



# Taxonomy and 18S rDNA-based phylogeny of *Henneguya multiradiatus* n. sp. (Cnidaria: Myxobolidae) a parasite of *Brochis multiradiatus* from Peruvian Amazon

Patrick Mathews, Omar Mertins, Luis Espinoza, Tiago Milanin, Gema  
Alama-Bermejo, F. Audebert, André Morandini

## ► To cite this version:

Patrick Mathews, Omar Mertins, Luis Espinoza, Tiago Milanin, Gema Alama-Bermejo, et al.. Taxonomy and 18S rDNA-based phylogeny of *Henneguya multiradiatus* n. sp. (Cnidaria: Myxobolidae) a parasite of *Brochis multiradiatus* from Peruvian Amazon. *Microbial Pathogenesis*, 2020, 147, pp.104372. 10.1016/j.micpath.2020.104372 . hal-02902791

**HAL Id: hal-02902791**

**<https://hal.science/hal-02902791>**

Submitted on 18 Jul 2022

**HAL** is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.



Distributed under a Creative Commons Attribution - NonCommercial 4.0 International License

**1 Taxonomy and 18S rDNA-based phylogeny of *Henneguya multiradiatus* n. sp.**  
**2 (Cnidaria: Myxobolidae) a parasite of *Brochis multiradiatus* from Peruvian**  
**3 Amazon**

4 Patrick D. Mathews<sup>a,b,\*</sup>, Omar Mertins<sup>c</sup>, Luis L. Espinoza<sup>d</sup>, Tiago Milanin<sup>e</sup>, Gema  
5 Alama-Bermejo<sup>f</sup>, Fabienne Audebert<sup>b</sup>, André C. Morandini<sup>a,g</sup>

6 <sup>a</sup> Department of Zoology, Institute of Biosciences, University of São Paulo, 05508-090  
7 São Paulo, Brazil

8 <sup>b</sup> Unité de Biologie des Organismes et Écosystèmes Aquatiques, Museum National de  
9 d'Histoire Naturelle, Sorbonne Université, CNRS, IRD, UCA, CP 26, 75005 Paris,  
10 France

11 <sup>c</sup> Department of Biophysics, Paulista Medical Scholl, Federal University of São Paulo,  
12 04023-062 São Paulo, Brazil

13 <sup>d</sup> Laboratory of Biology and Molecular Genetics, Faculty of Veterinary Medicine,  
14 National University of San Marcos, 2800 San Borja, Lima, Peru

15 <sup>e</sup> Department of Basic Sciences, Faculty of Animal Science and Food Technology,  
16 University of São Paulo, 13635-900 São Paulo, Brazil

17 <sup>f</sup> Institute of Parasitology, Biology Centre of the Czech Academy of Sciences, 37005  
18 České Budějovice, Czech Republic

19 <sup>g</sup> Marine Biology Center, University of São Paulo, 11612-109, São Sebastião, Brazil

20 \*Corresponding author at: Department of Zoology, Institute of Biosciences, University  
21 of São Paulo - USP, Rua do Matão, travessa 14, nº. 10, 05508-090 Cidade Universitária  
22 São Paulo, SP, Brazil. E-mail address: patrickmathews83@gmail.com (Patrick D.  
23 Mathews).

24

## ABSTRACT

A new myxozoan species belonging to the genus *Henneguya* was isolated from the serous membrane of the visceral cavity of the hog-nosed catfish *Brochis multiradiatus* from Peruvian Amazon. Whitish plasmodia, macroscopically visible, were found in four of the thirty examined fishes. Mature myxospores were ellipsoidal in shape in frontal view and had a total length of  $44.5 \pm 0.6 \mu\text{m}$  (43.9–45.1), spore body measured  $18.7 \pm 0.9 \mu\text{m}$  (16.8–19.6) in length,  $7.1 \pm 0.2 \mu\text{m}$  (6.6–7.4) in width and  $5.5 \pm 0.3 \mu\text{m}$  (4.9–5.6) in thickness. The two polar capsules were elongated and equal in size, measuring  $9.1 \pm 0.1 \mu\text{m}$  (8.8–9.4) in length and  $1.7 \pm 0.1 \mu\text{m}$  (1.6–1.8) in width, occupying half of the myxospore body. Polar tubules coiled in 10 to 11 turns perpendicular to the long axis of the polar capsule. The caudal appendage was not bifurcated and measured  $25.8 \pm 0.6 \mu\text{m}$  (24.7–26.5) in length. The sequencing of the 18S rDNA gene resulted in 1400 bp and this sequence did not match any of the myxozoans available in GenBank. Phylogenetic analysis placed the new species in a well-supported subclade of *Henneguya* spp. infecting callichthyid fishes, with *Henneguya loretoensis* being the closest species. This study is the first description of a myxozoan species, *Henneguya multiradiatus* n. sp. from a fish of the genus *Brochis*.

