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STUDIES ON THE OCCURRENCE OF ACTINOSPOREAN STAGES OF MYXOSPOREANS IN LAKE BALATON, HUNGARY, WITH THE DESCRIPTION OF TRIACTINOMYXON, RAABEIA AND AURANTIACTINOMYXON TYPES

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In the framework of a one-year survey, the actinosporean infection of the oligochaete fauna living in the mud and on the vegetation of Lake Balaton, Hungary was studied. A total of 10 types of actinospores were isolated from the oligochaetes *Tubifex tubifex* and *Limnodrilus hoffmeisteri* collected during the survey, which could be classified into the triactinomyxon, raabeia and aurantiactinomyxon groups. The drawings depicting the individual actinospore types are presented on a plate and their characteristic dimensions summarised in tables. The prevalence and seasonality of actinosporean infections observed in the two oligochaete species are illustrated graphically. Infection by actinospores showed pronounced seasonality. In the spring and summer the prevalence of triactinomyxon infection in *T. tubifex* exceeded 30 and 40%, respectively, while in the autumn it dropped to 6%. In *T. tubifex* raabeia infection of 3% prevalence was detected only in the summer period. In *L. hoffmeisteri* the peak of aurantiactinomyxon, raabeia and triactinomyxon infection occurred in the summer with a prevalence of 21, 10 and 8%, respectively. Actinosporean infection in the individual Oligochaeta species showed higher prevalence values than had been reported in the literature, which fact may be explained by the novelty of the examination technique used. Four types of actinospores found in Lake Balaton are identical with the actinospores already described. It cannot be determined with absolute certainty which stages of myxosporeans parasitic in Lake Balaton fishes are identical with the 10 actinospores described.

Key words: Actinospore, myxosporeans, Myxozoa, survey, Lake Balaton, triactinomyxon, raabeia, aurantiactinomyxon

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The first report on actinosporeans was published by Stolc (1899), who described these organisms found in Bohemia as parasites related to myxosporeans. Although nearly one hundred years have elapsed since their first description, until quite recently only few researchers had studied actinosporeans. Of them, Ikeda (1912) and Mackinnon and Adam (1924) detected tetractinomyxon and triactinomyxon forms in England, while in Poland Janiszewska (1955, 1957) performed detailed studies on the morphology, ecology and systematics of actinosporeans. The ultrastructure and biology of these parasites have been studied most intensively by Marques (1984), Lom and Dykova (1997), and Lom et al. (1997a). Research on actinosporeans gathered momentum after Wolf and Markiw (1984) had demonstrated that actinosporeans did not constitute an independent taxonomic unit but corresponded to fish-parasitic myxosporean stages developing in oligochaetes. After Wolf and Markiw (1984), other researchers also produced experimental evidence that in the developmental cycle of a given species of Myxosporea intrapiscine myxosporean and intra-oligochaete (El-Matbouli and Hoffmann, 1989; Ruidisch et al., 1991; El-Matbouli et al., 1992; Grossheider and Körting, 1992; El-Matbouli and Hoffmann, 1993; Kent et al., 1993; Yokoyama et al., 1993*a*; El-Matbouli et al., 1995; Kent et al., 1995; Uspenskaya, 1995; Yokoyama et al., 1995; Trouillier et al., 1996; Yokoyama, 1997; El-Mansy and Molnár, 1997*a*, 1997*b*) or intra-polychaete (Bartholomew et al., 1997) actinosporean stages alternated. Relying on these studies, Kent et al. (1995) proposed that the class Actinosporea should be merged into the class Myxosporea as a synonym of the latter, and that the names of actinosporean genera should in the future be used only for typing actinospores developing in oligochaetes. The major taxonomic changes of recent years are reflected in the works of Smothers et al. (1994), Kent et al. (1995), Siddall et al. (1995), and Schlegel et al. (1996), who reassigned phylum Myxozoa, earlier regarded by many authors as protozoa, from protozoan to metazoan parasites.

The actinosporean infection of oligochaetes in fish farms and natural waters in relation to the developmental cycle of myxosporeans has so far been studied among others by Hamilton and Canning (1987), Székely (1989), Burtle et al. (1991), Pote and Waterstrat (1993), Koller (1994), Pallós (1995), McGeorge et al. (1997), and El-Mansy et al. (1998*b*).

Myxosporean infections of fishes and intrapiscine myxosporeans are relatively well studied in Lake Balaton (Jaczó, 1940; Molnár and Székely, 1995; Székely and Molnár, 1996–1997), but no study has been done on actinosporean stages until now.

The present paper reports on a one-year survey made on the occurrence of actinospores of Myxosporea in oligochaete alternate hosts in Lake Balaton.

Materials and methods

The survey was carried out in Lake Balaton, Hungary, between March 1996 and March 1997. Water-weed and mud collected from the lake were transported to the laboratory for the isolation of oligochaetes and then actinospores. In the course of the one-year survey two oligochaete species, *Tubifex tubifex* (Müller) and *Limnodrilus hoffmeisteri* (Claparède) [identified according to Brinkhurst (1963)] were examined for the occurrence of actinospores.

The methods used for the isolation of actinospores were the same as those described by Yokoyama et al. (1991) and El-Mansy et al. (1998*b*). Actinospores found in this survey were measured and identified as described by Lom et al. (1997*b*).

