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Development of *Myxobolus dispar* (Myxosporea: Myxobolidae) in an oligochaete alternate host, *Tubifex tubifex*

Kálmán Molnár[1], **Amina El-Mansy**[2,3], **Csaba Székely**[1] and **Ferenc Baska**[1]

[1]Veterinary Medical Research Institute, Hungarian Academy of Sciences, H–1581 Budapest, P.O. Box 18, Hungary;

[2]National Institute of Oceanography and Fisheries, Cairo, Egypt;

[3]Department of Zootaxonomy, Synbiology and Hydrobiology, University of Eötvös Loránd, Budapest, Hungary

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Abstract. The development of *Myxobolus dispar* Thélohan, 1895, a myxosporean parasite of the gills of common carp (*Cyprinus carpio* L.) was studied in experimentally infected oligochaetes *Tubifex tubifex* Müller. After infection of uninfected tubificids with mature spores of *M. dispar,* development of actinosporean stages was first observed light microscopically 21 days after initial exposure. In histological sections, early pansporocysts were located in the gut epithelium of experimental oligochaetes, while advanced stages occupied mostly the outer layers of the gut and the coelozoic space. Mature pansporocysts, each containing 8 raabeia spores, appeared 199 days after initial exposure. Following damage of the intestinal wall and rupture of the pansporocysts, free actinosporean stages were found in the gut lumen of the oligochaetes. Actinospores of *M. dispar* emerged from the worms after 217 days of intra-oligochaete development. They were floating in the water and showed a unique raabeia form. Each raabeia spore had three pyriform polar capsules and a cylindrical-shaped sporoplasm with approximately 32 secondary cells. The spore body joined the three caudal projections without a style. Caudal projections were bifurcated at the end and the two main branches had further small bifurcations. The total length of the raabeia spore was approximately 158 µm. The prevalence of infection in 240 experimentally infected *Tubifex* specimens was 99.2%. No infection was found in the control oligochaetes.

Following the revelation by Wolf and Markiw (1984) that the extrapiscine development of *Myxobolus cerebralis* Hofer took place in an oligochaete alternate host (*Tubifex tubifex* Müller), several teams made efforts to reproduce their results or perform similar experiments with other myxosporeans. The life cycle of the following species belonging to the genus *Myxobolus* has been studied: *M. cotti* El-Matbouli et Hoffmann, a parasite of the bullhead *Cottus gobio*, *M. pavlovskii* (Akhmerov), a parasite of the silver carp *Hypophthalmichthys molitrix*, *M. carassii* Clokacheva, a parasite of the orfe *Leuciscus idus*, *M. arcticus* Pugachev et Khokhlov*,* a parasite of the sockeye salmon *Oncorhynchus nerca*, and *M. cultus* Yokoyama, Ogawa et Wakabayashi, a parasite of the goldfish *Carassius auratus* (El-Matbouli and Hoffmann 1989, Ruidisch et al. 1991, El-Matbouli and Hoffmann 1993, Kent et al. 1993, Yokoyama et al. 1995). From other myxosporean genera successful life-cycle studies have been completed for *Hoferellus*, *Ceratomyxa, Zschokkella, Myxidium, Thelohanellus* spp. and for the causative agent of proliferative gill disease of channel catfish (Styer et al. 1991, El-Matbouli et al. 1992, Grossheider and Körting 1992, Benajiba and Marques 1993, Yokoyama et al. 1993, Uspenskaya 1995, Trouillier et al. 1996, Bartholomew et al. 1997, Yokoyama 1997). In each case, various species of oligochaete were shown to be alternate hosts.

Myxobolus dispar was first described by Thélohan (1895). This parasite is one of the most commonly occurring myxosporeans of the gill of common carp (*Cyprinus carpio* L.), causing economic losses in fish farms (Molnár and Szakolczai 1980).

The work presented in this paper is a part of continuing experimental life cycle studies conducted on the most common myxosporeans of Hungarian fish species (El-Mansy and Molnár 1997a,b). In the experiments reported here, the oligochaete *Tubifex tubifex* was experimentally infected with *Myxobolus dispar* spores, and actinosporean stages belonging to the raabeia type developed in it.

MATERIALS AND METHODS

Spores of *Myxobolus dispar* were collected from mature cysts from the gills of 4- to 5-year-old common carp (*Cyprinus carpio*) collected from the Kis-Balaton Water Reservoir, Hungary.

