, 1938)	Crustacean Euphausiacea, (<i>Euphausia similis</i>)	F	Fish Aulopiformes, Syngnathiformes				Komaki, 1970; Shimazu, 1971
Psilostomidae	<i>Psilostomum progeneticum</i> Wisniewski, 1932	Amphipoda (<i>Pontogammarus</i> <i>bosniacus</i> , <i>Rivulogammarus</i> <i>spinicaudatus</i>)	F					Wisniewski, 1932; Buttner, 1950a (B, Y&W, T)
Microphallidae	<i>Quasimaritrema caridinae</i> (Yamaguti & Nishimura, 1944)	Decapoda (<i>Caridina</i> <i>denticulata</i>)	F	Birds Charadriiformes		Yes		Yamaguti & Nishimura, 1944; Yamaguti, 1958 (Y&W, T)
Opisthorchiidae	<i>Ratzia joyeuxi</i> (Brumpt, 1922)	Anura (<i>Discoglossus pictus</i>)	O	No	No	Yes, thin	+++	Buttner, 1951b; Buttner, 1955 (B)
Opisthorchiidae	<i>Ratzia parva</i> (Stossich, 1904)	Anura (<i>Rana esculenta</i> , <i>R. perezi</i> , <i>R. ridibunda</i>)	F	Reptiles Squamata	Yes	Yes	+	Fuhrmann, 1928; Lluch, Navarro & Roca, 1985 (B, Y&W, T)
Microphallidae	<i>Sogandaritrema progeneticus</i> (Sogandares-Bernal, 1962)	Decapoda (<i>Cambarellus puer</i> , <i>C. shufeldtii</i> , <i>Procambarus</i> <i>clarkii</i>)	O	No		No		Sogandares-Bernal, 1962; Lotz & Corkum, 1983
Zoogonidae	<i>Steganoderma formosum</i> Stafford, 1904	Decapoda (<i>Pagurus acadianus</i> , <i>P. pubescens</i>)	F	Fish Gadiformes, Pleuronectiformes, Scorpaeniformes	Yes	No		Bray, 1987; Marcogliese, 1996
Lepocreadiidae	<i>Stegodexamene anguillae</i> MacFarlane, 1951	Fish Osmeriformes (<i>Galaxias</i> <i>brevipennis</i> , <i>G. maculatus</i>), Perciformes (<i>Gobiomorphus</i> <i>cotidianus</i>)	F	Fish Anguilliformes		Yes	++	MacFarlane, 1951; Holton, 1984a
Cryptogonimidae	<i>Telogaster opisthorchis</i> MacFarlane, 1945	Fish Osmeriformes (<i>Galaxias</i> <i>brevipennis</i> , <i>G. maculatus</i>), Perciformes (<i>Gobiomorphus</i> <i>breviceps</i> , <i>Philypnodon</i> spp.), Salmoniformes (<i>Salmo</i> <i>trutta</i>)	F	Fish Anguilliformes		Yes		MacFarlane, 1945 (B)

For instance, in the obligate progenetic *Alloglossidium renale* (Macroderoidae), the whole metacercarial development up to egg production seems to be fixed and can be completed in less than 6 weeks, with no apparent contribution of extrinsic factors (Font & Corkum, 1976; Font, 1980).

At the intra-specific level, when progenesis is facultative (i.e. only adopted by certain members of the species), we might expect the involvement of proximal cues in the evolution toward progenetic development. Four main factors can be identified from the works of previous investigators: the internal host resources, the environmental instability, the vertebrate host unavailability and the developmental time.

