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ORIGINAL PAPER

Morphology and host–parasite interaction of *Henneguya azevedoi* n. sp., parasite of gills of *Leporinus obtusidens* from Mogi-Guaçu River, Brazil

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Abstract *Henneguya azevedoi* n. sp. is described from the piava (*Leporinus obtusidens*). Between 2005 and 2007, 60 fish were collected from the Mogi-Guaçu River near Cachoeira de Emas Falls located in the municipality of Pirassununga, state of São Paulo, Brazil. A total of 70% had plasmodia of the parasite. The plasmodia were white, spherical, and measured 40–200 μm in diameter. Histopathological analysis revealed that the development of the parasite was intralamellar and caused stretching of the epithelium, with accentuated deformation, as well as compression of the capillary and adjacent tissues. Ultrastructural analysis revealed that the wall of the plasmodium was a single membrane in direct contact with the host cells and contained pinocytic canals that extended into the plasmodium. The development of the parasite was asynchronous, with the earliest stages at the periphery and mature spores in the central region. Mature spores were elongated in the frontal view [mean±standard deviation (range)]: 45.2±0.6 (45.0–47.0) μm in total length, 10.0±0.07 (9.9–10.2) μm in body length, 35.6±0.9 (34.9–36.5) μm in caudal process length, and 4.4±0.4 (4.0–5.0) μm in body width. The polar capsules were elongated and equal in size: 3.8±0.3 (3.5–4.0) μm in length and 1.0 μm in width. The polar filaments were coiled in six to seven turns and perpendicular to the axis of the capsule. Scanning electron microscopy revealed smooth valves and a conspicuous rim around the spore body. This is the first time that a myxosporean has been reported in *L. obtusidens*.

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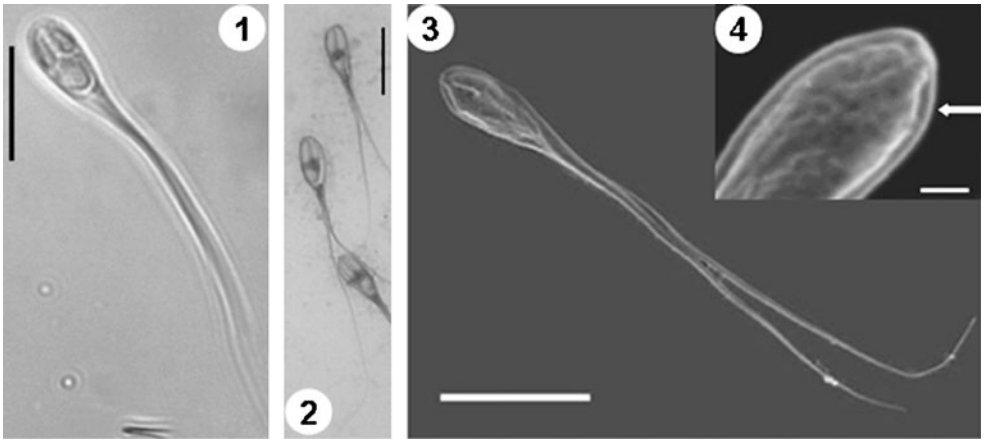
Introduction

Leporinus obtusidens Valenciennes, 1837, is a rheophilic omnivorous species from the family Anostomidae, which is popularly known as "piava" and occurs in the La Plata and São Francisco River basins (Santos 2000; Froese and Pauly 2009) in South America. This species can attain up a length of 76 cm (Froese and Pauly 2009). It has commercial and sport fishing importance and its fingerlings are very beautiful (Tataje and Zaniboni-Filho 2005). These characteristics make *L. obtusidens* an important species for cultivation on fish farms (Castagnolli 1992; Soares et al. 2000).

