Taxonomic problems, seasonality and histopathology of *Henneguya creplini* (Myxosporea) infection of the pikeperch *Stizostedion lucioperca* in Lake Balaton

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**Key words:** *Henneguya creplini*, Myxosporea, pikeperch, gills, development, histopathology

**Abstract.** Plasmodia of a *Henneguya* species measuring 70-900 µm and exhibiting season-dependent stages of development were detected throughout a three-year study on gill myxosporosis of Lake Balaton pikeperch (*Stizostedion lucioperca* (L.)). Sixty-five out of 160 fish (41%) examined in the period of study were infected by the parasite. Infection was the most prevalent (48%) among pikeperch specimens exceeding 40 cm in length. The highest prevalence of infection (58%) was recorded in 1995-1996 while the lowest (30%) in 1996-1997. The youngest plasmodia appeared in April, and started to develop within the capillaries of the secondary lamellae of the gill filaments. The round or ellipsoidal plasmodia which continued their gradual growth in the subsequent months of the year achieved a size of 800-900 µm by the late autumn months, but remained in intralamellar location throughout the developmental cycle. Mature spores developed in the plasmodia by the end of winter. On the basis of their shape and size, the spores were identified as *Henneguya creplini* (Gurley, 1894). However, because of the uncertain taxonomy of species assigned to the genus *Henneguya* the taxonomic position of the parasite requires further study. The host reaction consisting of epithelial proliferation and granulation tissue formation starts around the infected secondary lamella only after the maturation of spores and the disruption of plasmodia.

Lake Balaton, the biggest lake of Central Europe, is characterised by its shallowness. Due to periodical fish mortalities (e.g. Molnár et al. 1991), its parasite fauna is well studied. The pikeperch (*Stizostedion lucioperca* (L.)) is the heraldic animal and the most valuable fish species of the lake; therefore, regular monitoring of its health status is necessary. Reports on parasitic infections of the Lake Balaton fish population, including those of the pikeperch, have recently been published by Molnár and Székely (1995) as well as Székely and Molnár (1996-1997).

The earliest report on Myxosporea infection of Lake Balaton fishes was that of Rátz (1901). Keller (1910) described *Myxobolus oviformis* infection of the gills of Lake Balaton pikeperch. More detailed investigations were carried out by Jaczó (1941), who described the occurrence of five species of Myxosporea, including two new *Myxobolus* species and an unidentified *Henneguya* species in Lake Balaton fishes. The last mentioned species was detected in perch (*Perca fluviatilis*). Various *Henneguya* species are common parasites of freshwater fishes. In Europe they occur primarily in pike (*Esox lucius* L.) and in percid fishes (Donets and Shulman 1984, Lom and Dyková 1992). *Henneguya* species described from European percid fishes include *Henneguya creplini* (Gurley, 1894) recorded from a closely not identified organ of the ruffe (*Gymnosephalus cernuus* (L.)), *H. texta* (Cohn, 1895) and *H. minutus* (Cohn, 1895) parasitic on the gills of the perch (*Perca fluviatilis*), and *H. gigantea* Nemeczek, 1911 found on the gills of the pikeperch (*Stizostedion lucioperca*). The organ and tissue specificity of the above parasites is unknown; therefore, on the basis of spore size and shape different authors identified *Henneguya* species known from pike and percids also with the species *H. psorospermtica* Thélohan, 1895 and *H. oviperda* (Cohn, 1895) reported from pike; as a result, in the monograph of Donets and Shulman (1984) the pikeperch is indicated as the host of five *Henneguya* spp. (*H. gigantea, H. oviperda, H. psorospermtica, H. creplini, and H. nemeczeki*). Data on the seasonal occurrence of *Henneguya* spp. have been reported by Haaparanta et al. (1994) and Cone (1994).

This paper presents studies monitoring the infection of the gills of Lake Balaton pikeperch with the species *H. creplini* during a three-year period of observation.