Results

From the 1164 specimens of the two oligochaete species studied (*T. tubifex* and *L. hoffmeisteri*) a total of 10 actinospore types (Figs 1, 2.1 and 2.2) were isolated from Lake Balaton. The actinospores found belonged to three main groups (triactinomyxon, raabeia and aurantiactinomyxon). Of the 807 *Tubifex* specimens examined, 267 (33%) were infected with triactinomyxon and 9 (1%) with raabeia spores (Fig. 3). Of the 357 *Limnodrilus* specimens, 10 (3%) proved to be infected with aurantiactinomyxon, 7 (2%) with triactinomyxon, and 5 (1.4%) with raabeia spores (Fig. 4).

Infection with actinospores exhibited a pronounced seasonality. In the spring and summer the prevalence of triactinomyxon infection in *T. tubifex* exceeded 30 to 40%, while in the autumn and winter it dropped to 6 and 0%, respectively. Raabeia infection in *T. tubifex* was only observed during the summer. At that time its prevalence went up to 3% (Fig. 5). In *L. hoffmeisteri* the highest prevalence of actinospore infection occurred in the summer when it reached 21% with aurantiactinomyxon, 10% with raabeia and 8% with triactinomyxon spores (Fig. 6). The main parameters of the actinospores found are presented in Tables 1–3.

Discussion

Owing to the increased interest taken in myxosporean diseases and the successful progress of experimental studies in recent years, actinosporean infections of oligochaetes or polychaetes have been investigated by numerous authors, among others by Mackinnon and Adam (1924), Markiw (1986), El-Matbouli and Hoffmann (1989), Yokoyama et al. (1991), El-Matbouli and

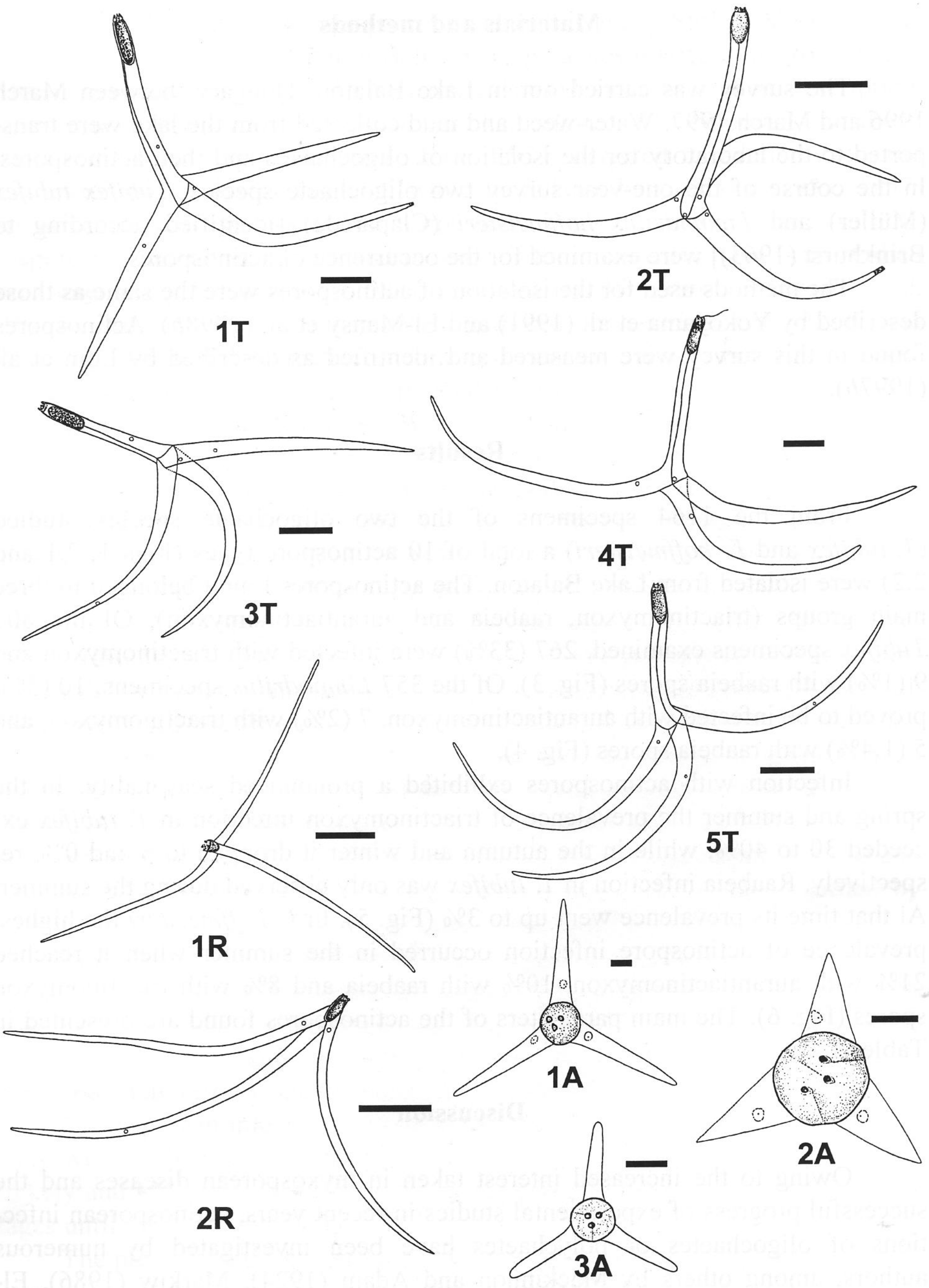

Fig. 1. Line drawings of actinospores found during a one-year survey of Lake Balaton oligochaetes. Triactinomyxon types: 1T, 2T, 3T, 4T and 5T, raabeia types: 1R and 2R, aurantiactinomyxon types: 1A, 2A and 3A. Bar = 50 μm