First, the internal host resources. It has been proposed that the production of eggs depends on the trophic quality of the host organisms or the particular organ in which the metacercariae are localized (MacFarlane, 1951 in *Stegodexamene anguillae*; Baer & Joyeux, 1961; Halton & Johnston, 1982 in *Proisorhynchoides gracilescens*). In *P. gracilescens* for instance (Bucephalidae), metacercarial cysts localized in the cranial cavity of second fish intermediate hosts become progenetic while those in the nasal or orbit regions remain sexually immature (Halton & Johnston, 1982). Such variability in the tendency to develop progenetically has been shown to mirror differences in the structure of the cyst wall, which is thin in the cranial cavity and thicker elsewhere (see above). To some extent, this reflects the usual relationship, pointed out by Dogiel (1964), between the degree of progenesis displayed by a parasite and its host specificity: parasite stages that undergo vigorous development are narrowly specific to their host. The author illustrated his opinion with the example of Microphallidae species for which the metacercariae undergo considerable development (sometimes even achieving egg formation) and that show a narrow specificity to their second intermediate hosts (Dogiel, 1964).

Second, the instability of the environment. It has been proposed by different authors that the occurrence of progenetic development may relate to some characteristics of the habitat; these may include unpredictable water levels (Holton, 1984a in *Coitocaecum parvum* and *Stegodexamene anguillae*; Poinar, Schwartz & Cameron, 1995 in *Alloglossidium anomophagis*), water salinity (Reimer, 1961 in *Bunocotyle meridionalis*), and water temperature (Buttner, 1951b in *Pleurogenoides medians*). Holton (1984a) thus suggested that trematode species are more likely to exhibit progenesis when they live in streams subjected to regular floods and droughts.

Third, the unavailability of the vertebrate host. A number of authors have remarked that progenetic metacercariae are particularly common when definitive hosts are absent in the area of study (Hickman, 1934 in *Coitocaecum parvum*; Bayanov,

1975 in *Prosotocus confusus*; Hine, 1978 in *Stegodexamene anguillae*), or temporally unavailable (seasonal migration of birds and fish, aestivation in frogs; Janardanan, Ramanandan & Usha, 1987 in *Pleurogenoides ovatus*). This may also apply to systems where definitive hosts are present but in such low abundance that the predatory rate is negligible (Chabaud & Biguet, 1954 in *Bunocotyle meridionalis*).

Fourth, the developmental time. For a number of authors, the time spent in the intermediate host is also believed to be an important trigger of progenesis (MacMullen, 1938 in various Leptophallidae; Grabda-Kazubska, 1976). Grabda-Kazubska (1976) stated that, in Leptophallidae, progenesis is the result of the extended duration of the metacercarial stage within the intermediate hosts. It could be that some internal developmental clock or other proximal cues may cause, beyond a certain time of encystment, the sexual maturation of the worm and egg production. In support of this idea, progenesis has sometimes been shown to be more pronounced among larger, and older, intermediate hosts (Erwin & Halton, 1983 in *Proisorhynchoides gracilescens*; Lefebvre & Poulin, 2005b, in *Coitocaecum parvum*).

Finally, 3 out of the 4 factors herein advanced (i.e. environmental instability, vertebrate host unavailability, developmental time) revolve around the fact that progenesis occurs when the probability of transmission to a definitive host is restricted. The mechanisms by which trematodes are able to detect the uncertainty of transmission are not yet fully understood. Nonetheless, parasites are now well known for their ability to detect signals from their immediate surroundings (physiological and biochemical conditions of their hosts) or external environment (host habitats) and to adjust their developmental schedule in consequence (Sukhdeo & Bansemir, 1996; Thomas *et al.* 2002). In this context, recent experiments by Poulin (2003) are particularly relevant. The author experimentally demonstrated that the opoecolid *Coitocaecum parvum* can accelerate its development and reach precocious maturity in its crustacean intermediate host in the absence of chemical cues emanating from its fish definitive host. Thus, progenesis is the preferred strategy when opportunities for transmission to definitive hosts are perceived to be limited (Poulin, 2003).

(3) What about the viability of progenetic generations?