Oligochaetes *Tubifex tubifex* and *Limnodrilus hoffmeisteri* (Claparéde), identified according to Brinkurst (1963), were collected from a muddy pool in a forest near the top of a hill north of Budapest, Hungary, where no fishes live. They were transferred to sterilised mud, and propagated in the laboratory in aerated aquaria. The worms were fed on some drops of granulated fish food, and pieces of chicken faeces were added to increase the organic matter content of the mud. In addition,

Address for correspondence: K. Molnár, Veterinary Medical Research Institute, Hungarian Academy of Sciences, H-1581 Budapest, P.O. Box 18, Hungary. Phone: ++36 1 252 2455; Fax: ++36 1 252 1069; E-mail: kalman@novell.vmri.hu

oligochaete specimens of *Branchiura sowerbyi* (Beddard) collected from a fish pond were also used in the experiments. Normal tap-water was used throughout the experiments. The temperature of the room varied between 18°C and 22°C.

Between 300 and 700 oligochaetes were placed into a 5-litre aquarium, and 50 to 100 worms were placed into a small plastic cup of 500 ml volume. All dishes were permanently aerated and regularly supplied with fresh water to prevent evaporation and to refresh the water for the oligochaetes. The oligochaetes were infected by adding about 0.5 million *M. dispar* spores to the content of both dishes.

Oligochaete specimens from the same stock were maintained in a 5-litre aquarium as a control.

From the infected stocks, 240 *T. tubifex* and 240 *L. hoffmeisteri* specimens were examined for the presence of developmental stages. The same number of oligochaetes was checked from the control stock. In addition, 20 exposed and 20 control specimens of *B. sowerbyi* were checked regularly after infection with *M. dispar* spores.

The development of actinosporean stages of *M. dispar* was checked regularly by the following methods: (1) Twice a week 2 to 5 oligochaetes were selected from both dishes for examination. First the gross appearance (colour and movement) of the worms was examined. Afterwards they were carefully placed under a coverslip and examined alive at 200-fold magnification of the microscope for the presence of developmental stages. One or two of the worms showing alterations in gross appearance were squashed. (2) Three weeks after initial exposure, 72 oligochaetes were placed into 2-ml cell-well plates three times a week (Yokoyama et al. 1991), and after one day of incubation they were examined for the release of actinospores under a compound microscope. (3) Every second day, water from the aquaria and the small dishes was filtered through a fine mesh of 10 µm pore size. The filtrates were taken up in a drop of water and examined for the presence of actinospores. (4) As far as possible, 5 oligochaetes were sacrificed for histological purposes every week. A total of 38 infected *T. tubifex* specimens were fixed in Bouin's solution, embedded in Paraplast® wax, cut into 4 to 8 µm thick sections, and stained with haematoxylin and eosin. For electron microscopy, 5 infected *T. tubifex* specimens were fixed in 2% osmium tetroxide, washed several times with cacodylate buffer, dehydrated and embedded in Durcupan ACM resin. Semithin sections (0.5-1 µm) were made and stained with 0.1% methylene blue solution. Ultrathin sections were cut with glass knives, contrasted with uranyl acetate and lead citrate, and examined with a JEOL-100 transmission electron microscope.

Raabeia spores released by the oligochaetes were examined under a coverslip. They were recorded with the help of a video image program on videotapes as described by Székely (1997). Photographs were taken, drawings made and measurements of 50 actinospores recorded. In the description, all measurements are given in µm. The actinosporean stage of *M. dispar* was described using the terminology of Janiszewska (1957) as modified by Lom et al. (1997).

RESULTS

Light microscopy

The development of *Myxobolus dispar* was followed in *Tubifex tubifex*. Over a period of 217 days, 238 of the examined 240 *T. tubifex* specimens (99.2%) were infected by actinosporeans (including developmental stages and released spores). Both *T. tubifex* specimens kept in the aquarium and those in the plastic cups were infected. Heavily infected specimens could be selected by their pale colour and sluggish movement. No infection was found in *Limnodrilus hoffmeisteri* and in the control *Tubifex* specimens. *B. sowerbyi* specimens, both the infected ones and the controls, released some aurantiactinomyxon stages. In live *T. tubifex* the first sign of infection was recorded 21 days after initial exposure with *M. dispar* spores. In that phase developmental stages were seen in the gut epithelium and in the coelom of some of the segments of the worms. Later on these stages grew in number and size. From crushed *T. tubifex* specimens pansporocysts were obtained, each of which contained 8 developing raabeia spores.

