

New data on *Microphallus breviatus* Deblock & Maillard, 1975 (Microphallidae: Digenea) with emphasis on the evolution of dixenous life cycles of microphallids

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Abstract Infection by intramolluscan stages of *Microphallus breviatus* Deblock & Maillard, 1975 are common in *Hydrobia ventrosa* mudsnails in Iceland. Cercariae encyst inside the daughter sporocysts and develop there into metacercariae that become infective for the definitive hosts which are probably charadriiform waders. The adult stage was obtained in 1-day-old chicks that were experimentally infected with metacercariae from naturally infected hydrobians. New data are presented on the morphology and biology of the cercariae, and the adult is described for the first time. Comparisons are made between *M. breviatus* and closely related species. Differential diagnosis of *M. breviatus* is given. The morphological specializations in larvae of the hermaphroditic generation of the microphallids accompanying transition from trixenous life cycles to dixenous ones are considered, and the applicability of the term “life-cycle truncation” to microphallids with dixenous life cycles is discussed. Also, reasons for the broad distribution of dixenous life cycles within the family Microphallidae are reviewed.

Introduction

Microphallus breviatus Deblock & Maillard, 1975 was first described after the studies on sporocysts, cercariae, and

metacercariae discovered in the mudsnail *Hydrobia ventrosa* at the Mediterranean coast of France (Deblock and Maillard 1975). The parasite has a dixenous life cycle; cercaria does not leave the mudsnail but encysts inside the daughter sporocysts, where the development of the metacercaria also takes place under protective covers of the cyst.

In a study on the trematode larvae fauna of intertidal snails in Iceland (Skirnisson and Galaktionov 2002), we paid attention to some new morphological details of the *M. breviatus* cercariae. In an infection experiment, we managed to attain the adult stage of the species after having fed chicks with the metacercariae. In this study, we describe some previously unknown morphological features of the cercariae, describe for the first time the adult stage of *M. breviatus*, and discuss the evolution of dixenous life cycles of microphallids.

Materials and methods

H. ventrosa Montagu, 1803 snails infected with intramolluscan stages of *M. breviatus* were collected in August–September 1998, 2000, and 2002 at the two sites in Iceland. Galgahraun, the first collection site (64°05′48″N, 21°57′30″W), is a system of silted channels connected to the sea in a lava field close to Reykjavik. Melabakkar, the second collection site (64°45′50″N, 22°25′40″W), is a salt marsh peninsula dotted with ponds of various shapes and sizes on the southern part of the Snæfellsnes peninsula, 80 km northwest of the study area in Galgahraun. Altogether, 530 snails from Galgahraun and 4,539 snails from Melabakkar were dissected. Prevalence values are presented in the article with the mean and the SE in parentheses.

Snails were examined at the Institute for Experimental Pathology at Keldur, University of Iceland. The specimens collected were kept in a marine aquarium at 5°C and

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dissected within 2 weeks of sampling. In each case, the shell was removed, and the molluscan soft tissues were carefully examined under a stereomicroscope for intramolluscan stages of *M. breviatus*. Species identification was carried out on the basis of descriptions made by Deblock and Maillard (1975) and Deblock (1980). Morphology of sporocysts, cercariae, and metacercariae was studied in vivo using a Leitz Dialux 20B microscope. Photographs were taken with a Leica Wild MPS 32 photomicrography camera. Measurements of cercariae and daughter sporocysts were made on heat-killed individuals in seawater under light cover-glass pressure. Not less than 20 cercariae and daughter sporocysts were measured.

To obtain the adult stage, two 1-day-old chicks were fed *per os* with cysts of fully formed *M. breviatus* metacercariae that were derived from infected hydrobians. The cysts were mixed with water and administered to the birds with a small pipette. The chicks were dissected 5 days p.i. and examined for the presence of adult worms. Worms found were fixed in 70% ethanol, stained with aluminous carmine, cleared in isobutyl alcohol and xylene, and mounted in Canada balsam. Fifteen adult worms mounted in this manner were measured.

Measurements (length×width) are presented in micrometers, with the mean in parentheses. Drawings were made with the aid of a camera lucida.

Results

Hydrobians infected with *M. breviatus* were found at both collection sites but in a very different prevalence of infection. In Galgahraun, the prevalence varied from 23 to 32% (27.5 ± 4.1) and remained quite stable throughout the study period, but on the salt marsh in Melabakkar, considerably lower prevalence values varied between 0 and 3.2% (1 ± 0.2).