**Keywords:** Cnidaria, Endocnidozoa, Hog-nosed catfish, Myxosporean, 18S rDNA sequencing, Peru

## 1. Introduction

Myxozoans are microscopic endoparasites with complex life cycles involving invertebrate and vertebrate hosts [1]. Recently, due to synapomorphies and cnidarian-specific genes, myxozoans were placed within the phylum Cnidaria and currently represent about 20% of the known cnidarian species diversity around the world [1].

While predominantly known to infect freshwater and marine fishes, myxozoans can also infect other groups of vertebrates such as amphibians, reptiles, birds, and terrestrial small mammals [2]. Within fish-infecting myxozoans, *Henneguya* Thélohan, 1892, is one of the largest genera, with more than 195 described species within a wide geographical range [3]. *Henneguya* spp. are histozoic parasites and they show high host-specificity and organ- or tissue tropism, with some species inducing severe henneguyosis in wild and cultured fish [4–7].

It is well known that the growing global pet trade, including aquarium market, plays a role in the spread of pathogens [8]. According to Hallett et al. [9], the aquatic pet trade would very likely stand as a primary mode for international transport of myxozoan parasites. In fact, there are some reports about the introduction of myxosporeans through commercial transfers of pets with some cases of ecological and economic impacts [10–12]. As such, there is a growing need for myxozoans screening during parasitological surveys in these aquatic pet animals.

The armored catfish corydoradines are members of the family Callichthyidae. With over 190 described species, it is one of the most diverse siluriform assemblages in the Neotropics [13]. These neotropical freshwater catfishes are endemic to South America [13]. Among these corydoradines, *Brochis multiradiatus* Orcés V., 1960 is found in the Napo River in Ecuador and Peru [14]. It can reach up to 6.7 cm in length and is largely marketed in the aquarium trade, being one of the most popular in the Chinese ornamental fish market [15]. Although corydoradines are highly appreciated in the international aquarium trade, there are few parasitological surveys about this fish, especially those concerning myxozoan parasites.

To our knowledge, nothing is known about myxozoan parasites infecting any member of the genus *Brochis*. Herein, based on morphological, biological/ecological traits and

molecular data, we described a new *Henneguya* species infecting the ornamental fish *B. multiradiatus* from the Amazon region of Peru, a key supply region of wild ornamental fishes for the international aquarium trade.

## 2. Material and methods

In September 2019, thirty wild specimens of *B. multiradiatus* were collected by a local fisherman. The fishes were caught in the Napo River, in an adjacent area of the village Cabo Pantoja (0°57'25"S, 75°27'11"W), Department of Loreto, Peru. The fish were transported alive to the field laboratory where they were euthanized by neural pithing and examined. The procedures were approved by the Federal University of São Paulo-UNIFESP Ethics Committee (CEUA No. 9209080214), in accordance with Brazilian law for scientific use of animals (Federal Law No. 11794, dated 8 October 2008). The family and current status of the host fish (valid species name or synonym) were reviewed using FishBase [14].

Morphometric analyses were performed on mature myxospores following the criteria outlined by Lom and Arthur [16]. Measurements and photographs were taken from 30 myxospores using a computer equipped with Axiovision 4.1 image capture software coupled to an Axioplan 2 Zeiss microscope (Carl Zeiss AG, Oberkochen, Germany). The dimensions of the myxospores were given in micrometers ( $\mu\text{m}$ ) and expressed as the mean  $\pm$  standard deviation, followed by the range in parentheses. Prevalence of infection [(number of infected fish/total number of fishes examined)  $\times 100$ ] was calculated according to Bush et al. [17]. Smears containing free myxospores were air-dried, fixed with methanol and stained with Ziehl-Neelsen to mount on permanent slides that were deposited in the cnidarian collection of the zoology Museum of the University of São Paulo - USP, São Paulo, Brazil (MZUSP).