This question makes sense only for facultative progenetic species. Indeed, obligate progenetic species only produce progenetic eggs and their survival in nature provides the best evidence of the viability of their offspring. This is the case for all members of the 3 blood fluke families, i.e. Sanguinicolidae, Schistosomatidae, Spirorchidae, that display an obligate 2-host cycle by way of progenesis (Poulin &

Cribb, 2002). This should also hold for species that belong to families or genera mainly using typical 3-host life-cycles, but for which adults have never been found in a vertebrate definitive host (i.e. obligate progenetic species as listed in Table 1). In this regard, an interesting example is provided by the obligate progenetic *Paralepoderma brumpti* (Leptophallidae) for which the complete viability of 10 progenetic generations was demonstrated in the laboratory (Buttner, 1953, 1955). Buttner (1951b; 1955) also investigated *Ratzia joyeuxi* (Opisthorchiidae) and was successful in running 3 successive cycles from progenetic eggs. For facultative progenetic species, the viability of progenetic eggs and subsequent larval stages has either not been experimentally tested or if so then only partially ($N=4$ species, see Table 1). Though negative results may be caused by artificial laboratory conditions, it is worth noting that, in some other reports, eggs produced by progenetic metacercariae failed to hatch or were incapable of infecting the first mollusc host (Cheng, 1957 in *Crepidostomum cornutum*, Winstead & Couch, 1981 in *Proctoeces* sp.).

(4) What are the benefits of progenesis?

The potential benefits of progenesis appear to revolve around 1 major key point: the subsequent reduction in the number of transmission events before reproduction, with the simpler life-cycle being easier to complete. By adopting progenetic development, all metacercariae are potential breeders while in normal 3-host life-cycles a great number of metacercariae die with their intermediate hosts or do not successfully establish in the definitive hosts (Buttner, 1951c; Grabda-Kazubska, 1976; Font, 1980; Poulin & Cribb, 2002). Progenesis is thus a reproductive insurance strategy (see Wang & Thomas, 2002).

In addition, some other authors argue that progenesis, and its associated low genetic diversity (see question 5 and the comments about parthenogenesis and self-fertilization), may favour highly specialized trematode species, well adapted to stable, conservative habitats (Grabda-Kazubska, 1976). Similarly, the limited dispersal generally associated with progenesis (due to the absence of the more vagile vertebrate host) has sometimes been considered as an advantageous feature when, for example, the first mollusc host has a very local distribution (Jamieson, 1966).

(5) What are the costs of progenesis?

The main disadvantage commonly attributed to progenetic life-cycles rests on the genetic basis of egg formation. For some authors, progenesis must be achieved via parthenogenesis, since male reproductive organs have been described as immature at

the time progenetic eggs are observed (MacFarlane, 1939 in *Coitocaecum parvum*; Buttner, 1951b in *Ratzia joyeuxi*; Bray, 1987 in *Steganoderma formosum*). This may be true for some species (e.g. *Ratzia joyeuxi*) but, in most cases, further or later studies have revealed that both male and female reproductive systems are fully functional, and active sperm has been observed in many species ($N=19$ in the present list, Table 1). More sophisticated observational and experimental investigations (labelled sperm, autoradiography, transplantation) also support the frequent use of self-fertilization in the process of progenetic egg formation (Khalil & Cable, 1968; Nollen, 1978; Marcogliese, 1996).

In the eventuality of parthenogenesis, progenetic eggs would result from asexual (clonal) reproduction. On the other hand, if progenetic eggs are produced by self-fertilization, this constitutes the most severe case of inbreeding. In both cases, the absence of genetic exchange leads to a loss of genetic variability (homozygosity), and may, in the long term at least, reduce the adaptiveness of the parasite to potential changes in the environment. The deleterious effect of homozygosity is a cornerstone of evolutionary biology (Maynard-Smith, 1998; West, Lively & Read, 1999), and is commonly advanced by parasitologists to explain why progenesis is not more widespread (Grabda-Kazubska, 1976; Font, 1980).