From live *Tubifex tubifex,* actinospores were first released into the water 217 days post infection, and the actinospore-release continued for about 1.5 months after their first appearance. The released actinosporean stages proved to be raabeia types but, due to their bifurcated tails, they represented an unusual form of raabeia stages.

Histology

Developing actinosporean stages were found only in *T. tubifex*. *L. hoffmeisteri* and *B. sowerbyi* specimens were free of infection. The first developing stages in the gut epithelium were young pansporocysts 21 days after initial exposure. Forty-eight days after initial exposure with *M. dispar* myxospores, larger pansporocysts of advanced stage were located also in the muscular layer of the intestine. These stages were round to oval in shape with a dark cytoplasm (Fig. 1). As the development progressed, in addition to pansporocysts still being located in the epithelium, more and more pansporocysts were found in the muscular layer of the gut and among chloragogen cells surrounding the intestine (Fig. 2). In addition, specimens were located in the ovary among the oocytes.

Mature pansporocysts were formed 199 days after initial exposure. They were mostly located in the coelom between the chloragogen cells of the gut and the worm's cuticle (Fig. 3), with fewer pansporocysts remaining in the epithelium and in the muscular layer of the gut. At that time each pansporocyst contained 8 raabeia spores in which the three polar capsules, the sporoplasm containing approximately 32 secondary cells and the projection of caudal processes were easily detected (Figs. 3, 4). At higher magnifications the contours of

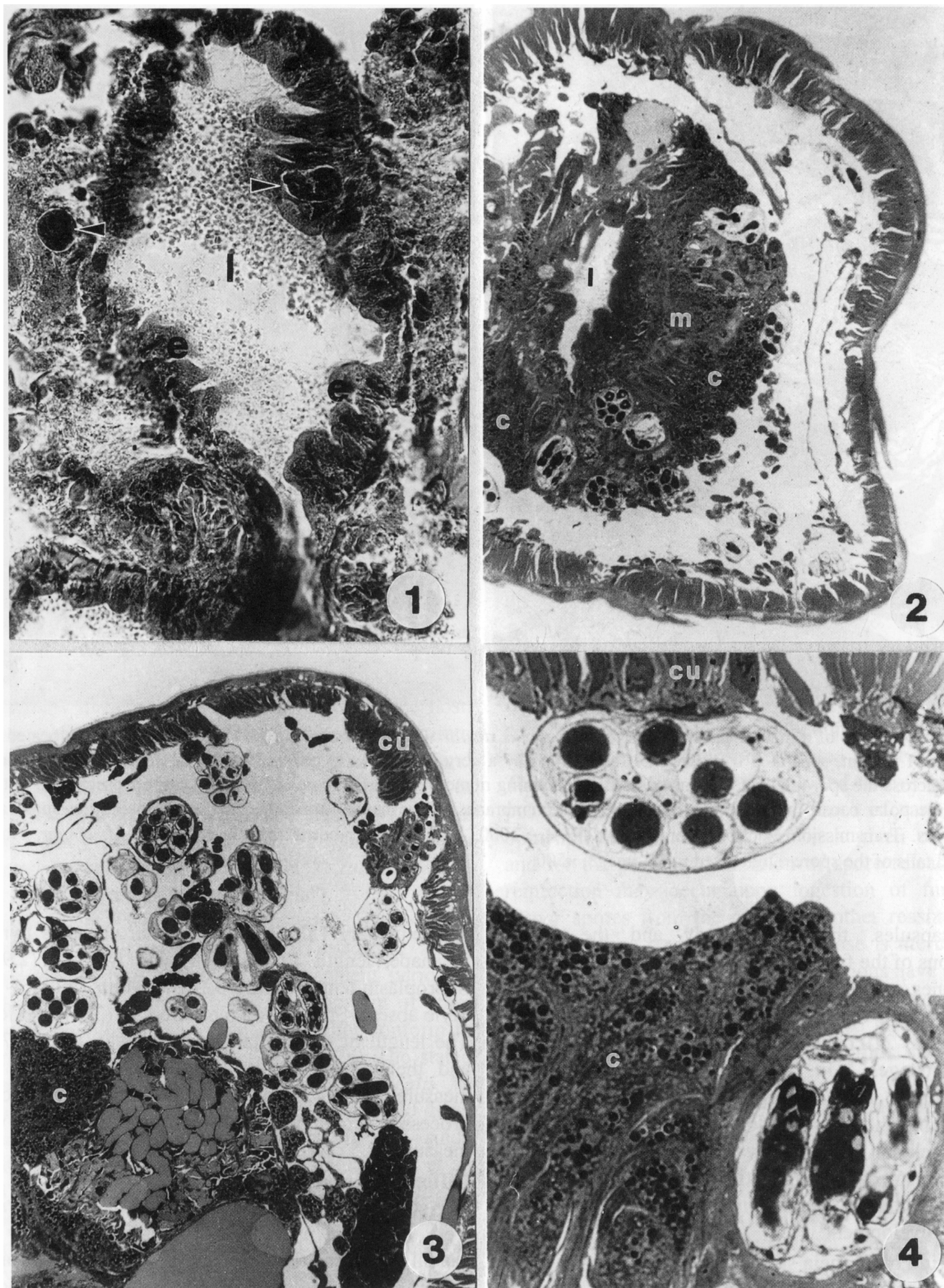
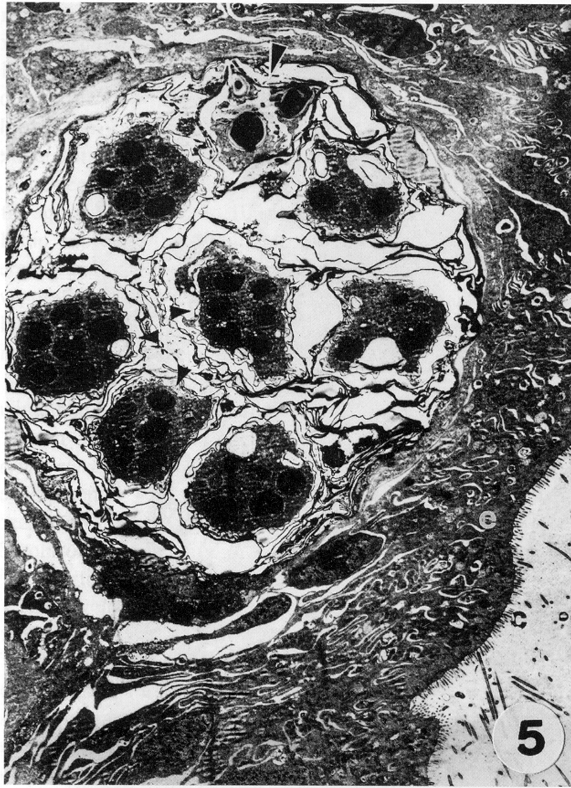