**MATERIALS AND METHODS**

Three- to six-year-old specimens of pikeperch (*Stizostedion lucioperca*) and Volga pikeperch (*S. volgensis* (Gmelin)) caught in the western and central basin of Lake Balaton were included in the survey. The fish were obtained from commercial fishermen in the fishing period (from March to December), with exception of May when fishing is forbidden. This study on the gill myxosporosis of pikeperch and Volga pikeperch was a part of the general faunistic survey previously reported by Molnár and Székely (1995) and Székely and Molnár (1996-1997). The studies started in April
1994 and finished at the end of March 1997 (Table 1.). During that period a total of 160 pike perch and 47 Volga pike perch specimens exceeding 16 cm in body length were examined. Fishes less than 16 cm in size were excluded from evaluation, as by routine examination it could not be determined whether they represented well-developed fry or runted two-year-old specimens. Prior to this survey, some orienting data on the gill infection of pike perch were already available from studies that had occasionally been performed in the given habitat on other parasitoses since 1984 (Molnár 1995).

The fish were selected on board of a fishing-boat, and transported in oxygen-filled plastic bags to the laboratory where they were kept in aerated aquaria until killed by cutting through the head with a pair of scissors. The fish were necropsied and organs excised for parasitological examination. The gills were examined in detail for infection by Myxosporea. Haemibranchia from infected gills were fixed in Bouin’s solution and, after embedded in paraffin, 4 µm thick sections were stained with haematoxylin and eosin. Spore measurements were taken directly from fresh material after video recording and image analysis (Székely 1997), and unless otherwise stated, they are expressed in micrometres. For further studies, some spores were preserved in glycerol-gelatin under coverslips as permanent preparations. Plasmodia were measured with an ocular micrometer.

**RESULTS**

Plasmodia representing different developmental stages but not containing spores occurred in the period lasting from April to October 1994 when regular examination of the gills of pike perch was started. In the same year it was found that the plasmodia which had been oval in shape and averaged 71-81 × 41-51 µm in size in April, reached a size of 100-120 × 75-85 µm by June, while in August round plasmodia of 150 µm average size and short-ellipsoidal plasmodia measuring 155 × 135 µm were detectable (Fig. 1). At the same time, round plasmodia measuring 38-51 µm, i.e. much smaller than the above plasmodia, appeared in the secondary lamellae close to the base of the gill filaments. In November, the larger plasmodia could be seen in certain fish specimens as rounded forms 300-340 µm in size, or as 470-480 × 150-160 µm forms flattened parallel with the plane of the gill filaments. The size of smaller plasmodia occurring in the gills of the same fish varied between 38 and 108 µm. Spores (Fig.1, inset) were first found in 1995, when favourable weather conditions allowed us to collect fish as soon as in February and March. By the end of the winter, the size of the spore-containing plasmodia had markedly increased, and larger cysts located close to the tips of the gill filaments reached 800-900 × 650-750 µm, while those occurring near the base of the gill filaments were 460-480 × 270-400 µm in size. Both the large and the smaller plasmodia were filled with typical *Henneguya* spores of identical shape and size. In 1996, when the first fish were examined in April, mostly young developing plasmodia were found, accompanied by only remnants of the previous year’s generation represented by disrupted, degenerated plasmodia and some spores stuck within them. On the other hand, in 1997 the mild spring enabled us to follow up the development of spore-containing plasmodia from early March up to the time of spore discharge, i.e. the end of March. Based upon the shape and dimensions of the spores, the myxosporean found in Lake Balaton pike perch was identified as *Henneguya creplini*.

**Table 1.** Number and size categories of pike perch examined in the survey.

<table>
<thead>
<tr>
<th>Examination periods</th>
<th>Total No. of examined fish</th>
<th>Size categories (total length of fish in cm)</th>
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<tbody>
<tr>
<td></td>
<td>16-29</td>
<td>30-39</td>
</tr>
<tr>
<td>April 1994 to March 1995</td>
<td>59</td>
<td>13</td>
</tr>
<tr>
<td>April 1995 to March 1996</td>
<td>36</td>
<td>3</td>
</tr>
<tr>
<td>April 1996 to March 1997</td>
<td>65</td>
<td>9</td>
</tr>
</tbody>
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Fig. 1. Several large and many small *Henneguya creplini* plasmodia on gill filaments of pike perch (*Stizostedion lucioperca*). × 2.5. Inset (i): Spore in frontal view. x 2000.
Morphological data

Vegetative stages. Spore-containing plasmodia were round or ellipsoidal, measuring from 300 to 900 in size. They were located in the capillary network of the secondary lamellae and contained about 10-50 x 10^3 spores.