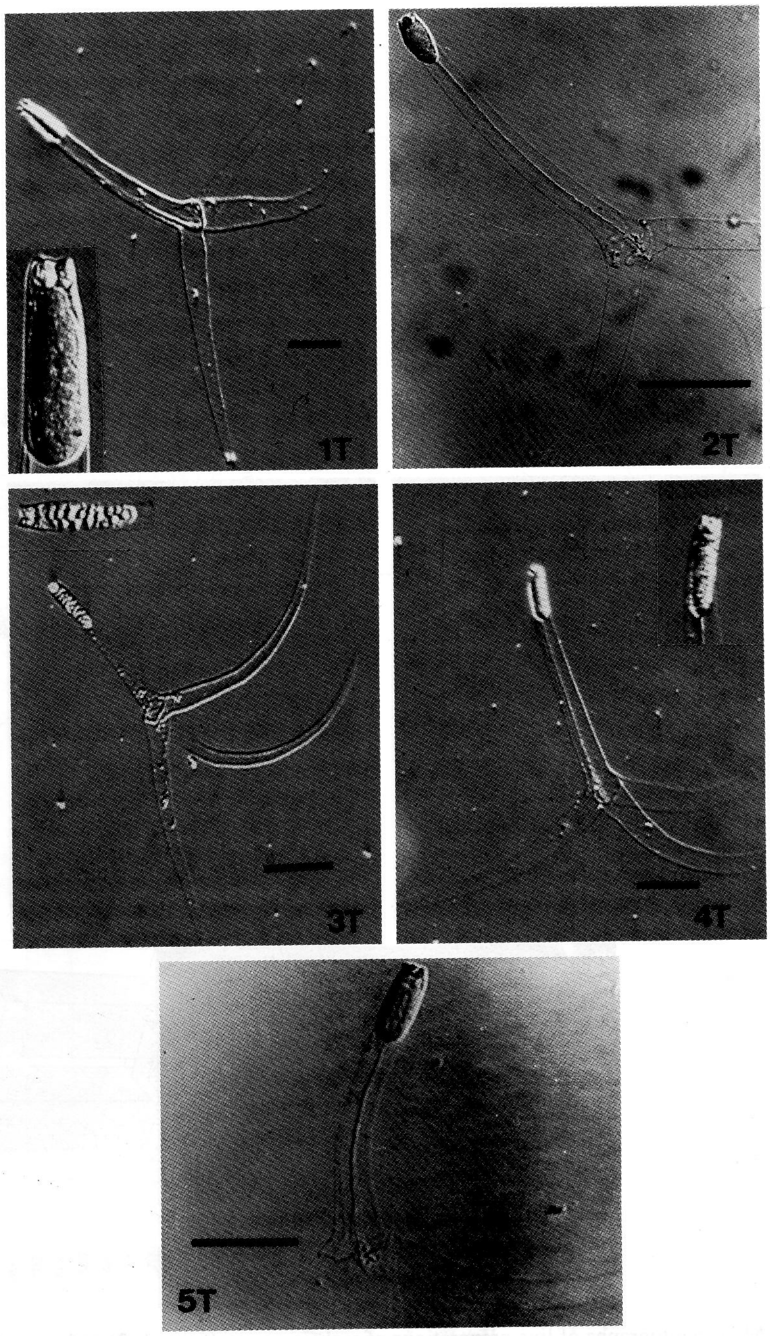

Fig. 2.1. Microphotographs of live preparations of triactinospores (types 1–5) found during a one-year survey of oligochaetes in Lake Balaton. Bar = 50 μm