Daughter sporocysts

The daughter sporocysts invade the gonads of hydrobians and end up in fully substituting their tissues and thus castrating infected individuals. The sporocysts are sac-like organisms of irregular shape. Their sizes vary greatly ($720\text{--}1,200\times 200\text{--}430$). Young sporocysts contain cercariae and encysted metacercariae at different stages of their development (Fig. 1a), but mature sporocysts exclusively contain encysted metacercariae that are infective for the definitive host (Fig. 1b).

Cercariae

M. breviatus has monostome cercariae that belong to the Ubiquita group of the xiphidiocercaria (which includes in accordance with Lühe (1909) tailed xiphidiocercariae with

oral sucker and undeveloped digestive system and ventral sucker) (Figs. 1c and 2a). The cercariae are small, 83–115 (102) long and 40–72 (54) wide at the midbody. Their surface is covered with small spines which decrease in size from the anterior to the posterior body end. The tail is slightly shorter than the body, 79–108 (91) long and 7–14 (10) wide at the base. The diameter of the oral sucker is 25–32 (27). The lanceolate stylet is 9–11 (10) long and 2 wide at the base (Fig. 2b). The external refractive layer of the stylet (cutting edges) is not pronounced.

As typical for most microphallid cercariae, there are four pairs of penetration glands. Cytions with light (when observed in vivo) nuclei are situated in the middle of the larval body. The ducts of the two anterior pairs are slightly swollen (Fig. 1c), but the degree of swelling is different (Fig. 2a,c). At first, these ducts pass together but then separate, forming a characteristic bend, at the level of the border of the first third of the cercarial body. The ducts of the two posterior pairs of the penetration glands are narrow. As a rule, they are masked (except in the distal regions) by the more developed ducts of the anterior glands. The gland ducts extend dorsally around the oral sucker and open at either side of the stylet. The openings of the two posterior glands are situated close to the stylet tip but those of the two anterior pairs are situated behind them. In vivo observations of cercariae demonstrate that secretory material in the anterior gland ducts is in the form of rough grains and that in the posterior gland ducts is in the form of small grains. Also, it is noteworthy that the lumina of the ducts of the penetration glands contain much less secretion in *M. breviatus* cercariae than in typical free-swimming cercariae of microphallids which have trixenous life cycles.