Description of spores (n=50): Mature, fresh spores (Fig. 2) elongated ellipsoidal. Total length 43 (38-49), spore length 14.3 (13-15), spore width 5.5 (5-6.5), spore thickness 5 (4.8-5.5), caudal appendage (tail) length 29 (25-34). Two polar capsules elongated, equal or slightly different in size, length 7 (6.5-7.5), width 1.8 (1.7-2). Coils of polar filament 10 to 11. Length of the extruded polar filaments 76 (70-80). Sporoplasm binucleated, rounded at the tail end. Spore wall thin, smooth, comprised of two equal valves. Sutural edge indistinct without edge markings. Membranaceous envelope or iodoniphilous vacuole not seen. Tail bifurcated. The bifurcation starts at the end of the spore body.

Seasonality. The development of plasmodia and the appearance of spores showed a clear seasonality and synchronicity. During the three-year study, the young plasmodia of *H. creplini* repeatedly appeared in the gills of fish in April and gradually increased in size to form spores in next winter. Spore excretion ceased by the beginning of April. Due to these characteristics, a development period lasting from April to next March, rather than a regular calendar year, seemed to be a feasible basis for studying the seasonal incidence.

During the three-year cycle between April 1994 and the end of March 1997, 41% of the 160 examined specimens of >16 cm pikeperch proved to be infected by *Henneguya creplini*. When considering total prevalences of the three years for each size category the 16-29 cm showed the lowest prevalence of infection (24%) and the highest prevalence of infection (48%) was recorded for fish exceeding 40 cm in body length (Fig. 3). No *Henneguya* infection was found in the gills of fish shorter than 16 cm.

Certain differences were also found in the prevalences of infection observed in different years of the study period. The moderate prevalence (42%) observed in the 1994-1995 cycle was followed by a relatively high prevalence (58%) in 1995-1996 and a rather low prevalence (30%) in 1996-1997 (Fig. 4). Although infection was present throughout the study period, minor differences in its prevalence did occur (Fig. 5). While in the period between February and May infected and infection-free fish specimens were found in nearly equal number, between August and November the number of uninfected fish markedly exceeded that of the infected specimens.

The 47 specimens of Volga pikeperch, collected from the same habitat during the three years of the study, also proved to be infection free.

Intensity of infection. The intensity of infection was very variable. In most cases, 10-20 plasmodia per hemibranchium were recorded, but up to 20-30 plasmodia were also found per gill filament. In general, the intensity of infection was moderate, consisting of up to 30-60 plasmodia in the eight hemibranchia, and the infection was never as severe as recorded in a pikeperch from the river Danube (Molnár and Szakolczai 1980).

Histopathology. The youngest plasmodia were found in the blood vessels of secondary lamellae, extending from the mid-part to the tip of the gill filaments (primary lamellae), disrupting the pillar cells and occupying the lumen of capillaries (Fig. 6). At higher magnification it was clear that the plasmodium was located within the capillary network of the secondary lamella, surrounded by large numbers of endothelial cells and erythrocytes. Within the plasmodium, the ectoplasm (which appeared to be structureless histologically) and the endoplasm containing the nuclei of different vegetative developmental stages, were distinguishable. Plasmodia started their development in the central region of the secondary lamellae and in these cases the original structure of the secondary lamella was still discernible near the tip and occasionally also near the basis of the secondary lamellae (Fig. 7). At that stage, the plasmodium was surrounded by the capillary endothelium; however, occasionally erythrocytes could also be seen in its direct surroundings. More advanced plasmodia occupied the entire length of the secondary lamella pushing the neighbouring secondary lamellae aside (Fig. 8). Even when plasmodia reached a size equal to 4-6 secondary lamellae it was clear that the development of the plasmodium was restricted to a single secondary lamella (Fig. 8). In gills fixed in and after September, large plasmodia located near the tip of the gill filaments occurred together with smaller plasmodia developing near the base of the gill filaments, which markedly differed from the former in size (Fig. 9). These plasmodia did not cause complete deformation of the secondary lamellae even when they reached the fully developed stage; as a result, the distal end of the secondary lamellae exhibited normal structure. Forms representing a transitional stage between the small and the large plasmodium type could not be found. The plasmodia fixed in February, which were surrounded by a thin ectoplasm and filled with spores, were usually round shaped. Around plasmodia of the smaller type the capillary network separated in two parts by the plasmodium was well discernible even at that stage. That capillary network set out from the artery of the gill filaments (primary lamellae), disrupting the pillar cells and occupying the lumen of capillaries (Fig. 10). Between the ectoplasm of the plasmodium and the endothelium of the capillary network a pale-staining space, indicative of the presence of erum, was often seen. At the end of the
Fig. 2. Schematic representation of spores of *Henneguya creplini*. (a) frontal view; (b) lateral view. Bar = 10 µm.

