2 Digenean trematodes

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1 Introductory remarks

Trematodes of the class Digenea belong to the phylum Platyhelminthes (see Gibson et al. 2002 for a recent update on taxonomy). They are parasites with complex life cycles and often use micromammals as definitive hosts. Trematodes are distributed all around the world. In Europe, for example, monographs or articles that deal with the helminthofauna of small mammals have always reported the ubiquitous presence of digenean trematodes (López-Neyra 1947; Prokopic and Genov 1974; Merkusheva and Bobkova 1981; Genov 1984; Goüy de Bellocq et al. 2002). In this chapter, we offer general information on the trematode faunas of micromammals, with a focus on parasites of small mammals of the Iberian Peninsula. Recent extensive studies of helminths in this Peninsula provide an opportunity to investigate various aspects of the ecology of these helminths.

2 Distribution of trematodes among small mammals

Available data on digeneans parasitic in small mammals are summarized in Tables 1-4. These tables have been compiled from an extensive bibliographical search (CAB Abstracts 1973-2005) with additional data from Yamaguti (1971), Gibson et al. (2002) and Jones et al. (2005), and show the records of trematode families in mammalian families belonging to four orders (Insectivora, Rodentia, Lagomorpha and Chiroptera). In general, small mammals harbour a great variety of trematodes representing a total of 37 families. Rodentia harbours the most diverse trematode fauna consisting of 30 families, while Lagomorpha have the least diverse spectrum of trematodes with seven families only.

Parasitic digeneans belonging to 19 families have been recorded from four families of Insectivora (Table 1). All of these digenean families have been reported for Soricidae. They were found mainly in the most extensively studied genera such as *Crocidura*, *Neomys* and *Sorex*. In contrast, among tenrecids (represented by 10 genera), only *Limnogale mergulus* was found to be parasitized by trematodes (omphalometrid *Neoglyphe polylecithos* and plagiorchiid *Plagiorchis limnogale*; Yamaguti 1971).

Table 1. Trematodes parasitic in Insectivora

	Erinaceidae	Soricidae	Talpidae	Tenrecidae
Brachylaimidae	+	+	+	
Cyathocotylidae		+	+	
Dicrocoeliidae	+	+		
Diplostomidae	+	+	+	
Echinostomatidae	+	+	+	
Heterophyidae		+	+	
Lecithodendriidae	+	+		
Microphallidae		+	+	
Nanophyetidae		+	+	
Omphalometridae		+	+	+
Opisthorchiidae		+		
Panopistidae	+	+		
Plagiorchiidae		+	+	+
Pleurogenidae		+		
Prosthogonimidae		+		
Psilostomidae		+		
Schistosomatidae	+	+		
Strigeidae		+		
Troglotrematidae		+	+	

Among Rodentia, data on trematodes are available for 13 of 29 recent families (Table 2). Of these, Muridae show the most diverse trematode fauna with 29 of the 30 digenean families recorded for Rodentia. The least diverse trematode faunas occur in four rodent families that each harbour a single digenean family. These rodent families are Chinchillidae with *Lagidium viscacia boxi* parasitized by *Fasciola hepatica* (Fasciolidae) (Led et al. 1979); Dasyproctidae with *Dasyprocta agouti* parasitized by two species of Cladorchiidae (*Cladorchis pyriformis* and *Stichorchis giganteus*) (Yamaguti 1971); Erethizontidae with *Erethizon dorsatum* parasitized by *Schistosoma douthitti* (Schistosomatidae) (Choquette et al. 1973); and Heteromyidae with *Liomys pictus* parasitized by *Brachylaima bravoae* (Brachylaimidae) (Yamaguti 1971).

Table 2. Digenean trematodes parasitic in Rodentia

	Cas	Cav	Chi	Das	Dip	Ech	Ere	Het	Hyd	Mur	Myc	Myx	Sci
Achillurbaniidae										+			
Brachylaimidae								+		+		+	+
Cladorchiidae	+	+		+					+	+	+		
Collyriclidae										+			
Dicrocoeliidae	+									+	+	+	+
Diplostomidae										+		+	+
Echinostomatidae	+									+	+		
Fasciolidae	+	+	+							+	+		
Gastrodiscidae	+									+	+		
Gymnophallidae										+			
Leucochloridiidae										+			
Leucochloridio-morphidae										+			
Heterophyidae										+			
Lecithodendriidae										+		+	+
Microphallidae										+			
Nanophyetidae										+			
Notocotylidae		+			+				+	+	+		
Nudacotylidae									+	+			
Omphalometridae										+			+
Opisthorchiidae	+									+			
Panopistidae										+		+	
Paragonimidae										+			
Paramphistomidae						+							
Plagiorchiidae	+				+					+		+	+
Prosthogonimidae										+			
Psilostomidae	+									+			
Schistosomatidae	+	+			+	+	+			+			
Strigeidae										+			
Troglotrematidae										+		+	
Zygocotylidae										+			