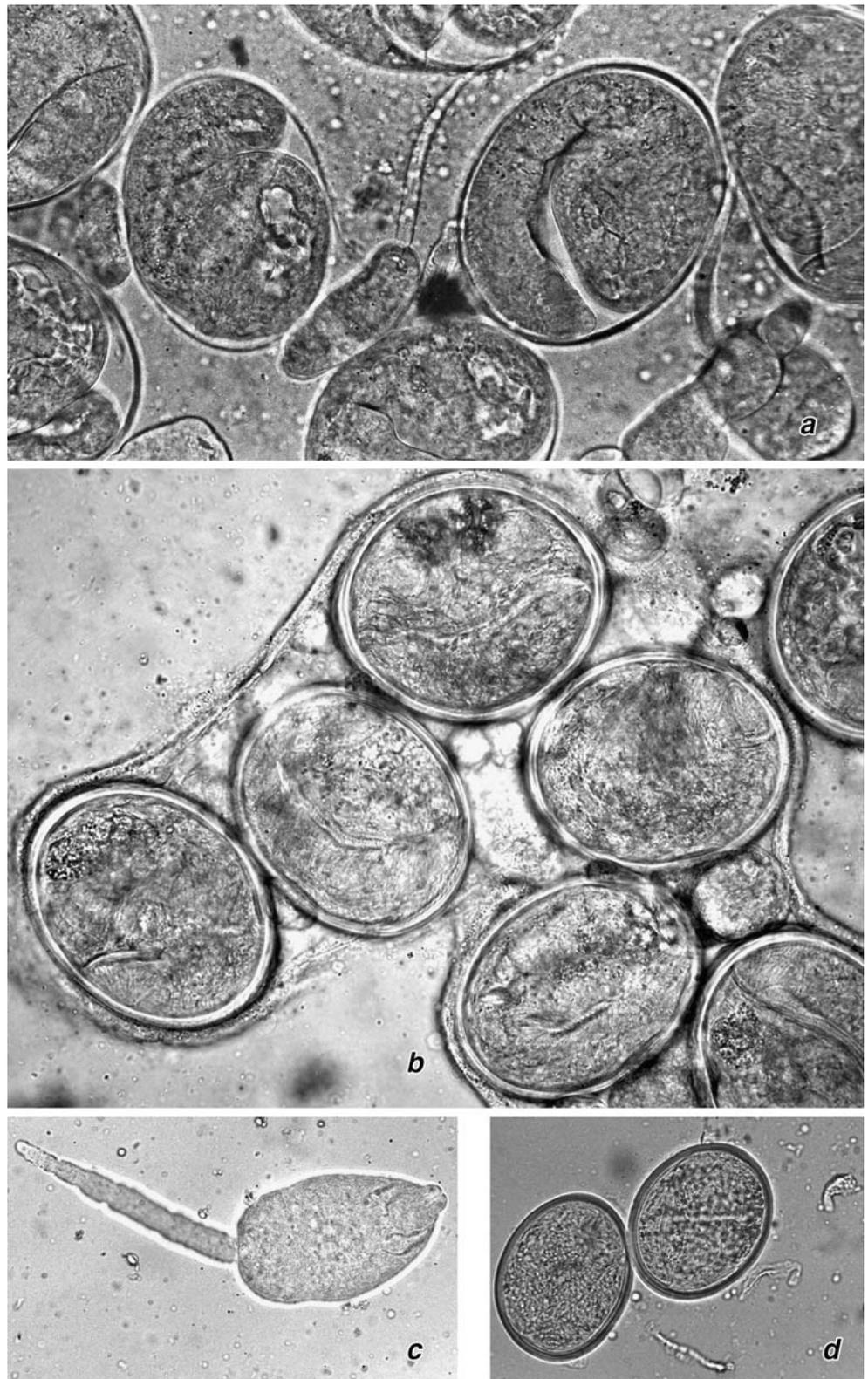
The flame cell formula is $2[(2 + 2) + (2 + 2)] = 16$. The genital primordium is represented by a compact group of cells in the posterior third of the larval body in front of the bladder. The alimentary tract primordium cannot be distinguished in fully formed cercariae during in vivo observations.

The cercariae do not leave the sporocysts. Extracted from sporocysts, they do not swim but slowly move by body contractions and tail beatings. The beatings, however, are not strong and frequent enough to allow movement of the larva in water column. The cercaria sheds the tail shortly before encystment inside the daughter sporocyst. Tails are preserved for a long time and can even be found in sporocysts which only contain fully formed metacercariae that are infective for the definitive host (Fig. 1d). Such tails immediately catch the eye during dissection of infected snails and are a useful character for preliminary species identification.

Metacercariae

The mature metacercaria is encased in an oval cyst of the size $99\text{--}140$ (124) \times $82\text{--}100$ (90) (Fig. 1b,d). In vivo microscopic observations indicate that the cyst wall consists

Fig. 1 Intramolluscan stages of *Microphallus breviatus*. **a** Cercariae and young, newly encysted metacercariae isolated from a young daughter sporocyst. **b** Daughter sporocyst containing fully formed encysted metacercariae. **c** Fully formed cercariae isolated from the young daughter sporocyst. **d** Fully formed encysted metacercariae and shed cercarial tails isolated from daughter sporocysts