Myxosporean parasites have been described infecting freshwater fish in both cultivated and natural environments in several parts of the world (Lom and Dyková 2006). Myxosporeans of the genus *Henneguya* Thelohan, 1892, have been reported infecting wild and farmed fish; some species are important pathogenic parasites (Feist and Longshaw 2006; Lom and Dyková 2006). Among Brazilian fish fauna, myxozoans from the genus *Henneguya* are the



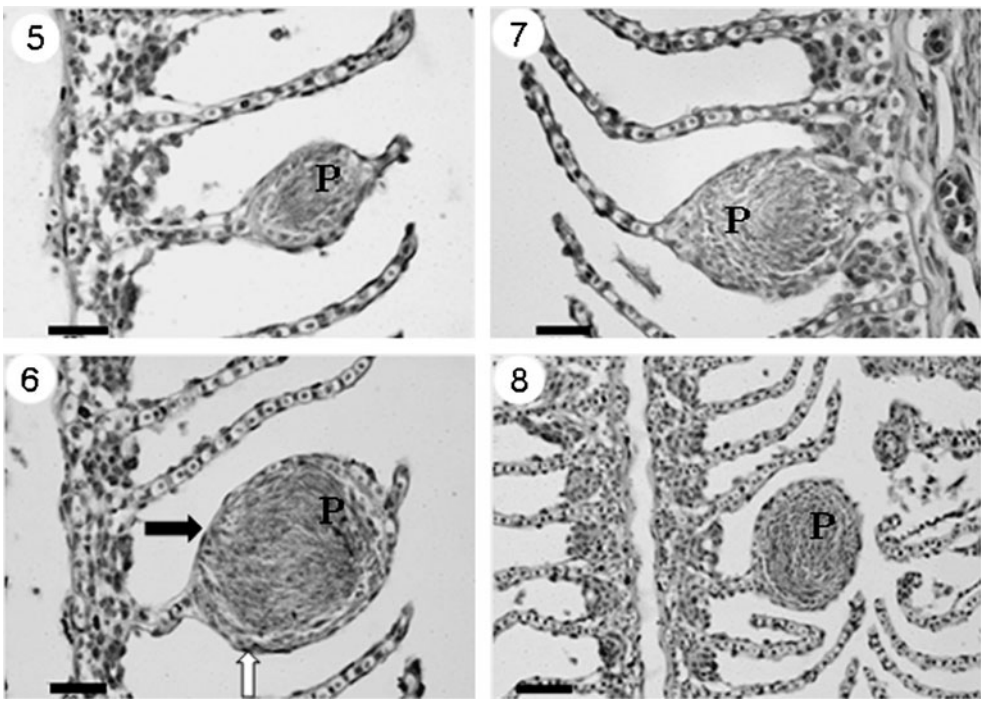
Figs. 1–4 Spores of *H. azevedoi* n. sp. from gills of *L. obtusidens*. *1* Fresh preparation. *Scale bar*, 10 μm *2* Fixed spores. Giemsa stain. *Scale bar*, 10 μm *3* Scanning electron microscopy of spore in frontal view. *Scale bar*, 10 μm *4* Scanning electron microscopy of anterior end of spore showing the rim surrounding the spore (*arrow*). *Scale bar*, 3 μm

most common, with 38 valid species, and of these species, only *Henneguya leporinicola* (Martins et al. 1999) and *Henneguya schizodon* (Eiras et al. 2004) have been found in species of Anostomidae (Eiras et al. 2008).

The present study is part of an ongoing investigation into the diversity of Myxosporea parasites of wild and farmed freshwater fish of commercial importance in Brazil. Light and electron microscopy were employed to investigate the morphology and histopathology of a new species of *Henneguya* found infecting gill filaments in wild specimens of *L. obtusidens* from the Mogi-Guaçu River in the state of São Paulo.

Materials and methods

Sixty fish were caught about 200 m downstream from the Cachoeira de Emas power plant (21°55′37″ S, 47°22′03″ W) in the municipality of Pirassununga, state of São Paulo, Brazil. The fish were caught using cast nets and transported alive to the field laboratory mounted nearby, where they were measured, weighed, and submitted to necropsy. Plasmodia with mature spores were examined on fresh mounts under a light microscope. The morphological and morphometric studies of the spores were based on mature spores obtained from different specimens (n=30), as



Figs. 5–8 Histological sections of the gills of *L. obtusidens* showing plasmodia (*P*) of *H. azevedoi* n. sp. in the lamellae *5* and *6* Plasmodia developing in the median region of the lamella. Note in Fig. 6, the stretching and accentuated deformation of the epithelium (*white arrow*) and compression of the capillary and adjacent tissues (*black arrow*) *7* Plasmodium occupying the basal region of the lamella *8* Plasmodium occupying the apical region of the lamella. *Scale bars*, 20 μm