Fig. 3. *Henneguya creplini* infection of pike perch in Lake Balaton. I. Prevalence of infection in different size categories during three-year survey. n = no. of fish examined from different size categories.

Developmental cycle the mature spores were released from the plasmodia externally through the damaged wall of the secondary lamella; in some cases, however, the wall of the secondary lamellae remained intact and the ectoplasm of the plasmodium burst within the endothelial wall of the secondary lamellae. In the latter cases the plasmodium had shrunken and only few spores remained in it. The normally uniformly round wall of the ectoplasm became amorphous. Serum containing spores accumulated in the cavity of the secondary lamella, which had earlier been occupied by the plasmodium (Fig. 11). These latter spores were located practically within the bloodstream. At the end of March, intact plasmodia containing spores could be found only occasionally. In one instance, however, both the larger plasmodia located at the tip of filaments and the smaller ones located at the base of the filaments could be detected, and *Henneguya* spores were successfully isolated from both. At that time, most often only the site of the former plasmodium location could be detected on the gill filaments. In such cases the capillary network which had surrounded the plasmodium was seen around the degenerated, eosinophilic cellular substance left behind by the ectoplasm of the plasmodium. That substance consisted of cells of the proliferating granulation tissue and a few spores stuck within it (Fig. 12). In the majority of cases, the capillaries of the secondary lamellae were covered by a

Fig. 4. *Henneguya creplini* infection of pike perch in Lake Balaton. II. Prevalence of infection in different years. n = no. of fish examined for each sampling time.

Fig. 5. *Henneguya creplini* infection of pike perch in Lake Balaton. III. Prevalence of infection in different seasons during three-year survey. n = no. of fish examined for each sampling time.
Figs. 6-9. Histological pictures of pikeperch gills infected by *Henneguya creplini*. H&E. **Fig. 6.** Young plasmodia (arrow) in capillary network of secondary lamellae. Around plasmodium, capillary network of secondary lamella and erythrocytes present in capillaries can be observed. × 500. **Fig. 7.** Young plasmodium located in mid-part of secondary lamella. The plasmodium has not yet affected position of neighbouring secondary lamellae. × 500. **Fig. 8.** Plasmodia of large type, not yet containing spores. Plasmodia have completely filled the secondary lamella and deformed neighbouring secondary lamellae. × 150. **Fig. 9.** Plasmodia of small type, not yet containing spores. Plasmodia infect basal part of single secondary lamella only. Distal part of secondary lamella is normal. × 200.
DISCUSSION

The three-year survey of the gill infection of Lake Balaton pikeperch revealed that the gill of this fish species is typically parasitized by a single *Henneguya* (Myxosporea) species. The taxonomical position of different *Henneguya* species is rather uncertain. The majority were reported simultaneously from pike and from percid fishes (Donets and Shulman 1984), although the phylogenetic distance between pike and percids makes unlikely that these fish species would be parasitized by the same species of Myxosporea. Precise identification of the parasite species is hampered by the extreme difficulty of identifying their type hosts. For example, in Gurley’s (1894) description of *Henneguya creplini* from pike, a certain proportion of the spores was derived from material collected from ruffe (*Gymnocephalus cernua*) half a century earlier. *H. acerinae* was first described by Schröder (1906) from *Gymnocephalus cernua*, and later from pikeperch by Nemeczek (1911). From pikeperch, Nemeczek (1911) recorded also another species designated as *H. gigantea*. The species described by Cohn (1896) as *H. texta* and *H. minuta* were reported from perch (*Perca fluviatilis*), Donets and Shulman (1984) later synonymized the species *H. acerinae* with *H. creplini*, whereas, after Tripathi (1953), they declared the new species described by Nemeczek (1911) as *H. acerinae* to be a distinct species designated *H. nemeczecki*.