However, experimental investigations on progenetic trematodes have given a more ambivalent view. Buttner (1953, 1955), in her remarkable experiments on the leptophallid *Paralepoderma brumpti*, was able to maintain 10 progenetic generations without any noticeable deleterious effect (egg productivity, egg hatching rate, infectivity of larval stages). Nollen (1971) showed that a selfing strain of the philophthalmid *Philophthalmus megalurus* (from isolated adults in the definitive bird host) exhibited no decreased performance (growth, egg shell formation, viable miracidia and cercariae) except for a lower infectivity to the definitive host when compared to a cross-fertilized strain after 3 successive life-cycles. Self-fertilization with the production of viable eggs has thus been described not only for progenetic metacercariae isolated in cysts (see examples in question 3 above), but also for single worm infection in the definitive host (Nollen, 1983). Self-fertilization is thought to be a common type of reproduction amongst many, if not most, trematodes even in the case of adults in the definitive host (Smyth, 1962; Nollen, 1983). The general impression remains that trematodes can survive utilizing self-fertilization, at least for short periods of time (Bush & Kennedy, 1994).

Progenesis may not only have consequences for offspring quality, it may also influence the quantity of offspring that can be produced. It has been repeatedly suggested that progenetic metacercariae in their second intermediate hosts are not as fecund, in

term of egg numbers, as adults could be in their definitive hosts (see Buttner, 1955; Jackson, Marcogliese & Burt, 1997 in *Hemiurus levinsemi*). The reasons mainly involve limited host resources (space and/or energy in the second hosts, generally an invertebrate) or accessibility of host resources (localization in the host, presence of a thick cyst wall of either parasite or host origin). However, there are also a number of reports of high fecundity in the second intermediate host, sometimes amounting to several thousand eggs (Nath & Pande, 1970 in *Halipegus mehransis*; Macy & Basch, 1972 in *Orthotremema monostomum*; Maillard, 1973 in *Aphalloides coelomicola*).

Another cost of the progenetic life-cycle may concern the limited egg dispersal in the environment (Font, 1980). Indeed, in the absence of vertebrate definitive hosts, that have larger habitats and greater displacements, we may expect a lower colonization potential for progenetic generations (vertebrate hosts being commonly viewed as 'transport hosts', see for instance Ewald, 1995).

(6) How are progenetic eggs released?

In trematodes with a 3-host life-cycle, adult worms are most often located in the intestine of the definitive host and eggs are released with the faeces into the external medium. In trematodes with a 2-host life-cycle, eggs are produced inside the intermediate host (body cavity, muscles) and most often within a metacercarial cyst. The unusual site of egg production leads to the question regarding the release of these eggs to the outside (i.e. the aquatic medium where they can hatch and infect a first intermediate mollusc host). From the literature, we have identified 5 ways used by trematodes for their eggs to reach the outside environment: (i) by host death, (ii) with host eggs, (iii) with host excretory products, (iv) by host predation, (v) by host skin rupture.

(i) *Host death.* Waiting for the natural death of their host seems to be the most common way used by progenetic species for their eggs to be released (DeGiusti, 1962 in *Allocreadium lobatum*; Deblock, 1975 in various microphallids; Lotz & Corkum, 1983 in *Sogandaritrema progeneticus*; Holton, 1984a in *Coitocaecum parvum*). Enzymes of the dying host (hepatopancreas fluid) may even induce or accelerate the liberation of the encysted metacercariae (Holton, 1984a in *Coitocaecum parvum*). A typical example is given by the obligate progenetic *Aphalloides coelomicola* (Cryptogonimidae) that releases its eggs within the body cavity of its fish host. The life-cycle of this trematode is synchronized with that of its host; progenetic egg production occurring at the end of the host reproductive season, i.e. at the end of the host life in this annual fish species (Maillard, 1973; Pampoulie *et al.* 2000). In that particular case, it

seems that the parasite has exploited a natural feature of its host for its eggs to be released. Sometimes, it seems that progenetic parasites may themselves favour the death of their host. In a number of invertebrate hosts, eggs are produced in the body cavity and their free distribution may accelerate host death by interference with or damage of vital organs (e.g. sinus in *Coitocaecum parvum*, Hickman, 1934). In *Microphallus opacus* (Microphallidae), the rapid excystment (less than 2 h even in tap water) following host death suggests the endogenous production of histolytic agents by the worms, rather than microbial or host derived enzymes (Caveny & Etges, 1971).