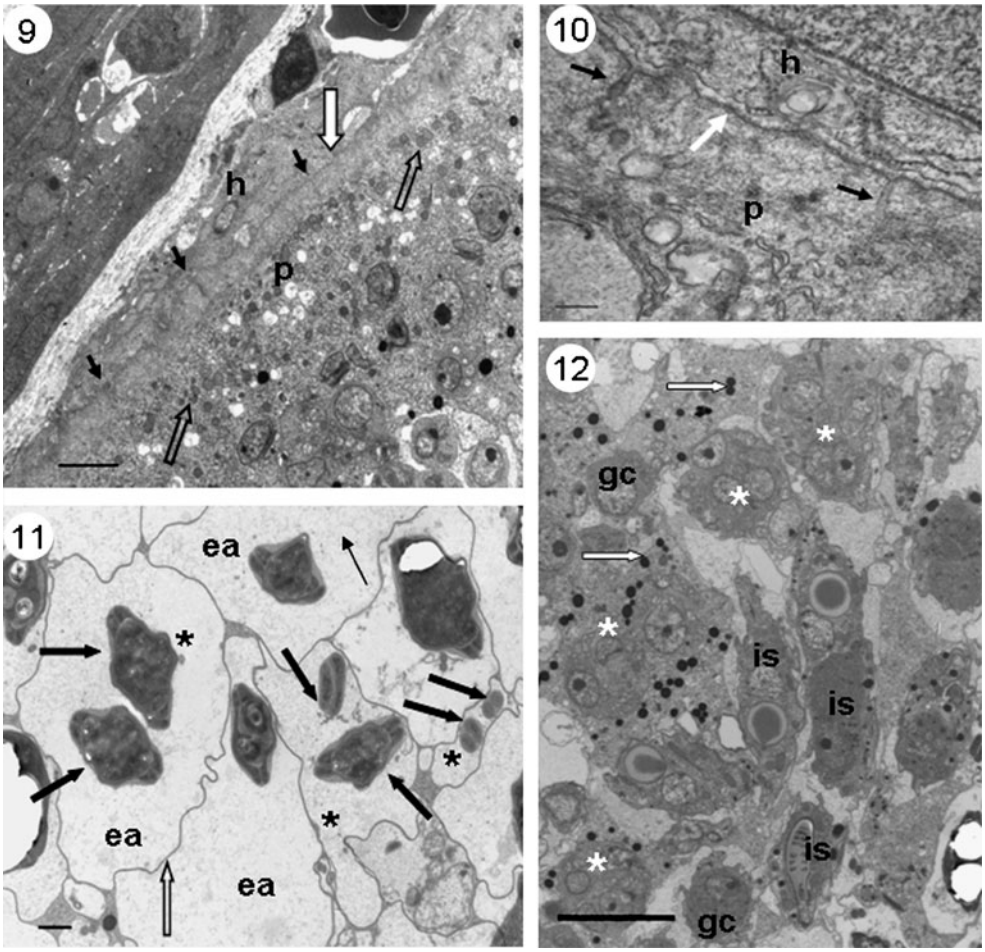


Fig. 9–12 Transmission electron microscopy of *H. azevedoi* n. sp. from gills of *L. obtusidens* *9* Image showing the interface host–parasite. Note the direct contact between the plasmodium (*P*) and the host cells (*h*), (*white arrow*), pinocytic canals (*black arrows*), and numerous mitochondria (*empty arrows*). *Scale bar*, 5 μm *10* Greater magnifications showing pinocytic canals (*black arrows*) and the plasmodial wall composed by a single membrane (*white arrow*). *Scale bar*, 0.5 μm *11* Plasmodium showing immature spores in transversal sections. Note that each sporoblast (*asterisks*) has two spores (*black arrows*) and a wide empathy area (*ea*) containing finely granular material (*thin arrow*) and well bounded by a membrane thin (*empty arrow*). *Scale bar*, 2 μm *12* Plasmodium with different developmental stages sporoblasts. Note generative cells (*gc*), young sporoblasts (*asterisks*), and immature spores (*is*) containing valve-forming materials (*white arrows*). *Scale bar*, 5 μm