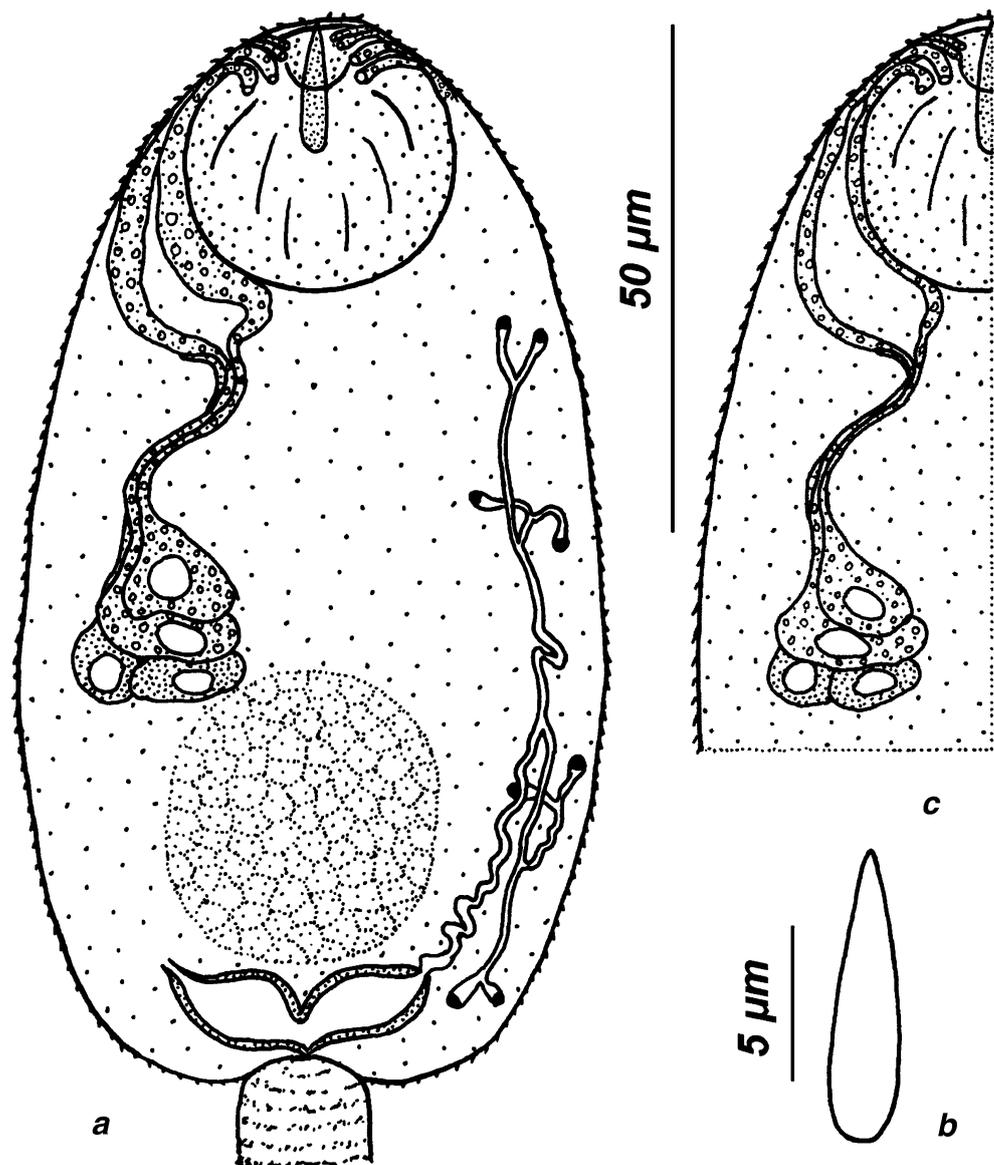


of two layers. Young metacercariae are surrounded with a thin single-layered cyst (Fig. 1a). Further morphological descriptions of *M. breviatus* metacercariae and their size characteristics are given by Deblock and Maillard (1975).

Adults

Mature adults were obtained in both of the experimentally infected chicks. The worms are pyriform and 202–

Fig. 2 Cercaria of *Microphallus breviatus*. **a** General scheme. **b** Cercarial stylet, *frontal view*. **c** Anterior part of the cercarial body showing a minimal rate of swelling of the ducts of the two anterior pairs of the penetration glands



338 (267) long (Fig. 3). Body width is 86–112 (103) at the level of the midesophagus and 133–184 (152) at the level of the testes. The body is covered with spines which are larger in the anterior region. The oral sucker is larger than the ventral one, the diameter of the former being 25–36 (31) but being 22–27 (24) of the latter. The prepharynx is short, 4–18 (8). The pharynx is oval, 18–22 (19) × 14–22 (18). The esophagus length varies greatly, 47–76 (58), mainly as a result of varying contraction level of the worms when fixed.

A large seminal vesicle, 24–42 (31) × 17–22 (19), is situated anteriorly to the ventral sucker. The male papilla is small, 10–11 (11) × 4–7 (6). Ovary size is 29–40 (32) × 32–54 (43), and testes size is 29–43 (36) × 43–76 (53). Vitellaria are represented by two compact groups of follicles, each 24–28 (26) × 10–18 (16) in size, situated behind the testes. Eggs are small, 14–18 (16) × 7–11 (9),

and their number reaches 200–300. In old adults, eggs fill almost all the posterior body region, masking the reproductive system organs.