For molecular studies, a plasmodium was dissected from the host tissue and fixed in absolute ethanol. The genomic DNA was extracted from a single plasmodium using DNeasy® Blood & Tissue Kit (Qiagen, Valencia, USA), in accordance with the manufacturer's instructions. The DNA concentration was measured using a NanoDrop 2000 spectrophotometer (Thermo Scientific, Wilmington, USA). Polymerase chain reactions (PCRs) were performed in accordance with Milanin et al. [18] and conducted in a final volume reaction of 25 µL, which comprised 10–50 ng of extracted DNA, 0.2 pmol for each primer, 12.5 µL of Dream Taq Green PCR Master Mix (Thermo Scientific) and nuclease-free water. Partial 18S rDNA sequence was amplified using the primer pairs ERIB1 [19] - ACT1r [20] and Myxgen4F [21] - ERIB10 [19] (Table 1), which amplified two fragments containing approximately 1.000 and 1.200 bp respectively. PCR amplification was done by initial denaturation at 95 °C for 5 min, followed by 35 cycles at 95 °C for 1 min, 64 °C (ERIB1-ACT1r) or 58 °C (Myxgen4F-ERIB10) for 1 min, 72 °C for 2 min, and then final elongation at 72 °C for 5 min. PCRs were performed in an AG22331 Hamburg Thermocycler (Eppendorf, Hamburg, Germany). PCR products were subjected to electrophoresis in 2.0% agarose gel (BioAmerica, Irvine, USA) in a TAE buffer (Tris-Acetate EDTA: Tris 40 mM, acetic acid 20 mM, EDTA 1 mM), stained with Sybr Safe DNA gel stain (Invitrogen by Life Technologies, Carlsbad, USA), and then analyzed with a Stratagene 2020E trans illuminator (Stratagene California, San Diego, USA). The size of the amplicons was estimated by comparison with the 1 Kb Plus DNA Ladder (Invitrogen by Life Technologies). PCR products were purified using USB® ExoSap-IT® (Thermo Fisher Scientific) in accordance to the manufacturer's instructions and sequenced using the same PCR primers plus two additionally MC5 and MC3 primers used to overlap the obtained amplification fragments [22]. Sequencing was performed at Paulista Medical

School, Federal University of São Paulo, using a BigDye® Terminator v3.1 Cycle Sequencing kit (Applied Biosystems Inc., California, USA) in an ABI 3130 automatic DNA analyzer (Applied Biosystems Inc.™). The obtained sequence was visualized, assembled and edited using BioEdit 7.1.3.0 software [23]. A standard nucleotide BLAST (blastn) search was conducted to verify the similarity of the sequence obtained in this study with other sequences available in GenBank [24]. Phylogenetic analysis was conducted using the most closely related myxozoans sequences with similarity > 80%. The sequences were aligned with ClustalW within BioEdit version 7.1.3.0 [23]. Phylogenetic analysis was performed using Maximum Likelihood (ML) method with a Kimura 2-parameter (K2P) evolution sequence model in MEGA 6.0 [25]. Bootstrap analysis (1000 replicates) was employed to assess the relative robustness of the branches in ML tree. *Ceratonova shasta* sequence was used as outgroup. The pairwise method with the p-distance model in MEGA 6.0 [25] was performed to evaluate the genetic distance between the myxozoan species clustering together with the new sequence obtained.

### 3. Results

Whitish plasmodia macroscopically visible measuring 2.1 to 3 mm in diameter and containing large quantities of myxospores belonging to the genus *Henneguya* were found in the serous membrane of the visceral cavity of wild specimens of *B. multiradiatus* (Fig. 1A). The prevalence of the myxozoan parasites in these fish hosts was 13.3% (4/30) and no signs of diseases were observed in the infected individuals.

#### *Henneguya multiradiatus* n. sp.

#### Taxonomic summary

Phylum: Cnidaria Verrill, 1865

Class: Myxosporea Bütschli, 1881

Order: Bivalvulida Shulman, 1959

Family: Myxobolidae Thélohan, 1892

Genus: *Henneguya* Thélohan, 1892

Type host: *Brochis multiradiatus* (Orcés V., 1960) (Siluriformes: Callichthyidae)

Site of infection: Serous membrane of the visceral cavity

Type locality: Napo River, adjacent area of the village Cabo Pantoja (0°57'25"S, 75°27'11"W), Department of Loreto, Peru.

Prevalence: 13.3 % (4/30).

Type of material: Syntypes-air-dried slide stained with Ziehl-Neelsen deposited in the cnidarian collection of Zoology Museum of the University of São Paulo - USP, São Paulo, Brazil (MZUSP 8508). Partial 18S rDNA sequence (1400bp) was deposited in GenBank under accession number MT415832.

Etymology: The specific name (*H. multiradiatus*) is based on host species name.