proposed by Lom and Arthur (1989). The dimensions of the spores (in micrometers) were expressed as the mean± standard deviation (range). Smears containing free spores were stained with Giemsa's solution and mounted in low-viscosity mounting medium (Cytoseal^{TM}) as permanent slides to be deposited in the museum collection. For histological analysis, fragments of infected organs were fixed in 10% buffered formalin and embedded in paraffin. Serial sections 4 μm in thickness were stained with hematoxylin/eosin and Sirius red. For the scanning electron microscopy, free spores were deposited on a coverslip coated with poly-L-lysine and fixed for 2 h at room temperature with 2.5% glutaraldehyde in 0.1 M sodium cacodylate buffer (pH 7.2). After washing in the same buffer, the preparations were dehydrated in ethanol, critical point-dried by CO_2, coated with metallic gold, and examined in a JEOL JSM 35 microscope operating at 15 kV. For the transmission electron microscopy, plasmodia were fixed in 2.5% glutaraldehyde in 0.1 M cacodylate buffer (pH 7.4) for 12 h, washed in a glucose–saline solution for 2 h, and post-fixed in OsO_4, all done at 4°C. After dehydration in an acetone series, the material was embedded in EMbed 812 resin. Ultrathin sections double stained with uranyl acetate and lead citrate were examined in an LEO 906 electron microscope operating at 60 kV. The effects of the sex of the host on the prevalence of the parasite were assessed using the χ^2 test, with the level of significance set at $p<0.05$.

Results

Among the 60 adult fish (30–50 cm) examined, 42 (70%) had plasmodia of an unknown species of *Henneguya* infecting the gills. There was no significant difference in the prevalence of infection with regard to the sex of the host [males, 74% (20/27); females, 66% (22/33); $\chi_1^2=0.38$, $p>0.53$].

Description *Henneguya azevedoi* n. sp. (Figs. 1–17)

Vegetative stages (Figs. 5, 6, 7, 8, 9, 10, 11, 12, 13, 14, 15, 16, and 17): plasmodia white, spherical, 40–200 μm in diameter, located throughout lamellae, but most commonly in distal region (Figs. 5, 6, 7, and 8). Histological analysis: plasmodia intralamellar, causing stretching of epithelium,