Differential diagnosis

The adult stage of *M. breviatus* is small, even for microphallids, and certainly cannot be attributed to any species in the identifications keys of Belopolskaya (1963) and Deblock (1971). Deblock and Maillard (1975) indicate the similarity of *M. breviatus* metacercariae and those of *Microphallus limuli* Stunkard, 1951. Morphometric characteristics of adults of these two species also turned out to be similar. However, in *M. limuli*, the adult body is broad and leaf-shaped, the oral and the ventral sucker are of the same size, and the esophagus (100–130, in accordance with

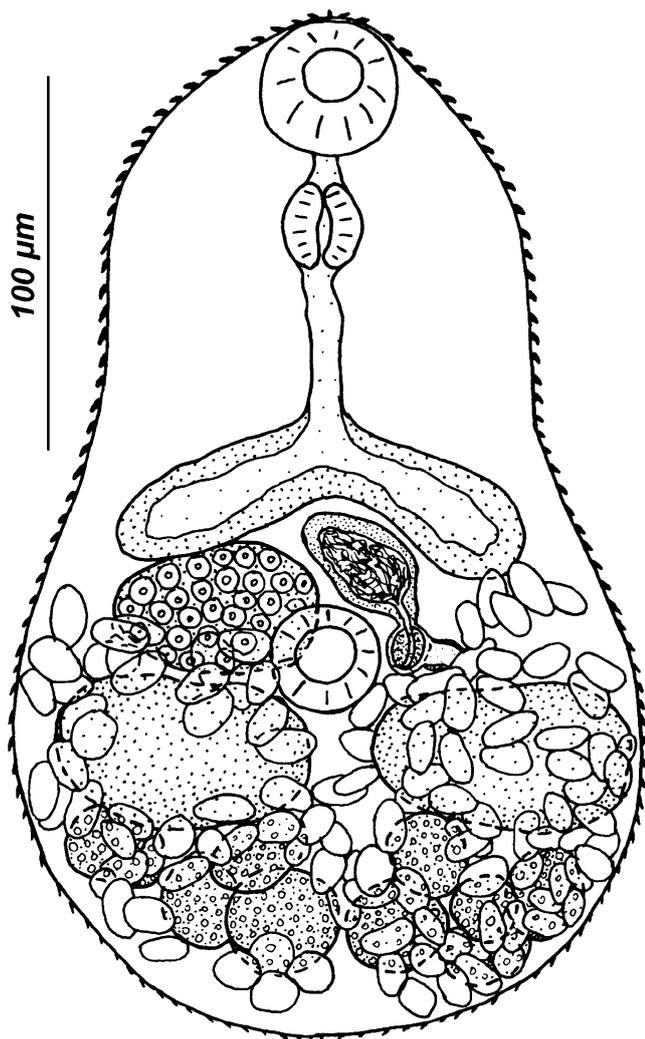


Fig. 3 Adult of *Microphallus breviatus*

Stunkard 1951) is much longer than in the adults of *M. breviatus*. Finally, *M. limuli* has a trixenous life cycle; actively swimming cercariae, formed in sporocysts parasitizing *Hydrobia minuta*, penetrate the second intermediate host (the horseshoe crab *Limulus polyphemus*) and encyst there (Stunkard 1968).

According to morphometric characteristics, *M. breviatus* adults are also similar to adults of microphallids of the “*pygmaeus*” group (Galaktionov 1980, 1983, 1984). At the same time, even the smallest of the latter, *Microphallus triangulatus* and *Microphallus* sp. I Galaktionov (1980) (*M. pseudopygmaeus*), are slightly larger (body length 310–400) than *M. breviatus* adults and also have a larger male papilla (15–22 in diameter) and larger eggs (25–27×10–15) (Galaktionov 1980, 1984). Furthermore, metacercariae of all microphallids of the “*pygmaeus*” group develop inside the daughter sporocysts without encystment and lack the stage of cercaria with pronounced tail (Galaktionov and Dobrovolskij 2003).