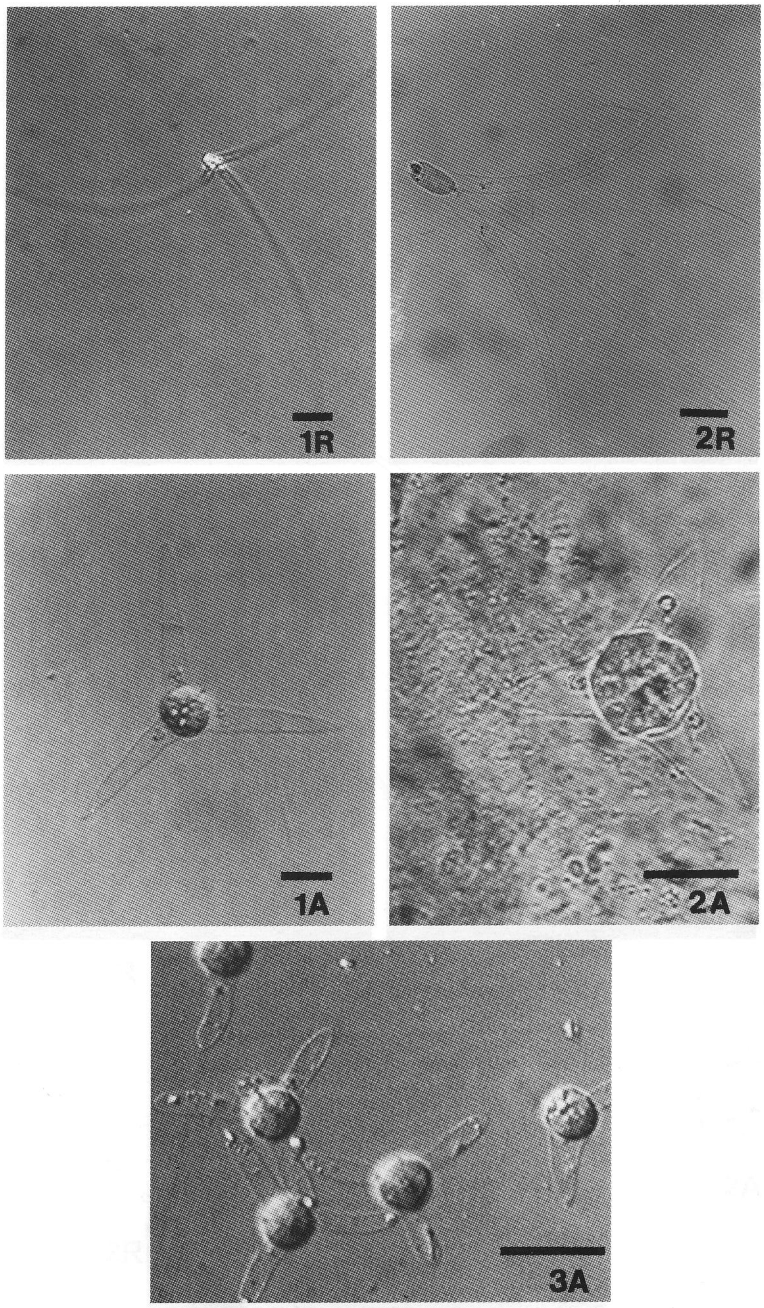

Fig. 2.2. Microphotographs of live preparations of raabeia spores (types 1–2) and aurantiactino-myxon spores (types 1–3) found during a one-year survey of oligochaetes in Lake Balaton. Bar = 20 μm

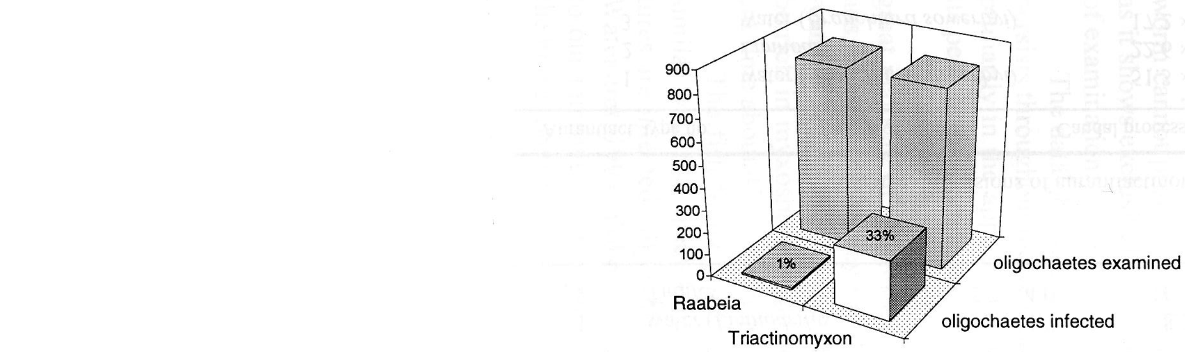

Fig. 3. Prevalence of infection in *Tubifex tubifex* (all year)

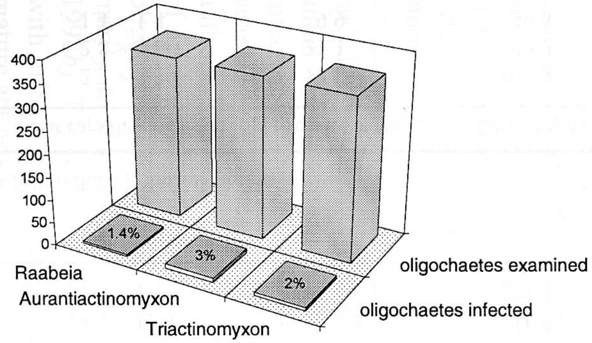

Fig. 4. Prevalence of infection in *Limnodrilus hoffmeisteri* (all year)

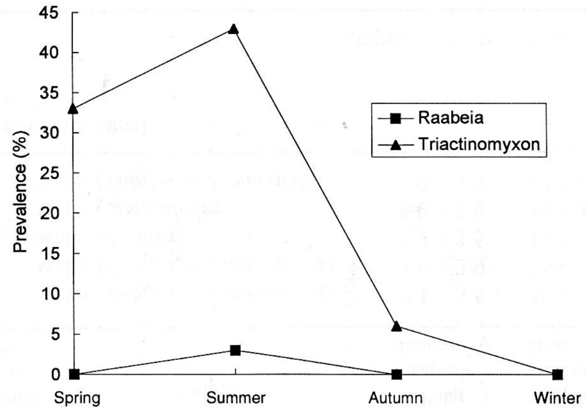

Fig. 5. Seasonality of actinosporean infection in *Tubifex tubifex*

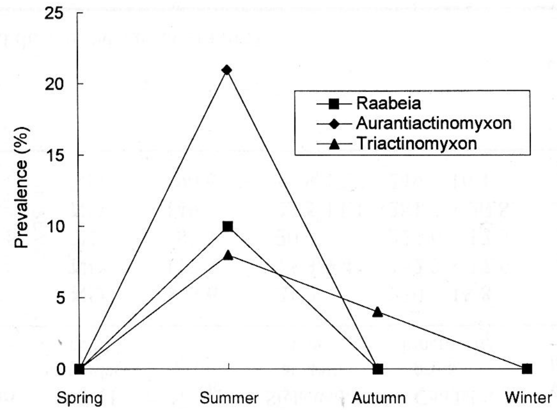

Fig. 6. Seasonality of actinosporean infection in *Limnodrilus hoffmeisteri*

All-year and seasonal prevalence of actinosporean infection of oligochaetes in Lake Balaton, Hungary from March 1996 to March 1997