### **Morphological characterization**

Mature myxospores were ellipsoidal in shape from the frontal view, measuring  $44.5 \pm 0.6 \mu\text{m}$  (43.9–45.1) in total length,  $18.7 \pm 0.9 \mu\text{m}$  (16.8–19.6) in spore body length,  $7.1 \pm 0.2 \mu\text{m}$  (6.6–7.4) in width and  $5.5 \pm 0.3 \mu\text{m}$  (4.9–5.6, n=5) in thickness (Figs. 1B and 2). Two elongated polar capsules, equal in size, measuring  $9.1 \pm 0.1 \mu\text{m}$  (8.8–9.4) in length and  $1.7 \pm 0.1 \mu\text{m}$  (1.6–1.8) in width, occupying half of myxospore body (Figs. 1B-C and 2). Polar tubules had 10 to 11 coils, perpendicular to long axis of polar



capsule (Figs. 1C and 2). Non-bifurcate caudal appendage, measuring  $25.8 \pm 0.6 \mu\text{m}$  (24.7–26.5) in length (Figs. 1B and 2).

#### **Molecular characterization and phylogenetic analysis**

Partial 18S rDNA sequence obtained from mature myxospores of *H. multiradiatus* n. sp. resulted in 1400 bp with a CG content of 49.4% and did not match any other myxozoans available in GenBank. The comparison of the new sequence obtained by BLAST revealed the highest sequence similarity to *Henneguya loretoensis* Mathews, Naldoni and Adriano 2017 (GenBank accession number MF434827.1, query coverage 99%, maximum identities 98.2%). The phylogenetic analysis placed *H. multiradiatus* n. sp. in a well-supported subclade of *Henneguya* parasites of callichthyids fish, including *Henneguya loretoensis*, and *Henneguya guanduensis* Abdallah, Azevedo, Luque and Bomfim 2007 (Fig. 3). This subclade, was close to a lineage formed by *Henneguya* species described from Amazonian cichlids. 18S rDNA pairwise comparisons between *H. multiradiatus* n. sp. described and the closest relatives resulted in 1.8% to *H. loretoensis*, 5.3% to *H. guanduensis*, 6.1% to *Henneguya peruviansis* Mathews, Mertins, Pereira, Maia and Adriano 2018, 7.6% to *Henneguya jariensis*, 9.5% to *Henneguya tapajoensis*, 7.2% to *Henneguya tucunare* Zatti, Atkinson, Maia, Bartholomew and Adriano 2018 and 8.6% to *Henneguya paraensis* Velasco, Videira, Nascimento, Matos, Gonçalves and Matos 2016.

#### **4. Discussion**

The Peruvian Amazon is the second largest portion of the Amazon rainforest concentrating a high aquatic biodiversity, with several commercially exploited fish species for human consumption and global aquarium trade [26,27]. However, little is known about the diversity of myxozoans in this region, with only three species

described to date: *Henneguya loretoensis*, *Henneguya peruviansis* and *Myxidium peruviansis* [28–30]. In contrast, over 40 myxozoan species have been described in the Brazilian Amazon region [31–33], indicating that there are likely many more myxozoan parasites to be identified in Peruvian Amazon, considering the recognized high diversity. This study reports, for the first time, a myxozoan species infecting a fish from the genus *Brochis* in the Amazon basin.

For robust identification and description of new myxosporeans taxa, it has been recommended, that the studies integrate multiple characters, including morphology, biological traits, host ecology factors and molecular data [34]. Following these delineated criteria for classifying myxozoans, we described a novel *Henneguya* species, *Henneguya multiradiatus* n. sp. from an important Amazonian ornamental fish. In the morphological comparison, considering the twenty-two *Henneguya* species previously described to infect fishes from Amazon basin, the most morphologically similar species to the new species were *Henneguya torpedo* Azevedo, Casal, Matos, Alves and Matos, 2011 and *Henneguya testicularis* Azevedo, Corral and Matos, 1997. Nevertheless, these differ from *H. multiradiatus* n. sp. in myxospore body length ( $28.5 \pm 0.3 \mu\text{m}$  in length for *H. torpedo*,  $14.0 \mu\text{m}$  for *H. testicularis* and  $18.7 \pm 0.9 \mu\text{m}$  to the new species), number of coils of the polar tubule (12 to 13 in *H. torpedo*, six to seven in *H. testicularis* and ten in the new species) and in the length of the caudal appendage, which is substantially larger in the new species ( $19.6 \pm 0.4 \mu\text{m}$  in *H. torpedo*,  $13.5 \mu\text{m}$  in *H. testicularis*, and  $25.8 \pm 0.6 \mu\text{m}$  in *H. multiradiatus* n. sp.). Plasmodia of *H. multiradiatus* n. sp. were located in the serous membrane of the visceral cavity, while *H. torpedo* and *H. testicularis* were described infecting brain, spinal cord, and testis respectively [35,36]. On the same premise, host species and locality of collection are indispensable traits for accurately distinguishing new histozoic platysporines species,