Cas Castoridae, *Cav* Caviidae, *Chi* Chinchillidae, *Das* Dasyproctidae, *Dip* Dipodidae, *Ech* Echimyidae, *Ere* Erethizontidae, *Het* Heteromyidae, *Hyd* Hydrochaeridae, *Mur* Muridae, *Myc* Myocastoridae, *Myx* Myoxidae, *Sci* Sciuridae.

All seven trematode families characteristic of Lagomorpha were found in Leporidae (Table 3). In contrast, only two trematode species from two families have been reported for Ochotonidae: *Dicrocoelium dendriticum* (Dicrocoeliidae) in *Ochotona alpina* (Gvozdev and Orlov 1985) and *Ochotona hyperborea* (Sakamoto et al. 1982) and *Hasstilesia ochotonae* (Hasstilesiidae) in *Ochotona rutila* (Zdarska and Soboleva 1990).

Table 3. Digenean trematodes parasitic in Lagomorpha

	Ochotonidae	Leporidae
Dicrocoeliidae	+	+
Echinostomatidae		+
Fasciolidae		+
Hasstilesiidae	+	+
Heterophyidae		+
Nudacotylidae		+
Schistosomatidae		+

Table 4. Digenean trematodes parasitic in Chiroptera

	Emb	Hip	Meg	Mol	Mor	Nat	Noc	Nyc	Phy	Pte	Rhl	Rhp	Ves
Anenterotrematidae	+			+	+	+			+				+
Brachylaimidae												+	+
Cyathocotylidae								+					
Dicrocoeliidae	+	+	+	+				+	+	+	+	+	+
Diplostomidae									+				
Echinostomatidae			+										
Heterophyidae							+						+
Lecithodendriidae	+	+	+	+	+	+	+	+	+	+	+	+	+
Mesotretidae											+		+
Microphallidae									+		+		+
Notocotylidae					+								+
Nudacotylidae									+				
Plagiorchiidae	+	+	+	+	+	+	+		+		+	+	+
Pleurogenidae													+
Rhopaliidae									+				

Emb Emballonuridae, *Hip* Hipposideridae, *Meg* Megadermatidae, *Mol* Molossidae, *Mor* Mormoopidae, *Nat* Natalidae, *Noc* Noctilionidae, *Nyc* Nycteridae, *Phy* Phyllostomidae, *Pte* Pteropodidae, *Rhl* Rhinolophidae, *Rhp* Rhinopomatidae, *Ves* Vespertilionidae.

Finally, 15 digenean families were found in 13 families of Chiroptera (Table 4). Vespertilionidae and Phyllostomidae harbour the richest digenean faunas (10 and eight parasite families, respectively). Lecithodendriidae parasitize all of the 13 chiropteran families. Plagiorchiidae and Dicrocoeliidae are also well represented (recorded in 11 and 10 chiropteran families, respectively). Representation of the remaining trematode families among chiropteran families is more restricted, including Cyathocotylidae with *Prohemistomum azimi* parasitizing *Nycteris thebaica* (Nycteridae) (Saoud and Ramadan 1977); Diplostomidae with *Neodiplostomum vaucheri* parasitizing *Chrotopterus auritus* (Phyllostomidae) (Dubois

1983); Echinostomatidae with *Echinochasmus megadermi* and *E. perfoliatus* found in *Megaderma lyra* (Megadermatidae) (Salem 1975); Nudacotylidae with *Nudacotyle* species reported from the phyllostomid genera *Carollia*, *Artibeus* and *Phyllonycteris* (Zdzitowiecki 1980; Zdzitowiecki and Rutkowska 1980; Vélez and Thatcher 1990); Pleurogenidae with *Maxbraunium baeri* parasitic on *Myotis siligorensis* (Vespertilionidae) (Yamaguti 1971); and Rhopaliidae with *Rhopalias coronatus* found in *Carollia perspicillata* (Phyllostomidae) (Marshall and Miller 1979).