(ii) *Host eggs.* This is the exit route of the facultative progenetic *Stegodexamene anguillae* (Lepocrea-diidae) that encysts in small fish as intermediate hosts. While non-progenetic metacercariae are mainly found in the muscles, progenetic metacercariae occur in the ovaries of female fish hosts, from where they are expelled at the time of fish spawning (MacFarlane, 1951). It is worth noting that the progenetic metacercariae in their cysts filled with their own eggs have approximately the same diameter as fish eggs, and thus benefit from the fish's reproductive efforts.

(iii) *Excretory products.* In these cases, progenetic metacercariae are located in the excretory organs of their hosts, such as antennary glands or the intestinal tracts. Typical examples are provided by species of the genus *Alloglossidium* (Macroderoididae) that mature in various crustacean and leech intermediate hosts (Font & Corkum, 1976; Font, 1980). Sometimes, as for *Alloglossidium macrodellensis*, the metacercariae grow and encyst in the coelom or muscles of their second leech hosts before migrating to the lumen of the intestine where they excyst and start egg production (Corkum & Beckerdite, 1975).

(iv) *Host predation.* In species that use this route, eggs are ingested along with their intermediate hosts, and expelled with the faeces of predators. Predation of the prey host may occur either by the historical definitive host as in the cases of facultative progenesis, or by any other trophic predators (Bayanov, 1975 in *Prosotocus confusus*; Madhavi & Swarnakumari, 1995 in *Orthotremema monostomum*). For instance, Bayanov (1975) did not demonstrate but strongly suspected that progenetic eggs of *P. confusus* (Pleurogenidae) are dispersed through predation of the odonate intermediate hosts by anurans (facultative definitive hosts) and insectivorous birds (alternative predators in the food chain).

(v) *Host skin rupture.* This seems to apply only to the obligate progenetic *Ratzia joyeuxi* (Opisthorchiidae) that encysts right under the epidermis of its

amphibian hosts. While growing, metacercariae deform the skin and at maturity, progenetic cysts fall off and then excyst in the external environment (Buttner, 1951b).

(7) *Is progenesis a clear-cut strategy?*

In other words, are egg-producing worms at the metacercarial stage able to further reproduce in a definitive host, or does progenesis in the intermediate host prevent the continuation of the normal 3-host cycle? Again, this question needs to be investigated at 2 levels, according to the obligate or facultative character of progenesis. For those species with no demonstrated historical definitive host, progenesis is obviously a clear-cut strategy. In the eventuality of occasional ingestion by a vertebrate host, these species do not appear to extend further their reproductive life-span, either because they do not establish or because they rapidly die without any further development (Joyeux, Noyer & Baer, 1930; Buttner, 1950b in *Paralepoderma brumpti*; Buttner, 1951b in *Ratzia joyeuxi*). For facultative progenetic species, egg production in the intermediate host probably does not preclude egg production in the definitive host. In the event that the intermediate host gets eaten by a suitable definitive host, excystment and the presence of conspecific adults would allow mating and cross-fertilization (Caveny & Etges, 1971 in *Microphallus opacus*).