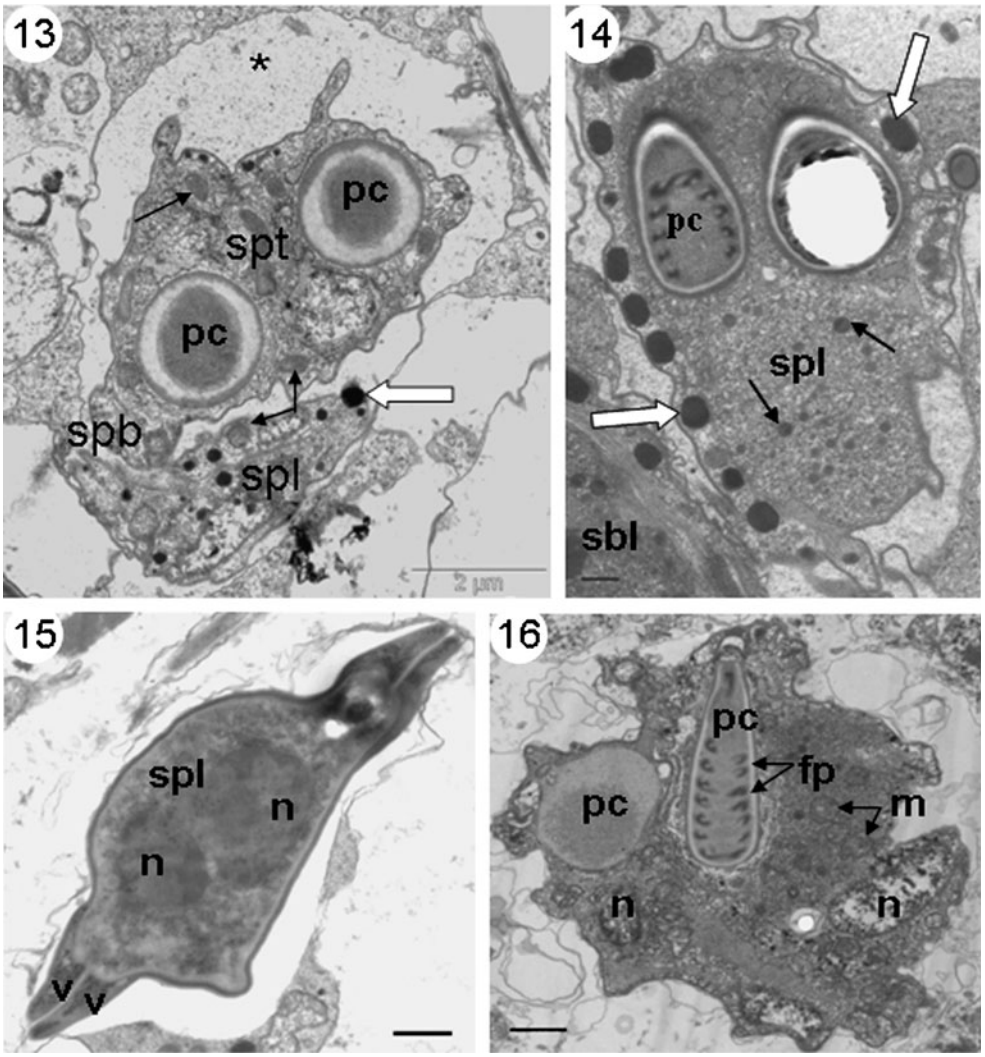


Fig. 13–16 Transmission electron microscopy of *H. azevedoi* n. sp. from gills of *L. obtusidens* *13* Sporoblast (*spb*) with two developing spores, one in the transversal section (*spt*) and the other in the longitudinal section (*spl*). Note the polar capsules (*pc*), wide empathy area (*asterisks*), several mitochondria (*thin arrows*), and valve-forming materials (*white arrow*). *Scale bar*, 2 µm *14* Immature spores in longitudinal section. Note the polar capsule (*pc*), the sporoplasms (*spl*) with sporoplasmosomes (*thin arrows*), and valve-forming materials (*white arrow*). *Scale bar*, 2 µm *15* Transversal section of an immature spore in sporoplasm level (*spl*) showing the sporoplasm nuclei (*n*) and each one of the valves (*v*). *Scale bar*, 5 µm *16* Longitudinal section of an immature spore showing the polar capsules (*pc*) with its polar filaments (*pf*), nuclei (*n*) of capsulogenic cells, and mitochondria (*m*). *Scale bar*, 2 µm

with accentuated deformation and compression of capillary and adjacent tissues; no inflammatory infiltrate observed (Figs. 5, 6, 7, and 8); direct contact between plasmodial wall and host cells observed in ultrastructural analysis (Figs. 9 and 10); Plasmodium wall composed of single membranes and with pinocytotic canals (Fig. 10); spore development asynchronous, with numerous mitochondria and generative cells in cortical zones (Fig. 9); mature spores centrally located and sporoblasts and immature spores between central and cortical zones (Figs. 12, 13, 15, and 16); sporoblasts disporic, with a wide empty area bounded by thin membrane at advanced stages of development (Figs. 11 and 13); valve-forming materials found in developing spores (Figs. 12, 13, and 14); sporoplasm binucleate with numerous sporoplasmosomes (Figs. 14 and 15).

Mature spores: elongated in frontal view, with ovoid spore body and two caudal process [45.2±0.6 (45.0–47.0) µm in total length, 10.0±0.07 (9.9–10.2) µm in body length, 35.6±0.9 (34.9–36.5) µm in caudal process length, 4.4±0.4 (4.0–5.0) µm in body width]; polar capsules elongated and equal in size [length=3.8±0.3 (3.5–4.0) µm, width=1.0 µm]; occupying one third of spore body length (Figs. 1, 2 and 17); polar filament with six to seven coils perpendicular to the longitudinal axis of capsule (Figs. 16 and 17). Scanning electron microscopy showed symmetrical, smooth valves, and rim around the spore body (Figs. 3 and 4).

Type host: *Leporinus obtusidens* (Valenciennes, 1837) (Osteichthyes, Anostomidae)

Site of infection: gill lamellae.

Prevalence: 70%.

Locality: Mogi-Guaçu River near Cachoeira de Emas Falls, Pirassununga, state of São Paulo, Brazil.