3 Small mammals as experimental models for studies of Digenea

Several small mammals have been used in experiments to investigate the life cycles of parasites and to serve as models of human infections. Although the ideal scenario would be to monitor in the laboratory the entire trematode life cycle, it has not always been possible. Often, only the adult stage has been studied. In both situations, the availability of adult trematodes required experimental infection of the definitive hosts, usually rodents. However, some experimental models involved also lagomorphs and, on rarer occasions, bats and insectivores (see Yamaguti 1971 for details).

Among rodents, most experimental infections with digeneans have been carried out on Muridae, though guinea pigs (Caviidae: *Cavia porcellus*) has also been frequently used in experiments. Among murids, Murinae (*Mus* and *Rattus*) have been used for experimental infections mainly by Brachylaimidae, Echinostomatidae, Heterophyidae, Paragonimidae, Plagiorchiidae and Schistosomatidae. Other Murinae, such as *Apodemus*, *Mastomys*, *Praomys*, *Thallomys*, *Arvicantis* and *Bandicota* have been less frequently used, although they also have been experimentally infected with Fasciolidae, Brachylaimidae, Schistosomatidae and Paragonimidae. Gerbillinae of the genus *Meriones*, especially *M. unguiculatus*, have been extensively used in experiments with digeneans. Another gerbilline, *Tatera indica*, has also been experimentally infected with Fasciolidae (Sahba et al. 1972) and Schistosomatidae (Massoud 1973). Among Cricetinae, *Mesocricetus auratus* has served as experimental model mainly for investigations with Schistosomatidae, Echinostomatidae and Heterophyidae. Other cricetines (*Phodopus*, *Tscherskia* and *Cricetulus*) have also been used in experiments with digeneans of particular public health importance such as *Fasciola hepatica*, *Dicrocoelium dendriticum*, *Opistorchis felineus*, *Clonorchis sinensis* and *Schistosoma mansoni* (Gitsu and Kovalenko 1983; Zelya and Sergeeva 1987; Terasaki et al. 2003; etc.). Additional models include schistosomatids in *Cricetomys* sp. and *Saccostomus campestres* (Crycetominae); *Schistosomatium*, *Notocotylus* and *Nudacotyle* in *Microtus pennsylvanicus* and *M. montanus*; and *Euryhelmis* in *Ondatra zibethica* (Arvicolinae); as well as some schistosomatids, brachylaimids, heterophyids and opisthorchiids in Sigmodontinae (*Sigmodon*, *Holochilus*, *Holochistus*, *Nectomys*, *Zygodontomys* and *Peromyscus*) (Pitchford 1975; Zajac and Williams 1981; Gitsu and Kovalenko 1983; Kawazoe and Pinto 1983; McKown et al. 2000; Terasaki et al. 2003).

Representatives of other rodent families (Echimyidae, Dasyproctidae, Hystricidae, Myoxidae, Sciuridae and Myocastoridae) have rarely been used for experimental infections with digeneans. Nevertheless, *Myocastor coypus* (Myocastoridae) has been described as a useful experimental model for *Fasciola*, *Schistosoma*, *Paragonimus* and *Clonorchis* (Kuntz et al. 1975; Hatsushika et al. 1979). *Paragonimus skrjabini* and *Brachylaima ruminae* have been maintained in *Hystrix hodgnosi* (Hystricidae) and *Eliomys quercinus* (Myoxidae) (Yamaguti 1971; Mas-Coma and Montoliu 1986). Finally, *Proechimys* (Echimyidae), *Dasyprocta* (Dasyproctidae), *Marmota* and *Callosciurus* (Sciuridae) have been infected with some *Schistosoma* species (Chiu and Kao 1973; Anderson et al. 1991).

4 Digeneans and Iberian small mammals

The mammal fauna of the Iberian Peninsula comprises 65 species of small mammals (14 Insectivora, 21 Rodentia, four Lagomorpha and 26 Chiroptera; Palomo and Gisbert 2002). Continuous extensive studies of the helminth fauna of Iberian small mammals started in the mid 70s (beginning with insectivores and rodents, then involving bats and, finally, hares and rabbits). At present, detailed information on the helminth faunas and, in particular, on trematodes, of a substantial number of the Iberian micromammalian species is available. The information provided here has been extracted from our own studies that included detailed examination of around 7000 individual hosts (500 Insectivora, 5500 Rodentia and 1000 Lagomorpha). Data on trematodes parasitic in Chiroptera were taken from the literature.