When determining the taxonomic position of the species found in the gills of pikeperch in this study, *H. lobosa, H. oviperta* and *H. psorospermica* known from pike were ruled out despite morphological similarity of their spores, and only the species recorded from percids were taken into account for the identification of the species. Among them, *H. gigantea* markedly differs from the species found in the present study in the markedly longer caudal appendage of the spores. Cohn (1896), who described and compared several *Henneguya* species by the generic name *Myxobolus*, failed to find substantial size differences between spores of *H. psorospermica* and *H. creplini*. The species described by him as *H. minuta* was distinguishable from *H. psorospermica* only in that it formed much smaller plasmodia in the gills of perch than the species also recorded by him from the gills of perch with the name of *H. texta* and identical in spore size with *H. psorospermica*. The spore dimensions of the species found here correspond also to *H. nemeczecki* regarded as a pikeperch parasite. Nevertheless, according to Nemeczek (1911), the latter species is characterised by the non-bifurcated caudal appendage. It should be mentioned that in the present case the two caudal appendages were stuck together in some of the spores, and could be distinguished only by immersion microscopy using higher magnification. Proper identification of *Henneguya* species will become possible only after a general revision of the genus. Based upon the morphology of spores, the parasite found in the current work in the gills of pikeperch is tentatively identified as *Henneguya creplini*, and regarded as *H. creplini* (s. l.). Reliable species identification will probably continue to be based on the morphological characters and the chances of determining the host specificity will remain unlikely for a long time. Certain observations suggest that *Henneguya* species may also have a relatively strict host specificity; namely, during my studies I could not detect *Henneguya* spores or developmental stages from the closely related Volga pikeperch (*S. volgensis*) in the same habitat. In that case, only *Henneguya* species recorded from the pikeperch can be taken into account.

The fact that a larger and a smaller plasmodium can develop near the tip and the base of the gill filaments, respectively, in the same pikeperch specimen, raises the possibility that two different species might be involved here. This, however, seems to be at variance with the lack of shape and size differences between spores derived from the two types of plasmodia. The simultaneous occurrence of two types of plasmodia differing in size was observed in the gills of perch (*Perca fluviatilis*) already by Cohn (1896), who described them as two distinct species, *Myxobolus (Henneguya) textus* and *Myxobolus (Henneguya) minutus*, despite the morphological identity of the spores. Another explanation for the common occurrence of small and large plasmodia on the same gill filament could be a subsequent reinfection. The latter possibility is supported by the fact that spores released from such smaller plasmodia did not differ morphologically from those contained by the markedly larger plasmodia developing in locations close to the tip of the gill filaments.

Reliable answers to this latter problem and other questions concerning the specificity of myxosporeans will only be made possible by the experimental reproduction of the developmental cycle, which now seems to be increasingly feasible, as well as by tests developed for the analysis of DNA structure, such as the PCR technique (Bartholomew et al. 1995, Andree et al. 1997).
Figs. 10-13. Histological pictures of pikeperch gills infected by *Henneguya creplini*. H&E. **Fig. 10.** Spore-filled plasmodium of small type in secondary lamella capillary network separated into two parts. At basal and distal ends of secondary lamella capillary structure is intact. × 300. **Fig. 11.** Plasmodium containing mature spores burst within capillary network of secondary lamella. Spores can be found both in shrunken plasm inum and in lumen of capillary network. × 300. **Fig. 12.** Disrupted plasmodium enclosed by granulation tissue after spore maturation. Remnants of ectoplasm are still surrounded by capillary network (arrow). × 200. **Fig. 13.** Traces of a passed-off *Henneguya* infection. In granulation tissue sticking together secondary lamellae, remnants of plasmodia (arrow) showing eosinophilic staining and masses of dark-staining macrophages can be seen. × 200.
Observations made in this study suggest that *Henneguya creplini* develops according to a strict annual cycle in Lake Balaton, which confirms the data presented by Shulman (1966), who observed similar seasonality in *H. creplini* infection of the pikeperch in Lake Shot. Infection started in April, when the young plasmodia of the parasite appeared in the secondary lamellae of the gill filaments. These plasmodia gradually grew in the subsequent months, but spores were formed within them only during winter. The disruption of plasmodia and spore release took place in February and March. A similar annual developmental cycle has been described for *Hoferellus cyprini* (Molnár et al., 1986) and *Myxobilatus legeri* (Molnár 1988). Nevertheless, no such annual cycle of development has been known so far for *Henneguya* species. Andrews (1979) and Haaparanta et al. (1994) who studied, in *P. fluviatilis*, the seasonal cycle of *Henneguya* species that they identified with *Henneguya psorospermica, H. creplini* and *H. doori*, failed to observe a clear season-dependent appearance of the spores. Andrews (1979) and Cone (1994) could not detect plasmodia in the gills of fish in the summer months, while Haaparanta et al. (1994) observed the simultaneous occurrence of different developmental stages, and detected plasmodia filled with spores not only during the spring peak but also in other months of the year. Narasimhamurthy and Kalavati (1984) reported the lack of seasonal variation in the prevalence of *H. waltairensis*. This latter observation, however, is not surprising, as the parasite fauna is less markedly influenced by temperature-related factors in the Indian subcontinent.