Besides *M. breviatus*, five other *Microphallus* species are known from hydrobiid snails, whose metacercariae encyst and reach the infective state inside the daughter sporocysts. Four of them, *Microphallus scolectroma* Deblock & Tran Van Ky, 1966, *Microphallus abortivus* Deblock, 1974, *Microphallus simillimus* Travassos, 1920 (Martorelli 1991) and *M. fusiformis* Reimer, 1963, lack the stage of tailed cercaria (Deblock 1980; Martorelli 1991; Montoliu et al. 1992) and are thus clearly different from *M. breviatus*. Adults of *M. scolectroma* and *M. abortivus* have not been described, but the characters distinguishing their metacercariae from those of *M. breviatus* are analyzed in detail in Deblock and Maillard (1975) and in Deblock (1980). Adults of *M. simillimus* are significantly larger (450×318) (Martorelli 1991) than those of *M. breviatus*. Adults of *M. fusiformis* have a characteristic spindle-like body (Reimer 1963), whose width in the widest region (60–66) is less than the width of the *M. breviatus* body, even at the level of midesophagus. Moreover, eggs of *M. fusiformis* are much larger (23–26×15–16), and their number in adults is less (20–60) (Montoliu et al. 1992) than in *M. breviatus*.

For the fifth species, *Microphallus pirum* Lebour, 1907 *sensu* (Deblock 1980) (= *Microphallus somateria* Kulatschkova, 1958), a tailed xiphidiocercaria of the Ubiquita group, similar to the cercariae of *M. breviatus*, has been described (Kulatschkova 1958; Deblock 1980). However, tailed cercariae were not found in an investigation on the larval development of *M. pirum* inside the daughter sporocysts parasitizing *Hydrobia ulvae* and *H. ventrosa* at the White Sea (that is, in the investigation area of Kulatschkova) (Galaktionov 1991a,b). Only a short rudimentary tail is formed during morphogenesis in these larvae; the degree of its development is similar to the analogous structure developing in metacercariae of the microphallids of the “*pygmaeus*” group (Galaktionov and Dobrovolskij 2003). It is noteworthy that Lebour (1907) did not either describe tailed cercariae in *M. pirum* sporocysts. Galaktionov (1991b) suggested that the description of a tailed cercaria in *M. pirum* was due to some misunderstanding. Most probably, it was an erroneous interpretation of the double infection of *Hydrobia* snails by *M. pirum* and *Microphallus claviformis* (we often observed such double infections at the White Sea and in Iceland). At the final morphogenetic stages, cercariae of the latter species look very similar to the *M. pirum* cercariae from the original drawings of Kulatschkova deposited at the White Sea Biological Station (Zoological Institute, St. Petersburg, Russia) and presented in Deblock (1980). After contact with the second intermediate host, a crustacean, the cercariae of *M. claviformis* shed the tail and instantly form the so-called penetration cyst around the body which consists of the secretion from the anterior pairs of the penetration glands (Deblock 1980; Galaktionov 1991b;

Galaktionov and Dobrovolskij 2003). Protected by this temporary penetration cyst, the larvae penetrate through the crustacean body, and when they have reached their final settlement sites in the body, the larvae form a permanent cyst owing to secretion of the cystogenous glands.

Penetration cysts often form spontaneously on slides which have been prepared for in vivo microscopic observations. As a result, cercariae of *M. claviformis* can be erroneously identified as *M. pirum* larvae. Adults of *M. pirum* are clearly different from those of *M. breviatus*; they have a smaller body (130–160×95–100), smaller organs, and relatively few (15–20), rather large (21–27×10–13) eggs (Kulatschkova 1958; Deblock and Rosé 1964).

Discussion

M. breviatus has been reported only from the Mediterranean coast of France and from Iceland (Deblock 1980; Skirnisson and Galaktionov 2002). Its first intermediate host is solely *H. ventrosa*, but its natural definitive host is yet unknown. However, considerable differences in *M. breviatus* prevalence in hydrobians on the two Icelandic study sites allow us to make some suppositions. Whereas ducks, geese, and swans are similarly abundant in Galgahraun and Melabakkar but waders are much more abundant in the former area, where the high and stable infection prevalences of *M. breviatus* were observed for years, we consider that one or more wader species might be the natural definitive host of *M. breviatus*. Wader species which occur in both study areas belong to the genera *Tringa*, *Calidris*, *Charadrius*, and *Pluvialis* and have one or more representatives which can feed upon hydrobians when the snails lie exposed on mudflats.