4.1 Faunistic aspects

Forty-six species of digeneans have been found in Iberian micromammals. In fact, this number may be greater, because of some unclear and unresolved taxonomical issues (Mas-Coma and Montoliu 1986; Botella et al. 1993; Esteban et al. 1999; Gracenea and González-Moreno 2002). These 46 trematodes were recorded in 36 host species (10 Insectivora, 13 Rodentia, two Lagomorpha and 11 Chiroptera).

Table 5 shows the number of families, genera and species of trematodes that infect small mammals belonging to different orders and families, whereas numbers of digenean families and species recorded in each host species are shown in Fig. 1.

Table 5. Number of families, genera and species of trematodes recorded in Iberian small mammals

Hosts	Trematodes		
	Families	Genera	Species
INSECTIVORA			
Talpidae	4	4	4
Erinaceidae	2	2	3
Soricidae	8	9	11
RODENTIA			
Myoxidae	6	7	8
Muridae	10	12	15
LAGOMORPHA			
Leporidae	2	2	2
CHIROPTERA			
Rhinolophidae	3	5	8
Vespertilionidae	3	6	12
Molossidae	2	3	3

A high diversity of trematode species is the characteristic for Muridae and Soricidae, whereas the lowest number of trematode species has been found in Leporidae and Erinaceidae. One of the reasons for this is the high number of host species within both Muridae (17) and Soricidae (nine), and their broad distribution across the Peninsula. Among dormice (Myoxidae), trematodes have been found only in *Eliomys quercinus*, whereas no trematode has been recorded in *Glis glis*. Leporidae is the only family that does not have specific trematodes, but its members are hosts of euryxenous trematodes (*Fasciola hepatica* and *Dicrocoelium dendriticum*) that are frequently found in other mammals. Rhinolophidae and Vespertilionidae are parasitized by a relatively high number of genera and species of trematodes, although these belong to only few families. Bats are the most frequently infected by Plagiorchiidae and Lecithodendriidae (Botella et al. 1993; Esteban et al. 1990, 1992, 1999).

Each trematode family has been recorded in either one (Collyriclidae, Echinostomatidae, Fasciolidae, Mesotretidae, Nanophyetidae, Notocotylidae, Omphalometridae and Prosthogonimidae), two (Brachylaimidae, Microphallidae, Panopistidae, Plagiorchiidae, Psilostomidae, Troglotrematidae) or three orders of hosts (Dicrocoeliidae, Lecithodendriidae). The most speciose genera of digeneans found in Iberian small mammals are *Brachylaima*, *Plagiorchis* and *Prosthodendrium*, each represented by four species.