Table 1

Average dimensions of triactinomyxon types found during the survey (in µm)

Triactino-myxon type no.	Origin of spores	Polar capsule dimensions	Spore body dimensions	Secondary cell dimensions	No. of secondary cells	Style length	Style width at start/at end	Caudal process dimensions	Whole length
1	water (*Tubifex* or *Limnodrilus*)	7.1 × 3.5	50.6 × 12.9	ND	ND	123.6	21.2	230 × 18.8	404.1
2	water (*Tubifex* or *Limnodrilus*)	3.0 × 2.9	25.4 × 10.6	ND	ND	117.7	15.3/9.4	152.2 × 17.6	295.2
3	water (*Tubifex*)	4.7 × 3.5	44.7 × 11.8	3.5 × 3.5	21	87.1	20	224.6 × 17.5	360
4	water (*Limnodrilus*)	8.0 × 5.9	45 × 12.9	ND	ND	149	23.5/14.1	281.7 × 20.8	478.4
5	water (*Tubifex* or *Limnodrilus*)	5.9 × 3.5	37.7 × 13.5	ND	ND	90.6	12.9/17.7	249 × 16.1	377.8

ND = not determined

Table 2

Average dimensions of raabeia types found during the survey (in µm)

Raabeia type no.	Origin of spores	Polar capsule dimensions	Sporoplasm dimension	Spore body dimensions	Caudal process dimensions	Whole length (from polar capsules to the end of caudal process)
1	water (*Limnodrilus*)	5.9 × 4.7	8.2 × 12.4	14.1 × 12.4	202.8 × 8.2	216.9
2	*Tubifex*	5.7 × 4.0	16.0 × 6.8	21.7 × 7.7	209.4 × 6.6	231.1

Table 3

Average dimensions of aurantiactinomyxon types found during the survey (in µm)

Aurantiact. type no.	Origin of spores	Caudal process dimensions	Polar capsule dimension	Spore cavity diameter	Largest span
1	water (*Branchiura sowerbyi*)	51.3 × 9.5	2.3 × 2.3	18.8	103.2
2	*Limnodrilus*	22.6 × 11.7	2.8 × 2.0	21.1	52.2
3	water (*Branchiura sowerbyi*)	17.2 × 3.9	1.4 × 1.4	9.9	39.5

Hoffmann (1993), Kent et al. (1993), Yokoyama et al. (1993*a, b*), El-Matbouli et al. (1995), Kent et al. (1995), Uspenskaya (1995), Yokoyama et al. (1995), Trouillier et al. (1996), and Bartholomew et al. (1997). Most of the above-listed authors reported a relatively low (around 1%) prevalence of infection in oligochaete populations. Yokoyama et al. (1993*a, b*) were the only investigators who detected > 4% actinosporean infection in *Branchiura sowerbyi* in a goldfish-culturing pond. In a survey of the actinosporean infection of oligochaetes in natural waters of Hungary, Székely (1989) and Pallós (1995) also found similarly low levels of infection. In contrast, in the survey of El-Mansy et al. (1998*b*) and in the present study we obtained high prevalence values (e.g. triactinomyxon infection of *T. tubifex* showed a prevalence of 33–43% in certain periods of the year). These values are significantly higher than those reported earlier by other authors. The higher values recorded by us, however, do not mean that the level of actinospore infection is so much higher in Lake Balaton oligochaetes than in oligochaetes from other habitats. The observed difference can be attributed primarily to the different examination technique used by us (El-Mansy et al., 1998*b*). Today it is already well known that a given oligochaete can be infected with different actinosporean developmental stages for several months, while the mature actinospores will be excreted only after an about 3-month period of intra-oligochaete development. The fact that in this study individual oligochaete specimens were regularly examined over a 3-month period, greatly elevated the ratio of positive individuals and revealed that a single examination of a given worm cannot provide reliable data on the prevalence of actinosporean infection, as it shows exclusively the ratio of worms that release mature spores at the time of examination.

The data obtained by us indicate that actinospore infection of oligochaetes persists throughout the year and is characterised by seasonality manifesting itself primarily in the appearance of worms containing mature spores, which reaches its peak in the warmer months.

Although myxosporeans parasitise several lower ranked vertebrates, the great majority of species are known from fishes. Accordingly, the actinosporeans found in this survey should first of all be regarded as fish parasitic myxosporeans. It seems to be evident that a habitat harbouring several fish species must be rich in myxosporean species and evidently also in actinospores. At the present time about 41 fish species are known to live in Lake Balaton (Biró, 1995).

The fish fauna of cold waters is relatively deficient in species and, in a similar way, fish species (salmonids, goldfish and catfish) cultured in monocultures are infected only with a scarce number of myxosporean species (Pote and Waterstrat, 1993; Yokoyama et al., 1993*a, b*; McGeorge et al., 1997). In addition to our improved actinospore examination technique, this could also account for the higher prevalence of actinosporeans found by us in Lake Balaton oligochaetes.