Type material: One slide containing free spores fixed with methanol, stained with Giemsa's solution, and mounted in a low-viscosity mounting medium has been deposited in the collection of the Museum of Natural History, Institute of Biology, State University of Campinas, São Paulo State, Brazil (accession no. ZUEC 30).

Etymology: The specific name (*H. azevedoi*) is in homage to Dr. Carlos Azevedo, professor at the University

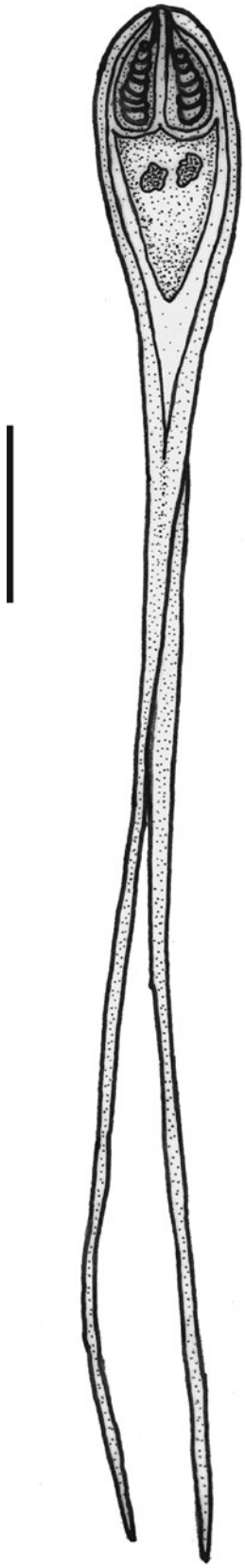


Fig. 17 Schematic representation of mature spores of *H. azevedoi* n. sp. *Scale bar*, 5 μm

of Oporto, Portugal, who has been contributing largely to improving our knowledge on the diversity of South American Myxosporea.

Discussion

The features of *H. azevedoi* n. sp. were compared with species of *Henneguya* parasites of South American fish (Azevedo et al. 2009; Eiras et al. 2009; Naldoni et al. 2011) and those of other regions (Eiras 2002). Among the 38 valid species of *Henneguya* described for the South American continent, only *H. leporinicola* (Martins et al. 1999), parasite of the gills of *Leporinus macrocephalus*, and *H. schizodon* (Eiras et al. 2004), infecting the kidney of *Schizodon fasciatus*, were found parasitizing fish of the family Anostomidae. However, the total length of the spores of these species (29.4 μm in *H. leporinicola* and 28.9 μm in *H. schizodon*) differs strongly from the size found in *H. azevedoi* n. sp. (45.2 μm). In the comparison with species of *Henneguya* parasites of other South American fish, *Henneguya astyanax* (Vita et al. 2003) and *Henneguya garavelli* (Martins and Onaka 2006), respectively, found infecting the gills of *Astyanax keithie* and *Cyphocharax nagell*, have total spore lengths similar to that observed in *H. azevedoi* n. sp. However, other dimensions in these species differ from those of *H. azevedoi* n. sp. In *H. astyanax* and *H. garavelli*: spore body length (15.2 and 13.6 μm, respectively), polar capsule length (5.0 and 5.4 μm, respectively), and the number of polar filament coils (eight to nine) are greater than those found in *H. azevedoi* n. sp.

Considering the species of *Henneguya* from other continents (Eiras 2002), *H. azevedoi* n. sp. differs from these species with regard to some characteristics, such as total spore length, spore body length, length of caudal process, spore width, length or width of polar capsules, number of polar filament turns, infection site, plasmodium shape and size, and phylogenetically distant hosts. Thus, based on the aforementioned differences in characteristics and the high host specificity demonstrated by species of *Henneguya* (Molnár 1998), the material studied here was considered a new species of Myxosporea.

The comparison between female and male hosts revealed no influence of sex on the prevalence of *H. azevedoi* n. sp. A number of authors have described similar findings (Gbankoto et al. 2001; Viozzi and Flores 2003; Milanin et al. 2010). However, other authors have reported significant difference between females and males regarding the prevalence of infection (Muzzall 1995; Gbankoto et al. 2003).