The ability and readiness of worms to copulate soon after the establishment in the definitive host is even thought to be a major advantage of precocious sexual maturation (Jackson *et al.* 1997; George-Nascimento *et al.* 1998). According to these authors, an increased rate of gamete production in the intermediate host may shorten the critical residence time necessary for maturation in the definitive host (i.e. the pre-patency time). This idea is supported by an inter-specific comparison of 3 cryptogonimid species (namely, *Caecincola latostoma*, *Cryptogonimus spinovum*, and *Textrema hopkinsi*), that are not fully progenetic but differ in their developmental timing. It revealed an inverse relationship between the developmental time of metacercariae in the intermediate hosts and the maturation period before egg production in the definitive hosts; the further the development in the intermediate host, the faster the reproduction in the definitive host (Greer & Corkum, 1980). This trend toward a shorter residence time in the definitive host could be a transitional step toward the evolution of what we now call progenesis.

DISCUSSION

In digenean trematodes, the number of hosts used in the life-cycle is an adjustment that helps to facilitate

the critical step of the transmission toward the definitive host. In some trematode taxa (Hemiuroidea, e.g. *Halipegus ovocaudatus*), the use of an additional intermediate host (4-host life-cycle) allows the concentration of the infective stages in order to increase their transmission efficiency to the definitive host (Kechemir, 1978). In contrast, the simplification of the life-cycle, as by way of progenesis, is probably an adaptive response to the uncertainty of the transmission toward the definitive host. Adopting the terminology of Bush & Kennedy (1994), progenesis is 'a good hedge against extinction' that 'can serve to perpetuate a parasite in those instances where the definitive hosts are absent'.

The phenomenon of progenesis is not restricted to trematodes among helminth parasites. Progenesis has been reported in Cestoda (Caryophyllidae, Hymenolepididae, Davaineidae; Poddubnaya, Mackiewicz & Kuperman, 2003), in Nematoda (Spirurida, Ascaridoidea; Anderson, 1988; Fagerholm & Butterworth, 1988), and in Monogenea (*Polystoma integerrimum*; Combes, 1967). In these groups also, precocious reproduction is thought to be an alternative transmission strategy that allows the parasite to compensate for the unpredictability in definitive host abundance (Adamson, 1986; Anderson & Bartlett, 1993; Poddubnaya *et al.* 2003).

Throughout this review, the importance of the metacercarial cyst has been highlighted for a number of evolutionary kind of questions about progenesis. The cyst mediates all communication between the metacercariae and its external world (either with the tissues of the host or with the habitat of the host), involving food and energy intake from the host or the way progenetic eggs are released. All these aspects depend on the presence and/or the permeability of the cyst wall. Cases of secondary loss of the cyst by maturing metacercariae are particularly significant in this regard. In extreme cases, where multiple progenetic metacercariae lie unencysted within the same intermediate host, the possibility of cross-fertilization may even be considered (see Font, 1980; Madhavi & Swarnakumari, 1995). The metacercarial cyst thus seems of major importance in the adoption and evolution of progenetic life-cycles in trematodes. As stated by Poulin & Cribb (2002) only the lineages that are free in their hosts and able to cross-fertilize have lead to a major radiation (e.g. blood flukes). There has been no radiation of a trematode taxon where cross-fertilization is impeded by the presence of a cyst wall.

In the future, several evolutionary questions could be answered by using comparative analyses that integrate data available from the literature. For example, it should be possible to rigorously verify the importance of the cyst wall by studying at the inter-specific level the average wall thickness in 3 groups of trematodes that display gradual variation in their degree of sexual maturation in the second

intermediate host (i.e. non-progenetic species, facultative progenetic species and obligate progenetic species). In addition, using facultative progenetic species, it should be possible to use experimental approaches to identify the proximate cues prompting the worms to adopt a truncated life-cycle, and to determine the genetic heritability of this strategy. The study of progenesis may eventually allow us to understand better how complex life-cycles evolved in the first place.

We thank Aneta Kostadinova for useful comments on an earlier draft. This study was supported by the foundation Basler Stiftung für Biologische Forschung (Basel, Switzerland).

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