The family Microphallidae is one of the few trematode families where species with dixenous life cycles are numerous. Cercariae of these species do not leave the molluscan host but develop into metacercariae, infective for the definitive host, inside the daughter sporocysts (Belopolskaya 1963; Deblock 1977). These species can be arranged in a distinct evolutionary series (Table 1). In this series, however, cercarial systems of organs associated with an existence in the external environment and with penetration into the second intermediate host (tail, stylet, penetration glands) and encystment (cystogenous glands) are gradually reduced (Belopolskaya 1963; Deblock 1977; Galaktionov 1991b). The first species in the series is *Maritrema murmanica* Galaktionov, 1989. Morphologically, its cercaria is a typical Ubiquita cercaria, which is a characteristic of microphallids with trixenous life cycles. However, the cercariae of *M. murmanica* do not leave the host (though they may swim in water under experimental conditions) but encyst inside the daughter sporocysts (Galaktionov 1989).

The cercariae of *M. breviatus* described in the present paper represent the next stage of somatic organization reduction (Table 1); their tail is so underdeveloped that the larvae are unable to swim. Also, the stylet and penetration glands are underdeveloped. Actually, the stylet has no cutting edges, and the ducts of the penetration glands are poorly filled with secretion. A similar reduction level is observed in cercariae of *Maritrema oocysta* Lebour, 1907 (see Deblock 1980 for a review).

Further transformations of morphogenesis of hermaphroditic generation (cercaria, metacercaria, adult) larvae of microphallids with dixenous life cycles are associated with the transfer of the differentiation of organ systems characteristic of mature organism (including digestive and repro-

Table 1 Some characters of cercariae and metacercariae of microphallids possessing dixenous life cycles

Species	Cercaria				Metacercarial cyst	
	Typical Ubiquita	Underdeveloped tail, stylet, and penetration glands	Reduced tail, loss of stylet, and penetration glands	Reduced tail, loss of stylet, penetration, and cystogenous glands	Present	Absent
<i>Maritrema murmanica</i>	+				+	
<i>Microphallus breviatus</i> , <i>Maritrema oocysta</i> , (possibly <i>M. syntomocyclus</i>)		+			+	
<i>Microphallus pirum</i> (possibly <i>M. scolectroma</i> , <i>M. abortivus</i> , <i>M. helicicola</i> , <i>M. simillimus</i> , <i>M. fusiformis</i> , <i>Atriophallophorus minutus</i>)			+		+	
“pygmaeus” group (<i>Microphallus pygmaeus</i> , <i>M. piriformes</i> , <i>M. pseudopygmaeus</i> , <i>M. triangulatus</i> , <i>M. calidris</i>), <i>Atriotrema</i> sp.				+		+

ductive organs) to earlier stages. This is accompanied by the further reduction of cercarial tail (it becomes a short and poorly differentiated appendage), the loss of the stylet, the loss of penetration glands, and the loss of tegument glands not associated with the production of cystogenous secretion. Such morphogenesis is characteristic of *M. pirum*. It is very likely that metacercariae are formed in the same way in *M. scolectroma*, *M. abortivus*, *Microphallus helicicola*, *M. simillimus*, *M. fusiformis*, and, possibly, also in *Atriophallophorus minutus* Price, 1934 (Deblock and Rosé 1964) (= *Levinseniella* sp. no. 17 Deblock, 1980) (Deblock 1974, 1977, Deblock 1980; Belopolskaya and Soboleva 1977; Martorelli 1991; Galaktionov 1991b; Field et al. 1998).

The series is completed by the microphallids of the “*pygmaeus*” group, currently comprising at least five species: *Microphallus pygmaeus* (Levinsen, 1881), *M. piriformes* (Odhner, 1905) Galaktionov 1983, *Microphallus* sp. 1 (*M. pseudopygmaeus*) Galaktionov, 1980, *M. triangularis* Galaktionov, 1984, and *M. calidris* Belopolskaya & Ryjkov, 1963 (see Galaktionov et al. 2004 for a review), and by *Atriotrema* sp. Galaktionov (1986). In these species, during morphogenesis of larvae of the hermaphroditic generation, the primordia of cystogenous glands are not formed and metacercarial development occurs inside the daughter sporocysts without encystment. It should be stressed that in microphallids of the “*pygmaeus*” group, and in species whose larval development is similar to that in *M. pirum*, the stage of cercaria retains in morphogenesis. It is clearly marked by the rudimentary tail, which is shed during transition to the next ontogenetic stage, that of the metacercaria (Galaktionov and Dobrovolskij 2003).