The ultrastructural characterization of the plasmodial wall of myxosporeans has fundamental importance in the

study of the host–parasite relationship since the structure of this wall differs among the different myxosporean species (Current and Janovy 1976; El-Mansy and Bashtar 2002; Adriano et al. 2005a) as well as among different clinical types of a single species (Current and Janovy 1978). The plasmodial wall functions as a nutrient transport system, supplying the nutrients necessary for plasmodial development through pinocytic canals (Hallett and Diamant 2001; El-Mansy and Bashtar 2002) and/or engulfing parts of the host cells through phagocytosis (Uspenskaya 1982; Lom and Dyková 1995, Adriano et al. 2005a; Naldoni et al. 2009). In the present study, the ultrastructural analysis revealed a plasmodial wall formed by a single membrane in direct contact with the host cells and with pinocytic canals entering the ectoplasm of the plasmodium, which is similar to the findings described by Current (1979), El-Mansy and Bashtar (2002), Adriano et al. (2005b), Matos et al. (2005), and Abdel-Ghaffar et al. (2008).

The sporogenesis of *H. azevedoi* n. sp. exhibited a similar development pattern to that of other species of *Henneguya* (Adriano et al. 2005a; Matos et al. 2005; Ali et al. 2007; Abdel-Ghaffar et al. 2008; Azevedo et al. 2008), with numerous mitochondria and generative cells in the periphery of the plasmodium, young sporoblasts and immature spores just below, and mature spores in the central area. However, the uniqueness of *H. azevedoi* n. sp. was the existence of a wide empty area in more mature sporoblasts occupied by a finely granular material, within which spores were immersed. Initially, this characteristic was thought to be the result of a fixation artifact. However, two factors suggest that these empty areas reflect actual conditions of this species of parasite: (1) empty areas were observed in different samples caught at different times throughout the study and not in samples of other myxosporean species fixed using the same method; (2) these empty areas were not observed in areas of development of young sporoblasts, but were clear in areas in which the spores were in the final development phase (almost mature or mature spores), which leads us to believe that these empty areas result from the natural contraction that the spores of *H. azevedoi* n. sp. undergo during the maturation process.

Several species of *Henneguya* induce pathogeny in their hosts, such as *Henneguya exilis* (Current and Janovy 1976), *Henneguya waltairensis* in *Channa punctatus* (Kalavati and Narasimhamurti 1985), *Henneguya creplini* (Molnár 1998), *Henneguya suprabranchiae* (El-Mansy and Bashtar 2002), *Henneguya piaractus* (Martins and Souza 1997; Adriano et al. 2005a), and *Henneguya pseudoplatystoma* (Naldoni et al. 2009). Using the classification proposed by Molnár (2002), the plasmodia of *H. azevedoi* n. sp. is of the intralamellar type, and the histological analysis revealed that the parasite causes stretching of the epithelium, with accentuated deformation, and compression of the capillary and adjacent tissues. The gill is the major respiratory organ, the primary site of nitrogenous waste excretion, and plays an important role in ionic balance (Noga 2000). According to Feist and Longshaw (2006), myxosporeans infecting the gills can compromise respiratory capacity when present in sufficient numbers. Deformation of the gill structures with compression of the capillary and adjacent tissues also has been reported by several authors (Haaparanta et al. 1994; Martins et al. 1999; Adriano et al. 2005a; Naldoni et al. 2009). The gills of *L. obtusidens* infected by *H. azevedoi* n. sp. had no inflammatory infiltrate and the plasmodial wall was in direct contact with the host cells. Many myxosporean species induce little or no host response, and the most common condition found in histological analyses is the encapsulation of the plasmodia by connective, fibrotic, and epithelioid tissue layers, isolating the parasite and preventing its dispersal to adjacent tissues (Sitjà-Bobadilla 2008). However, besides the absence of inflammatory infiltrate, *H. azevedoi* n. sp. also lacked encapsulation by connective tissue surrounding the plasmodial wall, leaving the parasite in direct contact with the host cells, similar to that observed in the interlamellar plasmodium of *H. exilis* (Current and Janovy 1976) and *H. pseudoplatystoma* (Naldoni et al. 2009).

The lack of inflammation infiltrate and of encapsulation by connective tissue associated with *H. azevedoi* n. sp. infection in *L. obtusidens* suggests a minimal pathologic impact and apparently did not compromise the health of this host. However, the more subtle impacts of this parasite on the respiration of its host remain to be determined.

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