since host-specificity and geography may play an important role in speciation [37]. Accordingly, differences were observed in the infected host, *e.g.*, *H. multiradiatus* n. sp. infecting *B. multiradiatus*, a Siluriform fish; *H. torpedo* infecting *Brachyhypopomus pinnicaudatus* (Hopkins 1991), a Gymnotiform fish; and *H. testicularis* infecting *Moenkhausia oligolepis* (Günther 1864), a Characiform fish. Besides, differences in the locality of these species were noted, with *H. multiradiatus* n. sp. found in the Napo River, a tributary of the upper Amazon River, near the village of Cabo Pantoja in Department of Loreto, Peru, and *H. torpedo* and *H. testicularis* found in the lower Amazon River, both near Belém city in Pará state, Brazil. In addition to the large geographic distance between these species (2, 965 km in straight line), the nonmigratory behavior of their hosts is an important ecological character for the separation of these species, taking in account that host behavior may drive both parasite endemism and the radiation within the Amazon basin [32]. Unfortunately, there is no molecular data available for *H. torpedo* and *H. testicularis* in GenBank, so it is not possible to compare them with *H. multiradiatus* n. sp. However, differences observed in the integrative comparison, including morphology, geography, biological traits in conjunction with the ecological characters of their hosts, are sufficient arguments to conclude that *H. multiradiatus* n. sp. is a separate species.

In our phylogenetic analysis, *Henneguya* spp. showed tendency to cluster, largely based on vertebrate host fish family, and this corroborates the results pointed out by other authors who evidenced that host group is a strong evolutionary signal within the Myxobolidae [32,38,39]. *Henneguya multiradiatus* n. sp. was placed in a well-supported subclade of parasites of callichthyids fishes, with *H. loretoensis* as the closet related species (Fig. 3). This close phylogenetic relationship was corroborated by the pairwise analysis, which showed a slight genetic divergence of 1.8% on their 18S rDNA

sequences. Nevertheless, there is no exact value for determining the level of genetic variation in 18S rDNA that equates to species differentiation within this enigmatic group of parasites [38,40]. In this context, species differentiation should be assessed for each individual case and always with the aid of biology and/or ecology traits of the organisms, such as their morphology, tissue and/or organ tropism, host species, geography, and host ecological aspects such as endemic character, migratory behavior and distribution [16,40]. In our study, remarkable morphometrical differences can be observed between these two corydoradines *Henneguya* parasites, with myxospores substantially larger in total length and width in the newly identified species ( $44.5 \pm 0.6 \mu\text{m} \times 7.1 \pm 0.2 \mu\text{m}$  vs  $36.2 \mu\text{m} \times 5.1 \mu\text{m}$  for *H. loretoensis*), larger body length ( $18.7 \pm 0.9 \mu\text{m}$  vs  $14.3 \pm 0.1 \mu\text{m}$  for *H. loretoensis*), longer polar capsules ( $9.1 \pm 0.1 \mu\text{m}$  vs  $5.1 \pm 0.1 \mu\text{m}$  in *H. loretoensis*), higher number of coils in the polar tubule (ten to eleven coils vs five coils in *H. loretoensis*) and the caudal appendage which is substantially longer ( $25.8 \pm 0.6 \mu\text{m}$  vs  $21.9 \pm 0.1$  in *H. loretoensis*). Furthermore, *H. multiradiatus* n. sp. the caudal appendage is not bifurcated, as occurs in *H. loretoensis*. Differences can also be outlined concerning the host-, tissue- and organ infected, with the new species proposed found in the serosa layer of the visceral cavity of *B. multiradiatus* n. sp. whereas *H. loretoensis* is found in gill filaments of *Corydoras leucomelas* Eigenmann and Allen, 1942, a host of a different genus. While these two corydoradines parasites inhabit the Amazon biome of Peru (*H. multiradiatus* n. sp. in Napo River and *H. loretoensis* Nanay River), they are separated by 381 km from each other. Another important point to consider in establishing *H. multiradiatus* n. sp. as a new species, is in regards to the endemic character and the absence of migratory reproduction, characteristics which are highly recognized to corydoradines fish [33].

In the present study, an integrative taxonomy approach was employed in the description of an unknown myxosporean. Given that these criteria are compelling evidence for the characterization of new species [16,40], we confidently considered that this isolate is a new species, *H. multiradiatus* n. sp. Hence, this new data contributes to increase the knowledge of the myxosporean diversity from the Amazon biome, as well to clarify the relationships of myxozoan parasites of corydoradines, an economic important assemblage of catfishes in the lucrative global aquarium industry.