The actinospores found during the present survey were defined on the basis of the old taxonomic terms (triactinomyxon, raabeia and aurantiactinomyxon) described by Janiszewska (1955, 1957) and Marques (1984); however, we agree with the view of El-Matbouli et al. (1992), Kent et al. (1993), Yokoyama et al. (1993*a*), Kent et al. (1995), Yokoyama et al. (1995), Trouillier et al. (1996), and McGeorge et al. (1997), i.e. that these cannot be regarded as independent taxonomic units. The accepted names are used only for denoting the type of developmental stage of a given myxosporean species. The number of the 10 actinospore types detected by us from Lake Balaton roughly corresponds to that of myxosporean species hitherto found in the lake. We do not venture to identify any of the detected actinospore types as a developmental stage of any of the myxosporean species occurring in the lake in question. However, based upon the experimentally proven developmental cycles reported in the literature (Wolf and Markiw, 1984; El-Matbouli and Hoffmann, 1989; El-Matbouli et al., 1992; Benajiba and Marques, 1993; El-Matbouli and Hoffmann, 1993; Kent et al., 1993; Uspenskaya, 1995; Yokoyama et al., 1995; El-Mansy and Molnár, 1997*a*, 1997*b*) it can be assumed that triactinomyxons and raabeias represent the developmental stages of species belonging to the *Myxobolus* genus, while aurantiactinomyxons may be the developmental stages of species included in the genera *Myxidium, Zschokkella, Hoferellus* or *Thelohanellus*.

Although a relatively large number of myxosporeans are known from Lake Balaton fishes (Molnár and Székely, 1995; Székely and Molnár, 1996–1997), their actinosporean stages have not been identified. Only three species (*Myxobolus drjagini, M. hungaricus* and *M. portucalensis*) can be regarded as exceptions, as their actinosporean stages have already been revealed in experimental studies (El-Mansy and Molnár, 1997*a*, 1997*b*; El-Mansy et al., 1998*a*). All of the three *Myxobolus* species developed in their *Tubifex* alternate hosts into triactinospores. In some dimensions (e.g. the length of the style and the caudal processes) these triactinospores resembled some triactinospores found during the survey but there were major differences in the shape of the spores and in the number of secondary cells in the sporoplasm. In a similar way, none of the 5 triactinospore types could be identified with triactinospores described by other authors (Hamilton and Canning, 1987; El-Matbouli and Hoffmann, 1993; McGeorge et al., 1997) who studied actinosporeans in waters inhabited by salmonid fishes. None of the triactinospores proved to be identical with the triactinospores found by us during a survey of actinosporeans of oligochaetes from a fish pond (El-Mansy et al., 1998*b*).

Both of the raabeia types found by us differed from the forms hitherto described (Janiszewska, 1957; Janiszewska and Krzton, 1973; Yokoyama et al., 1995; McGeorge et al., 1997). Although the raabeia types found by us in Lake Balaton oligochaetes have caudal processes similar in size to that described by

Yokoyama et al. (1995) from *Branchiura sowerbyi* and, moreover, type 2 even has spore body parameters identical with those of the latter, type 2 described by us has much larger polar capsules than that reported by the above-cited Japanese authors. On the other hand, both raabeia types found in our survey in Lake Balaton are identical with raabeia spores found by us during a survey of fish pond oligochaetes (types 1 and 2 from Lake Balaton are identical with types 2 and 4 from the fish ponds, respectively; El-Mansy et al., 1998*b*).

By their dimensions, all the 3 aurantiactinomyxon types differed from the forms described by Marques (1984), Trouillier et al. (1996), McGeorge et al. (1997), and Yokoyama (1997). The possible identity of spores found by us with the aurantiactinospores described by El-Matbouli et al. (1992), Grossheider and Körting (1992), and Benajiba and Marques (1993) could not be evaluated, as the authors did not give spore dimensions in these works. At the same time, two of the three aurantiactinomyxon types found in Lake Balaton correspond to the types found by us in a previous survey in a fish pond. In this way we have identified type 1 and type 3 from Lake Balaton with type 10 and type 5 from the fish pond, respectively (El-Mansy et al., 1998*b*).

A paper providing general and consistent guidelines on the description of actinospores on their own or as the alternative form of myxosporeans has been published only quite recently (Lom et al., 1997*b*). This is why it is often difficult to compare the forms found by us with those described in earlier works. It is to be hoped that in the future all descriptions will conform to the general guidelines, which would make it easier to compare the results obtained by different researchers. Identification of a species and its systematic position will be easier by the molecular biological methods applied by Andree et al. (1997) and Andree et al. (in press).

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References

Andree, K. B., Gresoviac, S. J. and Hedrick, R. P. (1997): Small subunit ribosomal RNA sequences unite alternate actinosporean and myxosporean stages of *Myxobolus cerebralis*, the causative agent of whirling disease in salmonid fish. J. Eukaryotic Microbiol. **44,** 208–215.

Andree, K. B., Székely, Cs., Molnár, K., Gresoviac, S. J. and Hedrick, R. P. (1998): Relationships among members of the genus *Myxobolus* (Myxozoa: Bivalvidae) based on Small Subunit Ribosomal RNA sequences. Int. J. Parasitol. (in press).

Bartholomew, J. L., Whipple, M. J., Stevens, D. G. and Fryer, J. L. (1997): The life cycle of *Ceratomyxa shasta*, a myxosporean parasite of salmonids requires a freshwater polychaete as an alternate host. J. Parasitol. **83,** 859–868.

Benajiba, M. H. and Marques, A. (1993): The alternation of actinomyxidian and myxosporidian sporal form in the development of *Myxidium giardi* (parasite of *Anguilla anguilla*) through oligochaetes. Bull. Eur. Ass. Fish Pathol. **13,** 100–103.

Biró, P. (1995): Structural changes and present status of fish population in Lake Balaton (in Hungarian). Halászat **86,** 22–24.