Pronounced differences were observed in the prevalence of infection by year. Whereas in 1995 infection was diagnosed in more than half of the fish examined, in 1996 the prevalence of infection declined markedly. Infection seems to increase with the age of fish, and it was not detected in fish of the younger age groups. This latter phenomenon can be easily explained by the fact that at the time of infection of the older fish, which possibly occurs in March, the pikeperch fry are yet rather small. In addition, it is difficult to explain why *Henneguya* was not detected in the Volga pikeperch, which lives in the same habitat and the fish sampled were of the same size. The absence of infection in the Volga pikeperch raises the possibility that the *Henneguya* species infecting the pikeperch is a rather species-specific parasite which is unable to infect even the closely related Volga pikeperch. While it is very difficult to decide that question, the possibility of host specificity is suggested by the example of specific *Thelohaneanellus* species parasitic only on the common carp (Akhmerov 1955).

Major seasonal differences were found in parasite prevalence. Markedly lower numbers of infected fish specimens were found between August and November than in the spring months. That difference, however, must reflect the margin of error typical of studies involving natural waters. For supporting this statement there are two reasons: 1) The season-dependent release of spores and the continuous growth of plasmodia clearly indicate that an infection started in spring will reach its final stage by the winter months. 2) In a given fish specimen the prevalence of a parasite with a strict annual development cycle cannot vary during the year.

*H. creplini* provoked a very weak host reaction. In all cases observed by us, the parasite developed according to a pattern that had been termed “intralamellar” by Current and Janovy (1978), irrespective of the intensity of infection. The plasmodia that started to develop in the capillary network of the secondary lamella, presumably in the pillar cells, were surrounded by circulating blood cells and plasma, and were encircled by the endothelium of the secondary lamellae. The presence of blood serum and occasionally some blood cells could be seen even around plasmodia already containing spores. The large plasmodia markedly increased the dimensions of the secondary lamella and deformed the neighbouring secondary lamellae; however, in conformity with the figures published by Cone (1979), Shariff (1982) and Kalavati and Narasimhamurthy (1985), they remained in intralamellar location and from the capillaries of the secondary lamellae they did not extend to the arteries of the primary lamellae (gill filaments). Dyková and Lon (1978), who studied the histopathological changes caused by *H. psorospermica* in the gills of pike and perch and by *H. creplini* in ruffe, found exclusively intralamellar infection in perch and ruffe. At the same time, in pike typical large interlamellar plasmodia were found, similar to those described by Current and Janovy (1978) for *Henneguya exilis*. Obviously, the majority of spores are released directly to the exterior through the injury of the secondary lamellae containing the plasmodium. However, in some cases disruption of the ectoplasm of the plasmodium was clearly followed by spore release into the lumen of capillaries. Such spores are transported via the blood stream to organs from which they get out of the fish, probably in a manner described for *Myxobolus cyprini* by Molnár and Kovács-Gayer (1985). Despite the fact that in some cases intensive infection was recorded, only moderate host reaction could be seen during the period of plasmodium development, which manifested itself in proliferation of the epithelium surrounding the infected secondary lamella. However, during the maturation of spores and the disruption of plasmodia the host reaction described by Dyková and Lon (1978) started, manifesting itself in intensive epithelial proliferation, overgrowth of the damaged plasmodium by granulation tissue and macrophages, and in cell necrosis.
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REFERENCES


COHN L. 1896: Über die Myxosporidien von Balaton for supplying fishes, as well as Dr. Cs. Székely and thanks the management of the Fisheries Company of Lake Balaton. Halászat 11: 108–109. (In Hungarian.)


MOLNÁR K., KOVÁCS-GAYER É. 1985: The pathogenicity and development within the fish host of Myxobolus cyprini Doflein, 1898. Parasitology 90: 549-555.


SHULMAN S. 1984: Myxosporidia of the fauna of the USSR. Nauka, Moscow, 504 pp. (In Russian.)