## Acknowledgments

The authors thank the São Paulo Research Foundation, FAPESP, for Post-Doc fellowship awarded to P.D. Mathews (grant no. 2018/20482-3 and 2019/13147-6). A.C. Morandini was funded by CNPq (309440/2019-0) and FAPESP (2015/21007-9). T. Milanin was supported by a Post-Doc fellowship from FAPESP (grant no. 2015/18807-3). L.L. Espinoza thanks Vice-rectorado de Investigación y Postgrado, Universidad Nacional Mayor de San Marcos for research financial support (grant no. A17080131). The authors thank Dr K. Liittschwager (USA) for revision of the English idiom.

## References

- [1] S.D. Atkinson, J.L. Bartholomew, T. Lotan, Myxozoans: Ancient metazoan parasites find a home in phylum Cnidaria, *Zoology* 129 (2018) 66–68. <https://doi.org/10.1016/j.zool.2018.06.005>
- [2] M. Lisnerová, I. Fiala, D. Cantatore, M. Irigoitia, J. Timi, H. Pecková, P. Bartošová-Sojková, C.M. Sandoval, C. Luer, J. Morris, A.S. Holzer, Mechanisms and drivers for the establishment of life cycle complexity in myxozoan parasites, *Biology* 9 (2020) 10. <https://doi.org/10.3390/biology9010010>

- 289 [3] J.C. Eiras, E.A. Adriano, Checklist of new species of *Henneguya* Thélohan, 1892  
 290 (Myxozoa: Myxosporea, Myxobolidae) described between 2002 and 2012, Syst.  
 291 Parasitol. 83 (2012) 95–104. <https://doi.org/10.1007/s11230-012-9374-7>
- 292 [4] L.M. Pote, L.A. Hanson, R. Shivaji, Small subunit ribosomal RNA sequences link  
 293 the cause of proliferative gill disease in channel catfish to *Henneguya* n. sp. (Myxozoa:  
 294 myxosporea), J. Aquat. Anim. Health 12 (2000) 230–240. [https://doi.org/10.1577/1548-](https://doi.org/10.1577/1548-8667(2000)012<0230:SSRRSL>2.0.CO;2)  
 295 8667(2000)012<0230:SSRRSL>2.0.CO;2
- 296 [5] A. Gupta, H. Kaur, 18S and 28S rDNA identity and phylogeny of two novel  
 297 myxosporeans infecting gills of cyprinid carps inhabiting a cold-water wetland in  
 298 northern India, Microb. Pathog. 120 (2018) 97–108.  
 299 <https://doi.org/10.1016/j.micpath.2018.04.042>
- 300 [6] R.T.A. Figueredo, J.E.F. de Oliveira, M.P.S.P. Vilhena, J. Berredo, W.J.P. Dos  
 301 Santos, E. Matos, M. Velasco, Henneguyosis in gills of *Metynnis hypsauchen*: an  
 302 Amazon freshwater fish, J. Parasit. Dis. 44 (2020) 213–220.  
 303 <https://doi.org/10.1007/s12639-019-01183-7>
- 304 [7] P. Katharios, P. Varvarigos, K. Keklikoglou, M. Ruetten, J. Sojan, M. Akter, M.C.  
 305 Cascarano, M.I. Tsertou, C. Kokkari, Native parasite affecting an introduced host in  
 306 aquaculture: cardiac henneguyosis in the red seabream *Pagrus major* Temminck &  
 307 Schlegel (Perciformes: Sparidae) caused by *Henneguya aegea* n. sp. (Myxosporea:  
 308 Myxobolidae), Parasit.Vectors 13 (2020) 27. [https://doi.org/10.1186/s13071-020-3888-](https://doi.org/10.1186/s13071-020-3888-7)  
 309 7
- 310 [8] N.P. Mohanty, J. Measey, The global pet trade in amphibians: species traits,  
 311 taxonomic bias, and future directions, Biodivers. Conserv. 28 (2019) 3915–3923.  
 312 <https://doi.org/10.1007/s10531-019-01857-x>