Brinkhurst, R. O. (1963): A guide for the identification of British aquatic Oligochaeta. Freshwater Biological Association Scientific Publication No. 22, p. 52.

Burtle, G. J., Harrison, L. R. and Styer, E. L. (1991): Detection of a triactinomyxid myxozoan in an oligochaete from ponds with proliferative gill disease in channel catfish. J. Aquat. Anim. Health **3,** 281–287.

El-Mansy, A. and Molnár, K. (1997*a*): Extrapiscine development of *Myxobolus drjagini* Akhmerov, 1954 (Myxosporea: Myxobolidae) in oligochaete alternative hosts. Acta Vet. Hung. **45,** 427–438.

El-Mansy, A. and Molnár, K. (1997*b*): Development of *Myxobolus hungaricus* Jaczó, 1940 (Myxosporea: Myxobolidae) in oligochaete alternate hosts. Dis. aquat. Org. **31,** 227–232.

El-Mansy, A., Molnár, K. and Székely, Cs. (1998*a*): Development of *Myxobolus portucalensis* Saraiva et Molnár, 1990 (*Myxosporea: Myxobolidae*) in the oligochaete *Tubifex tubifex* (Müller). Syst. Parasitol., (accepted).

El-Mansy, A., Székely, Cs. and Molnár, K. (1998*b*): Studies on the occurrence of actinosporean stages of fish myxosporeans in a fish farm of Hungary, with the description of triactinomyxon, raabeia, aurantiactinomyxon and neoactinomyxon types. Acta Vet. Hung. **46,** 259–284.

El-Matbouli, M. and Hoffmann, R. W. (1989): Experimental transmission of two *Myxobolus* spp. developing bisporogeny via tubificid worms. Parasitol. Res. **75,** 461–464.

El-Matbouli, M. and Hoffmann, R. W. (1993): *Myxobolus carassii* Klokaceva, 1914 also requires an aquatic oligochaete, *Tubifex tubifex* as an intermediate host in its life cycle. Bull. Eur. Ass. Fish Pathol. **13,** 189–192.

El-Matbouli, M., Fischer-Scherl, T. and Hoffmann, R. W. (1992): Transmission of *Hoferellus carassii* Achmerov, 1960 to goldfish *Carassius auratus* via an aquatic oligochaete. Bull. Eur. Ass. Fish Pathol. **12,** 54–56.

El-Matbouli, M., Hoffmann, R. W. and Mandok, C. (1995): Light and electron microscopic observations on the route of the triactinomyxon-sporoplasm of *Myxobolus cerebralis* from epidermis into rainbow trout cartilage. J. Fish Biol. **46,** 919–935.

Grossheider, G. and Körting, W. (1992): First evidence that *Hoferellus cyprini* (Doflein, 1898) is transmitted by *Nais* sp. *Bull.* Eur. Ass. Fish Pathol. **17,** 17–20.

Hamilton, A. J. and Canning, E. U. (1987): Studies on the proposed role of *Tubifex tubifex* (Müller) as an intermediate host in the life cycle of *Myxosoma cerebralis* (Hofer, 1903). J. Fish Dis. **10,** 145–151.

Ikeda, J. (1912): Studies on some sporozoan parasites of sipunculoids. I. The life history of a new Actinomyxidian, *Tetractynomyxon intermedium* g. et sp. nov. Archiv für Protistenkunde **25,** 240–242.

Jaczó, I. (1940): Examinations of myxosporeans of Lake Balaton fishes I. (in Hungarian). Magy. Biol. Kut. Munk. **12,** 277–289.

Janiszewska, J. (1955): Actinomyxidia. Morphology, ecology, history of investigations, systematics, development. Acta Parasitol. Polon. **2,** 405–443.

Janiszewska, J. (1957): Actinomyxidia II. New systematics, sexual cycle, description of new genera and species. Zoologica Poloniae **8,** 3–34.

Janiszewska, J. and Krzton, M. (1973): *Raabeia furciligera* sp. n. (Cnidosporidia, Actinomyxidia) from the body cavity of *Limnodrilus hoffmeisteri* Claparéde, 1862. Acta Protozool. **12,** 165–167.

Kent, M. L., Whitaker, D. J. and Margolis, L. (1993): Transmission of *Myxobolus arcticus* Pugachev and Khokhlov, 1979, a myxosporean parasite of Pacific salmon, via a triactinomyxon from the aquatic oligochaete *Stylodrilus heringianus* (Lumbriculidae). Can. J. Zool. **71,** 1207–1211.

Kent, M. L., Margolis, L. and Corliss, J. O. (1995): The demise of a class of protists: taxonomic and nomenclatural revisions proposed for the protist phylum Myxozoa Grassé, 1970. Can. J. Zool. **72,** 932–937.

Koller, E. (1994): Verbreitung von Actinosporea in zwei Salmoniden-Teichwirtschaften. Dipl.-Arb., Univ. München, 99 pp.

Lom, J. and Dykova, I. (1997): Ultrastructural features of the actinosporean phase of Myxosporea (Phylum Myxozoa): a comparative study. Acta Protozool. **36,** 83–103.

Lom, J., Yokoyama, H. and Dykova, I. (1997*a*): Comparative ultrastructure of *Aurantiactinomyxon* and *Raabeia*, actinosporean stages of myxozoan life cycles. Archiv für Protistenkunde, **148,** 173–189.

Lom, J., McGeorge, J., Feist, S. W., Morris, D. and Adams, A. (1997*b*): Guidelines for the uniform characterisation of the actinosporean stages of parasites of the phylum Myxozoa. Dis. aquat. Org. **30,** 1–9.