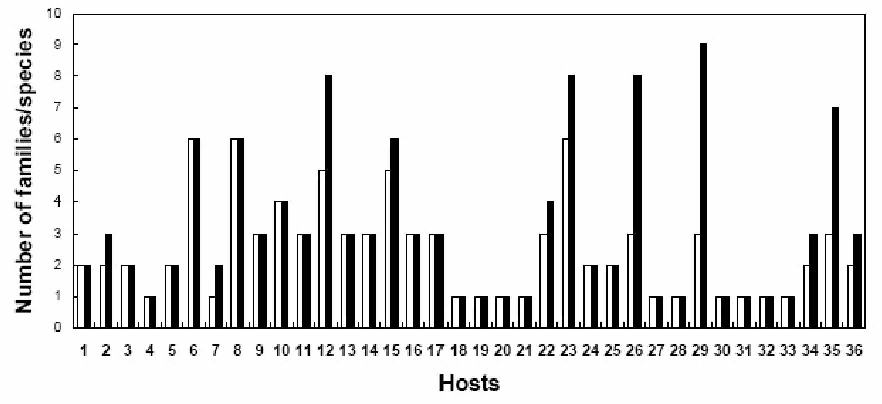

Fig. 1. Number of families and species of digenean trematodes recorded in different species of Iberian small mammals. 1 *Talpa europaea,* 2 *Talpa occidentalis,* 3 *Galemys pyrenaicus,* 4 *Erinaceus europaeus,* 5 *Atelerix algirus,* 6 *Crocidura russula,* 7 *Crocidura suaveolens,* 8 *Neomys fodiens,* 9 *Sorex minutus,* 10 *Sorex araneus,* 11 *Rattus rattus,* 12 *Rattus norvegicus,* 13 *Mus domesticus,* 14 *Mus spretus,* 15 *Apodemus sylvaticus,* 16 *Clethrionomys glareolus,* 17 *Microtus agrestis,* 18 *Microtus lusitanicus,* 19 *Microtus arvalis,* 20 *Microtus cabrerae,* 21 *Microtus duodecimcostatus,* 22 *Arvicola sapidus,* 23 *Eliomys quercinus,* 24 *Oryctolagus cuniculus,* 25 *Lepus granatensis,* 26 *Rhinolophus ferrumequinum,* 27 *Rhinolophus hipposideros,* 28 *Rhinolophus mehelyi,* 29 *Pipistrellus pipistrellus,* 30 *Myotis daubentonii,* 31 *Myotys nattereri,* 32 *Myotis myotis,* 33 *Eptesicus serotinus,* 34 *Plecotus auritus,* 35 *Miniopterus schreibersii,* 36 *Tadarida teniotis*

Among host species, the highest diversity of trematodes is characteristic of *Pipistrellus pipistrellus* (nine species), *Rattus norvegicus*, *Eliomys quercinus*, *Rhinolophus ferrumequinum* (eight species each) and *Miniopterus schreibersii* (seven species). All these hosts are broadly distributed across the Iberian Peninsula, and some of them (*P. pipistrellus*, *R. norvegicus*) live in peridomestic habitats (Palomo and Gisbert 2002). The lowest number of trematode species (one) is characteristic of herbivorous hosts that have a patchy distribution in Iberia (*Microtus* spp.) as well as Rhinolophidae and Vespertilionidae, which have been only occasionally studied for parasites.

The majority of Iberian digeneans show relatively low host specificity in terms of the number of host species they exploit. However, host specificity of some trematodes appears to be relatively high in terms of the taxonomic composition of the host spectrum. For example, all seven hosts of *Plagiorchis vespertilionis* and six hosts of *Mesotretes peregrinus* belong to Chiroptera; all six hosts of *Notocotylus neyrai* belong to Rodentia, whereas *Nephrotrema truncatum* has been recorded in five insectivores and one rodent. High host specificity is characteristic of Nanophyetidae, Collyriclidae, some Dicrocoeliidae and some Lecithodendriidae. Other trematode species have low host specificity in terms of both the number of host species used and their phylogenetic affinities. For example, some Psilostomidae can infect insectivores, rodents and birds (Montoliu et al. 1987; Cordero del Campillo et al. 1994).

The taxonomy of digenean trematodes in general, and those inhabiting the Iberian Peninsula in particular, is far from being clear. Many new species have been described during the last decades. Synonymy issues also need to be resolved (see Cordero del Campillo et al. 1994). Nevertheless, recent studies on spermiogenesis and spermatozoon of these digeneans may be helpful in clarifying the taxonomic issues (Ndiaye et al. 2004; Miquel et al. 2006). The use of molecular tools to determine phylogenetic relationships of digeneans is also growing (Littlewood et al. 1998; Cribb et al. 2001).

4.2 Ecological and zoogeographical aspects

The role of host factors such as host sex or age on the composition and structure of trematode assemblages is poorly known. Nevertheless, host sex has been shown to have no effect on trematode assemblages in *Talpa occidentalis* and *Erinaceus europaeus* (Casanova et al. 1996; Feliu et al. 2001). Prevalence of *Dicrocoelium dendriticum* did not differ between male and female *Oryctolagus cuniculus* (Blasco et al. 1996). No strong effect of host age and reproductive status on infection parameters of digenean trematodes has been found, although the highest prevalence of infection has been reported in adult rabbits, especially in pregnant females and in males with no scrotal testicles (Molina 1999). The variation in trematode infection among host individuals within host species can, however, be masked by seasonal effects. For example, intensity of infection of *Erinaceus europaeus* by *Brachylaima erinacei* increases substantially during summer and autumn (Feliu et al. 2001), whereas *Dicrocoelium dendriticum* is absent in its rabbit hosts in autumn (Molina et al. 1998).