Maritrema syntomocyclus Deblock and Tran Van Ky (1966) does not seem to fit the above series of morphogenesis transformation in hermaphroditic generation larvae of microphallid. Its cercariae were found, in small numbers, together with encysted mature metacercariae in sporocysts. Its larva, referred to as pseudo-cercariaeum, lacks tail and stylet but has penetration glands with narrow ducts and sparse secretion (Deblock and Tran Van Ky 1966; Deblock 1980). It looks very similar to a young metacercaria of microphallids with a trixenous life cycle, which has just penetrated the second intermediate host (Galaktionov 1991a,b; Galaktionov and Dobrovolskij 2003). Deblock and Tran Van Ky (1966) and Deblock (1980) seem to have dealt with a case of mature *M. syntomocyclus* infection, when, alongside with fully formed encysted metacercariae, a few young nonencysted larvae are retained, which, however, have already shed their tails. We repeatedly observed such composition of larvae in *M. breviatus* sporocysts. It seems unlikely that the tail is not developed at all in *M. syntomocyclus* cercariae, considering that its rudiment is present even in developing larvae of the microphallids of the “*pygmaeus*” group. If our assumption

is true, *M. syntomocyclus* should be placed near *M. breviatus* in the above evolutionary series. However, this question can only be clarified after a thorough investigation of the larval morphogenesis in *M. syntomocyclus*.

The above review of morphogenesis specialization in hermaphroditic generation larvae of microphallids with dixenous life cycles shows that in their case, the life cycle as such (that is, a sequence of ontogenetic stages) is not reduced. All ontogenetic stages of the hermaphroditic generation (cercaria—metacercaria—adult) are retained, though the larval morphogenesis is considerably different from that in species with trixenous life cycles (Galaktionov and Dobrovolskij 2003). What happens is a reduction of transmission ways due to the loss of the second intermediate host.

A true reduction of the life cycle may result from neoteny as, for instance, in *Paralepoderma* representatives. Adults of species with dixenous life cycle (*Paralepoderma brumpti*) and species with monoxenous cycle (*Paralepoderma progenetica*) are underdeveloped as compared with *Paralepoderma cloacicola* adults, which appear to possess a typical trixenous cycle. The level of development of somatic systems of organs in adults of *P. brumpti* and *P. progenetica* corresponds to that in metacercariae of *P. cloacicola*. Thus, the ontogenesis of the former two species is reduced at the expense of the adult stages, that is, neoteny takes place (Grabda-Kazubska 1976). The origin of schistosomatid blood parasites (Sanguinicolidae, Spirorchidae, Schistosomatidae) also appears to be associated with neoteny. In their case, the formation of dixenous life cycles was probably accompanied not only by the loss of the true definitive host (reduction of transmission ways of parasites in an ecosystem) but also by the reduction of the life cycle itself by the loss of the primary adult phase (Combes 1991, 2001). A detailed analysis of secondary transformation of trematode life cycles is available in the literature (Combes 2001; Poulin and Cribb 2002; Galaktionov and Dobrovolskij 2003). Here, we only note that such an analysis should involve not only life cycle schemes (holoxenous, dixenous, trixenous, etc.) but also the morphological–functional reconstructions that brought about the formation of a definite life cycle.

Among microphallids, species with dixenous life cycles are most numerous in the genus *Microphallus* (14 species). They are fewer in the genera *Maritrema* (three species) and *Atriophallophorus* (two species). Only one such species has been found in each of the genera *Odhneria* and *Atriotrema* (Deblock 1980; Galaktionov 1986; Montoliu et al. 1992). Undoubtedly, transition to dixenous life cycles occurred independently in the above genera and several times within each genus (at least in *Microphallus*). In our opinion, a high prevalence of species with dixenous life cycles in Microphallidae is associated with adaptation to transmission in marine coastal ecosystem, where the evolution of the family took place (Galaktionov and Dobrovolskij 2003). Environ-

mental factors of the intertidal zone, especially in the North, are very unfavorable for free-swimming cercariae, reducing considerably their chances of penetration into the second intermediate host. Under these conditions, the loss from the life cycle of the phase of free-living larva in the external environment, and a consequent loss of the second intermediate host, may be a selective advantage. This point of view is probably sustained by the fact that those were microphallids with dixenous life cycles which managed to colonize the Arctic (microphallids of the “*pygmaeus*” group, *Atriotrema* sp.) and the terrestrial ecosystems of alpine pastures (*Microphallus helicicola*) (Galaktionov and Dobrovolskij 2003; Skirnisson and Galaktionov 2002).

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