Mackinnon, D. L. and Adam, D. I. (1924): Notes on sporozoa parasitic in Tubifex. I. The life history of Triactinomyxon. Quart. J. Microsc. Sci. **68,** 187–209.

Markiw, M. E. (1986): Salmonid whirling disease: Dynamics of experimental production of the infective stage — the triactinomyxon spore. Can. J. Fish. Aquat. Sci. **43,** 521–526.

Marques, A. (1984): Contribution a la connaissance des Actinomyxidies: ultrastructure, cycle biologique, systematique. Ph.D. Thesis, Universite des Science et Techniques du Languedoc, Montpellier, France.

McGeorge, J., Sommerville, C. and Wootten, R. (1997): Studies of actinosporean myxozoan stages parasitic in oligochaetes from sediments of a hatchery where Atlantic salmon harbour *Sphaerospora truttae* infection. Dis. aquat. Org. **30,** 107–119.

Molnár, K. and Székely, Cs. (1995): Parasitological survey of some important fish species of Lake Balaton. Parasit. Hung. **28,** 63–82.

Pallós, A. (1995): Occurrence of actinosporean stages of myxosporeans in oligochaetes (in Hungarian). MSc Dissertation. University of Veterinary Science, Budapest. 37 pp.

Pote, L. M. and Waterstrat, P. (1993): Motile stage of *Aurantiactinomyxon* sp. (Actinosporea: Triactinomyxidae) isolated from *Dero digitata* found in channel catfish ponds during outbreaks of proliferative gill disease. J. Aquat. Anim. Health. **5,** 213–218.

Ruidisch, S., El-Matbouli, M. and Hoffmann, R. W. (1991): The role of tubificid worms as an intermediate host in the life cycle of *Myxobolus pavlovskii* (Akhmerov, 1954). Parasitol. Res. **77,** 663–667.

Schlegel, M., Lom, J., Stechmann, A., Bernhard, D., Leipe, D., Dyková, I. and Sogin, M. L. (1996): Phylogenetic analysis of complete small subunit ribosomal RNA coding region of *Myxidium lieberkuehni*: Evidence that Myxozoa are Metazoa and related to Bilateralia. Archiv für Protistenkunde **147,** 1–9.

Siddall, M. E., Martin, D. S., Bridge, D., Desser, S. S. and Cone, D. K. (1995): The demise of a phylum of protists: phylogeny of Myxozoa and other parasitic Cnidaria. J. Parasitol. **81,** 961–967.

Smothers, J. F., von Dohlen, C. D., Smith Jr., L. H. and Spall, R. D. (1994): Molecular evidence that the myxosporean protists are metazoans. Science **265,** 1719–1721.

Stolc, A. (1899): Actinomyxidies, nouveau groupe de Mesozoaires parent des Myxosporidies. Bull. Internat. de l'Acad. Sci. Boheme **22,** 1–12.

Székely, Cs. (1989): Fish-parasitic myxosporeans and a new method to control them (in Hungarian). Univ. Doctoral Dissertation. Agricultural University of Gödöllő. 75 pp.

Székely, Cs. and Molnár, K. (1996–1997): Preliminary survey of the parasite fauna of some important fish species in the Upper-Reservoir of the Kis-Balaton System. Parasit. Hung. **29–30,** 45–54.

Trouillier, A., El-Matbouli, M. and Hoffmann, R. W. (1996): A new look at the life-cycle of *Hoferellus carassii* in goldfish (*Carassius auratus auratus*) and its relation to "kidney enlargement disease" (KED). Folia Parasitol. **43,** 173–187.

Uspenskaya, A. V. (1995): Alternation of actinosporean and myxosporean phases in the life cycle of *Zschokella nova* (Myxozoa). J. Eukar. Microbiol. **42,** 665–668.

Wolf, K. and Markiw, M. E. (1984): Biology contravenes taxonomy in the Myxozoa: new discoveries show alternation of invertebrate and vertebrate hosts. Science **225,** 1449–1452.

Yokoyama, H. (1997): Transmission of *Thelohanellus hovorkai* Achmerov, 1960 (Myxosporea: Myxozoa) to common carp *Cyprinus carpio* through the alternate oligochaete host. Syst. Parasitol. **36,** 79–84.

Yokoyama, H., Ogawa, K. and Wakabayashi, H. (1991): A new collection method of actinosporeans. A probable infective stage of myxosporeans to fishes from tubificids and experimental infection of goldfish with the actinosporean, *Raabeia* sp. Fish Pathol. **26,** 133–138.

Yokoyama, H., Ogawa, K. and Wakabayashi, H. (1993*a*): Involvement of *Branchiura sowerbyi* (Oligochaeta: Annelida) in the transmission of *Hoferellus carassii* (Myxosporea: Myxozoa), the causative agent of kidney enlargement disease (KED) of goldfish *Carassius auratus.* Fish Pathol. **28,** 135–139.

Yokoyama, H., Ogawa, K. and Wakabayashi, H. (1993*b*): Some biological chararacteristics of actinosporeans from the oligochaete *Branchiura sowerbyi*. Dis. aquat. Org. **17,** 223–228.

Yokoyama, H., Ogawa, K. and Wakabayashi, H. (1995): *Myxobolus cultus* n. sp. (Myxosporea: Myxobolidae) in the goldfish *Carassius auratus* transformed from the actinosporean stage in the oligochaete *Branchiura sowerbyi.* J. Parasitol. **81,** 446–451.