Fig. 1. Histological section of the intestinal wall of a *Tubifex tubifex* 48 days after initial exposure. More developed pansporocysts (arrowheads) of *Myxobolus dispar* are located in the epithelium (e) and muscular layer of the intestinal wall. H&E, ×400. **Fig. 2.** Cross-section of a *T. tubifex* 199 days after initial exposure. Pansporocysts containing 8 actinospores are located in the muscular layer (m) of the intestinal wall and inside chloragogen cells (c). l – lumen of the gut. Semithin section, ×200. **Fig. 3.** Cross-section of a *T. tubifex* 199 days after initial exposure. The space between chloragogen cells (c) and the cuticle (cu) is filled with pansporocysts containing 8 raabeia spores each. Semithin section, ×300. **Fig. 4.** Cross-section of a *T. tubifex* 199 days after initial exposure. Note a pansporocyst with transversally sectioned spores between the cuticle (cu) and the chloragogen cells (c), and a pansporocyst with longitudinally sectioned spores among the chloragogen cells. Semithin section, ×1000.



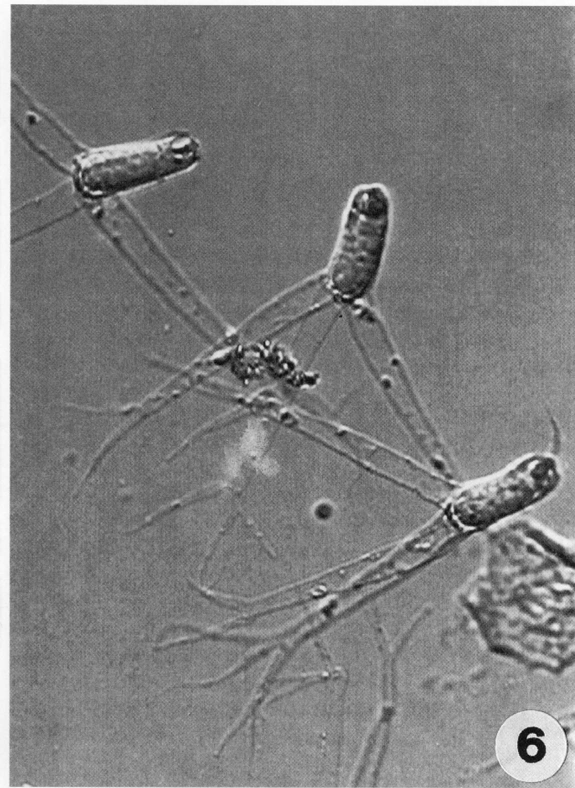


Fig. 5. Cross-section of a mature pansporocyst of *Myxobolus dispar* with 8 raabeia spores. The pansporocyst is located in the epithelium of the gut, separated from the intestinal lumen by a very thin layer (e) covered by cilia (c). Most of the spores are sectioned across the sporoplasm (small arrowheads) containing numerous secondary cells. One of the spores sectioned at the top shows three polar capsules (large arrowhead). Folded membranes of the caudal appendage are seen inside the space among actinospores. Transmission electron micrograph (TEM), ×2000. **Fig. 6.** Water-borne raabeia spores of *M. dispar*. Note the bifurcated tails of the spore. Digitalised video image, ×500.

the polar capsules, the spore body and the folded projections of the future raabeia spores were discernible. Membranes of the folded caudal appendages were located among the raabeia spores (Fig. 5). On post-infection day 210 the coelom still harboured hundreds of raabeia stages. In addition, however, mature pansporocysts and free spores were already being released into the intestinal lumen through the damaged gut epithelium. Interestingly enough, however, some pansporocysts containing actinospores were recovered from the intestinal epithelium even at that advanced stage of development.

Description of raabeia spores

Raabeia spores released from the body of *T. tubifex* and floating in the water were characterised by three pyriform polar capsules and a cylindrical sporoplasm containing approximately 32 secondary cells. Polar capsules and the sporoplasm formed the spore body. Each of the caudal processes was divided into two main branches each having a further small bifurcation, but some of them ended in a terminal claw-like structure (Fig. 6, 7). The whole length of the raabeia spore was approximately 158 (150-168). Polar capsules pyriform in shape, length 7.5 (5.9-8.6) and width 4 (2.9-4.7). Sporoplasm length 30 (28-32) and width 14 (11.4-15.5). Style absent. Spore body measured 37 (34-40) in length. The length of the caudal processes was 121 (117-124) and their width 10.8 (8.5-11.4). The terminal claw measured 6.2 (4.2-7.1) in length. Each of the caudal processes contained one spherical nucleus which measured 2.5 (2.4-2.6).

Differential diagnosis

Actinospores of *M. dispar* released from *T. tubifex* were identified as raabeia spores, although by their caudal processes they resembled echinoactinospores as well. Most of the spores found had straight processes like echinoactinospores but spores with slightly curved processes characteristic of raabeia spores also occurred. By their bifurcated caudal processes actinospores of *M. dispar* bore the closest resemblance to *Raabeia furciligera* Janiszewska et Krzton. Both species had branches (terminal claws) on their relatively straight caudal processes, but while Janiszewska and Krzton (1973) described the branches of *R. furciligera* as

unevenly located in the caudal processes, the processes of the *M. dispar* raabeia spores have regular bifurcations.

DISCUSSION

Myxobolus dispar is a well-known parasite of the common carp. In spite of its common occurrence, however, little is known about its pathogenicity and intrapiscine development. No studies have been done on the intra-oligochaete development of this species. The data obtained on its extrapiscine development show that this parasite follows the same pattern in its development as described by Wolf and Markiw (1984), El-Matbouli and Hoffmann (1989, 1993) and Ruidisch et al. (1991). The development of *M. dispar* was successfully accomplished in *Tubifex tubifex,* in which unique raabeia spores having bifurcated caudal processes developed. In their shape and size the spores resembled raabeia spores described by Janiszewska (1955, 1957) and Yokoyama et al. (1995), but they markedly differed from the latter by their bifurcated tails. Raabeia spores with bifurcated tails have already been described by Janiszewska and Krzton (1973), but the bifurcations of that species have irregular branches. It seems that the majority of *Myxobolus* species (*M. cerebralis, M. cotti, M. carassii*) form triactinospores in the alternate host. However, *M. pavlovskii* has been found to develop into a hexactinospore in *T. tubifex* (Ruidisch et al. 1991) and *Myxobolus cultus* into a raabeia-type actinospore in *Branchiura sowerbyi* (Yokoyama et al. 1995). The present study proves that *M. dispar* forms a characteristic actinosporean spore in *T. tubifex*, which might be designated as "bifurcoraabeia".