- [9] S.L. Hallett, A. Hartigan, S.D. Atkinson, Myxozoans on the move: dispersal modes, exotic species and emerging diseases, in: B. Okamura, A. Gruhl, J.L. Bartholomew (Eds.), *Myxozoan Evolution, Ecology and Development*, Springer, Switzerland, 2015, pp. 343–362.
- [10] A.C. Camus, M.J. Griffin, Molecular characterization and histopathology of *Myxobolus koi* infecting the gills of a koi, *Cyprinus carpio*, with an amended morphological description of the agent, *J. Parasitol.* 96 (2010) 116–124.
- [11] A. Sitjà-Bobadilla, Can myxosporean parasites compromise fish and amphibian reproduction? *Proc. Biol. Sci.* 276 (2009) 2861–2870.
- [12] A. Hartigan, D.N. Phalen, J. Šlapeta, Myxosporean parasites in Australian frogs: Importance, implications and future directions, *Int. J. Parasitol. Parasites Wildl.* 2 (2013) 62–68. <https://doi.org/10.1016/j.ijppaw.2012.12.002>
- [13] M.R. Britto, Phylogeny of the subfamily Corydoradinae Hoedeman, 1952 (Siluriformes: Callichthyidae), with a definition of its genera, *Proc. Acad. Nat. Sci. Philadelphia* 153 (2003) 119–154.
- [14] R. Froese, D. Pauly (2016) FishBase. <http://www.fishbase.org> (accessed Jan 2020).
- [15] B. Xu, H. Su, Q. Liu, L. Lv, K. Chen, T. Xiao, Complete mitochondrial genome of *Brochis multiradiatus*, *Mitochondrial DNA Part B* 5 (2020) 646–647. <https://doi.org/10.1080/23802359.2019.1711227>
- [16] J. Lom, J.R. Arthur, A guideline for the preparation of species descriptions in Myxosporea, *J. Fish Dis.* 12 (1989) 151–156.
- [17] A.O. Bush, K.D. Lafferty, J.M. Lotz, A.W. Shostaak, Parasitology meets ecology on these terms: Margolis et al. revisited, *J. Parasitol.* 83 (1997) 575–583.

- 336 [18] T. Milanin, P.D. Mathews, O. Mertins, L.E.R. Tavares, M.R.M. Silva, AAM. Maia,  
337 Molecular phylogeny of the gill parasite *Henneguya* (Myxosporea: Myxobolidae)  
338 infecting *Astyanax lacustris* (Teleostei: Characidae) from fish farm in Brazil, Microb.  
339 Pathog. 123 (2018) 372–376. <https://doi.org/10.1016/j.micpath.2018.07.037>
- 340 [19] J.R. Barta, D.S. Martin, P.A. Liberator, M. Dashkevich, J.W. Anderson, S.D.  
341 Feighner, A. Elbrecht, A. Perkins-Barrow, M.C. Jenkins, H.D. Danforth, M.D. Ruff, H.  
342 Profous-Juchelka, Phylogenetic relationships among eight *Eimeria* species infecting  
343 domestic fowl inferred using complete small subunit ribosomal DNA sequences, J.  
344 Parasitol. 83 (1997) 262–271.
- 345 [20] S.L. Hallett, A. Diamant, Ultrastructure and small-subunit ribosomal DNA  
346 sequence of *Henneguya lesteri* n. sp. (Myxosporea), a parasite of sand whiting *Sillago*  
347  *analis* (Sillaginidae) from the coast of Queensland, Australia, Dis. Aquat. Org. 46  
348 (2001) 197–212.
- 349 [21] A. Diamant, C.M. Whipps, M.L. Kent, A new species of *Sphaeromyxa*  
350 (Myxosporea: Sphaeromyxina: Sphaeromyxidae) in devil firefish, *Pterois miles*  
351 (Scorpaenidae), from the northern Red Sea: morphology, ultrastructure, and phylogeny,  
352 J. Parasitol. 90 (2004) 1434–1442.
- 353 [22] K. Molnár, E. Eszterbauer, C. Székely, A. Dan, B. Harrach, Morphological and  
354 molecular biological studies on intramuscular *Myxobolus* spp. of cyprinid fish, J. Fish  
355 Dis. 25 (2002) 643–652.
- 356 [23] T.A. Hall, BioEdit: a user-friendly biological sequence alignment editor and  
357 analysis program for Windows 95/98/NT, Nucleic Acids Symp. Ser. 41 (1999) 95–98.