On the other hand, the structure of trematode assemblages is strongly affected by the dietary habits of the host. For example, among rodents, trematode assemblages are richer in omnivorous and insectivorous (murines and *Eliomys quercinus*) than in herbivorous species (arvicolines) (Fig. 1). In some hosts, diet varies among geographic localities, and so does the composition of trematode assemblages, being poorer in individuals from localities where the diet is strictly herbivorous (see Torres and Feliu 1990 for an example with *Arvicola sapidus*). The life style of a host species also plays an important role in determining the composition of trematode assemblages. For example, among rodents, the richest trematode assemblages are found in terrestrial and/or semi-aquatic species, whereas the poorest assemblages are characteristic of subterranean or arboreal hosts (Feliu et al. 1992, 1997).

Different trematode species demonstrate various patterns of geographic distribution across Iberia. Some species are distributed across the entire Peninsula (e.g., *Plagiorchis vespertilionis*; Cordero del Campillo et al. 1994), whereas the distribution of other species is much more restricted. For example, *Dollfusinus frontalis*, a relatively common species in the Balearic Islands, has been recorded in the Eastern Peninsula only once (Galán-Puchades et al. 1994). Some species are endemic to the Pyrenees (e.g., *Brachylecithum eliomydis*, *Macyella apodemi*) or are detected in very specific habitats (deltas, albuferas; e.g., *Euparyphium albuferensis*, *Echinostoma friedi*). Finally, the distribution of some oioxenous or stenoxenous species mimics that of their hosts (e.g., *Ityogonimus* spp., *Matovius galemydis*; see Cordero del Campillo et al. 1994; Ribas 2005 for details).

4.3 Biological aspects

Although details of the life cycles of many trematodes inhabiting the Iberian Peninsula are still unknown, the available data allow to distinguish at least seven types of trematode life cycles (Table 6).

While the first intermediate hosts are either pulmonate gastropods or prosobranchs, the taxonomic affinity of the second intermediate hosts (in species with triheteroxenous life cycles) varies greatly (insects, annelids, crustaceans, pulmonate gastropods). Unfortunately, studies of the biological cycles of digeneans in Iberia are scarce and almost always focused on three families, namely Brachylaimidae, Echinostomatidae and Microphallidae. Nevertheless, a study on *Plagiorchis* (Plagiorchiidae), parasitic in *Apodemus sylvaticus* has been completed recently (Esteban et al. unpublished data). In addition, some information on a brachylaimid (*Brachylaima ruminate*) and on two panopistids (*Pseudoleucochloridium pericardicum* and *Dollfusinus frontalis*) parasitic in insectivores and rodents from regions geographically close to Iberia (eastern French Pyrenees and the Balearic Islands) is available (Mas-Coma and Montoliu 1986, 1987, 1995). The study of trematode life cycles may help to clarify some taxonomic issues (Gracenea et al. 1993; Esteban et al. 1997; Toledo et al. 2000; González-Moreno 2002; Gracenea and González-Moreno 2002).

Table 6. Types of life cycles for the Iberian digenean parasites of small mammals

Life cycle	Digenean species	First intermediate host	Second intermediate host
Terrestrial			
Triheteroxenous	*Brachylaima mascomai*	Pulmonate	Pulmonate
Triheteroxenous	*Dicrocoelium dendriticum*	Pulmonate	Insect
Aquatic			
Diheteroxenous	*Psilotrema spiculigerum*	Prosobranch	Metacercarie encysted on vegetation
Triheteroxenous	*Hypoderaeum conoideum*	Pulmonate	Pulmonate
Triheteroxenous	*Plagiorchis vespertilionis*	Pulmonate	Insect
Triheteroxenous	*Nephrotrema truncatum*	Prosobranch	Annelid
Triheteroxenous	*Maritrema feliui*	Prosobranch	Crustacean

5 Concluding remarks

Digenean trematodes are characteristic parasites of small mammals all over the world. In spite of the availability of faunistic data, it seems that still many species remain to be described. In particular, the use of molecular techniques and ultrastructural data of the spermatozoon and the spermiogenesis will undoubtedly help toward this end. The details of the life cycles of many species of trematode parasites of micromammals are still unclear, although some species have been thoroughly studied using experimental models. The relationships between a variety of host-related and environmental-related factors and the populations and communities of digenean trematodes also require further investigations.

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