Development was completed and actinospores released 217 days after the initial exposure, at an average temperature of 20°C. The prepatent period is very long when compared to the development of other known *Myxobolus* species, and it does not conform to data reported by El-Matbouli et al. (1992a) who stated that intra-oligochaete development for *M. cerebralis, M. cotti* and *M. carassii* occurred between 80 and 120 days.

The prevalence of infection found in this study considerably exceeds that reported by Yokoyama et al. (1995). While studying the development of *M. cultus* in *B. sowerbyi*, these authors found an about 20% infection with raabeia stages in *B. sowerbyi*; in the present study, however, the prevalence of infection with raabeia stages of *M. dispar* was as high as 99.2% in *T. tubifex*. In addition, the raabeia stages of *M. dispar* equally infected the gut epithelium and the coelom, while Yokoyama et al. (1995) recorded infection exclusively in the intestinal epithelium of *B. sowerbyi.*

Histological data suggest that early development of the species takes place in the intestinal epithelium, while more mature pansporocysts are located in the

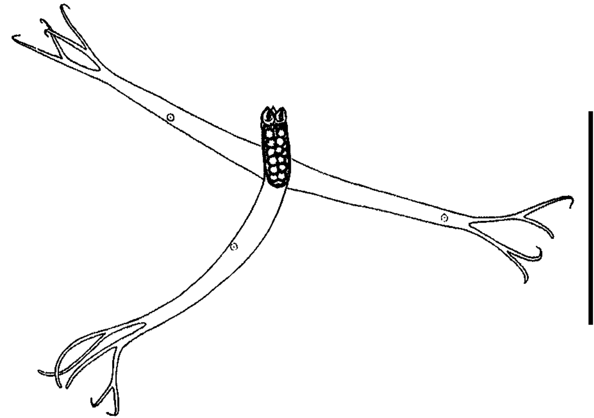


Fig. 7. Schematic illustration of the raabeia spore of *Myxobolus dispar*. Scale bar = 100 µm.

coelom. Despite this specific location, released actinospores were found primarily in the gut of *Tubifex*, which suggests that the spores find their way into the gut lumen and they are released from the infected oligochaetes partly through the anal opening.

A certain asynchronism was found in the intra-oligochaete development of *M. dispar*. Although 199 days after initial exposure the majority of raabeia stages finished sporogony, several very young pansporocysts were also observed in the epithelium. Furthermore, the release period of actinospores lasted about 1.5 months. This asynchronism can be attributed to two factors. A possible explanation for the presence of varied developmental actinosporean stages in a given oligochaete and for the prolonged duration of spore release is that reinfection may occur upon ingestion of further *M. dispar* spores from the mud. The other reason for the relatively long period of spore release is the coelozoic development. Although such observations have not been made, it is assumed that a certain proportion of spores developing in the coelom are released through injuries in the worm's cuticle or after the worm's death, rather than via the gut.

From these experiments it can be concluded that, of the three oligochaete species used, only *T. tubifex* is a good alternate host for *M. dispar*, since no development took place in *B. sowerbyi* and *L. hoffmeisteri.*

Lacking successful experimental infections of the common carp with bifurcoraabeia stages, the entire developmental cycle of *M. dispar* could not be clarified yet; however, by utilising field observations on pond-cultured common carp and by the analogy of infection with other *Myxobolus* species (Wolf and Markiw 1984, El-Matbouli and Hoffmann 1989), a tentative model of its development has been constructed.

Intrapiscine development takes place in the gills after infection of the carp with bifurcoraabeia spores, while intra-oligochaete development starts when this alternate

host becomes infected with the myxosporean spores of *M. dispar*.

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Contact:
Dr. František Moravec or Dr. Jiří Lom
Institute of Parasitology
Academy of Sciences of the Czech Republic
Branišovská 31, 370 05 České Budějovice
CZECH REPUBLIC

Phone: ++420 38 7775432; Fax: ++420 38 47743
E-mail: moravec@paru.cas.cz, or lom@paru.cas.cz
http://www.paru.cas.cz/Sympos.htm