- 358 [24] S.F. Altschul, T.L. Madden, A.A. Schaffer, J.H. Zhang, Z. Zhang, W. Miller, D.J.  
 359 Lipman, Gapped BLAST and PSI-BLAST: a new generation of protein database search  
 360 programs, *Nucleic Acids Res.* 25 (1997) 3389–3402.
- 361 [25] K. Tamura, G. Stecher, D. Peterson, A. Filipski, S. Kumar, MEGA 6: molecular  
 362 evolutionary genetics analysis version 6.0, *Mol. Biol. Evol.* 30 (2013) 2725–2729.
- 363 [26] J.S. Albert, T.P. Carvalho, J.A. Chuctaya, P. Petry, R.E. Reis, B. Rengifo, H.  
 364 Ortega, *Fishes of the Fitzcarrald, Peruvian Amazon*. Lulu Press, Raleigh, 2012.
- 365 [27] N.L.S. Rivadeneyra, O. Mertins, C.R. Cuadros, J.C.O. Malta, L.V. Matos, P.D.  
 366 Mathews, Histopathology associated with infection by *Procamallanus*  
 367 (*Spirocamallanus*) *inopinatus* (Nematoda) in farmed *Brycon cephalus* (Characiformes)  
 368 from Peru: a potential fish health problem, *Aquacult. Int.* 28 (2020) 449–461.  
 369 <https://doi.org/10.1007/s10499-019-00474-3>
- 370 [28] L.L. Espinoza, O. Mertins, G.S. Gama, A.C.M. Fernandes-Patta, P.D. Mathews, A  
 371 new *Myxidium* species (Myxozoa: myxosporea) infecting the gallbladder of the turtle  
 372 *Podocnemis unifilis* (Testudines: podocnemididae) from Peruvian Amazon, *Acta Trop.*  
 373 172 (2017) 75–79. <https://doi.org/10.1016/j.actatropica.2017.04.021>
- 374 [29] P.D. Mathews, J. Naldoni, E.A. Adriano, Morphology and small subunit rDNA-  
 375 based phylogeny of a new *Henneguya* species, infecting the ornamental fish *Corydoras*  
 376 *leucomelas* from the Peruvian Amazon, *Acta Trop.* 176 (2017) 51–57.  
 377 <https://doi.org/10.1016/j.actatropica.2017.07.017>
- 378 [30] P.D. Mathews, O. Mertins, J.O.L. Pereira, A.A.M. Maia, E.A. Adriano,  
 379 Morphology and 18S rDNA sequencing of *Henneguya peruviansis* n. sp. (Cnidaria:  
 380 Myxosporea), a parasite of the Amazonian ornamental fish *Hyphessobrycon loretoensis*

- 381 from Peru: A myxosporean dispersal approach, *Acta Tropica* 187 (2018) 207–213.  
 382 <https://doi.org/10.1016/j.actatropica.2018.08.012>
- 383 [31] E.A. Adriano, O.M.P. Oliveira (2017) Myxosporea in catálogo taxonômico da  
 384 fauna do Brasil. <http://fauna.jbrj.gov.br/fauna/faunadobrasil/152799> (accessed 18 Nov  
 385 2019).
- 386 [32] S.A. Zatti, S.D. Atkinson, A.A.M. Maia, J. Bartholomew, E.A. Adriano, Novel  
 387 *Henneguya* spp. (Cnidaria: Myxozoa) from cichlid fish in the Amazon basin cluster by  
 388 geographic origin, *Parasitol. Res.* 117 (2018) 849–859. [https://doi.org/10.1007/s00436-](https://doi.org/10.1007/s00436-018-5762-5)  
 389 018-5762-5
- 390 [33] P.D. Mathews, R.R.M. Madrid, O. Mertins, V.L.S. Rigoni, A.C. Morandini, A new  
 391 *Myxobolus* (Cnidaria: Myxosporea) infecting the ornamental catfish *Corydoras*  
 392 *schwartzi* from the Purus River in Brazil. *Eur. J. Taxon.* 620 (2020) 1–14.  
 393 <https://doi.org/10.5852/ejt.2020.620>
- 394 [34] S.D. Atkinson, P. Bartošová-Sojková, C.M. Whipps, J.L. Bartholomew,  
 395 Approaches for characterising myxozoan species, in: B. Okamura, A. Gruhl, J.L.  
 396 Bartholomew (Eds.), *Myxozoan Evolution. Ecology and Development*, Springer, Cham,  
 397 2015, pp.111–123.
- 398 [35] C. Azevedo, L. Corral, E. Matos, Light and ultrastructural data on *Henneguya*  
 399 *testicularis* n. sp. (Myxozoa, Myxobolidae), a parasite from the testis of the Amazonian  
 400 fish *Moenkhausia oligolepis*, *Syst. Parasitol.* 37 (1997)111–114.
- 401 [36] C. Azevedo, G. Casal, P. Matos, Â. Alves, E. Matos, *Henneguya torpedo* sp. nov.  
 402 (Myxozoa), a parasite from the nervous system of the Amazonian teleost  
 403 *Brachyhypopomus pinnicaudatus* (Hypopomidae), *Dis. Aquat. Org.* 93 (2011) 235–242.  
 404 <https://doi.org/10.3354/dao02292>

- 405 [37] M. Wang, Y. Zhao, C. Yang, The impacts of geographic and host species isolation  
 406 on population divergence of *Myxobolus lentisuturalis*, Parasitol. Res. 1189 (2019)  
 407 1061–1066. <https://doi.org/10.1007/s00436-019-06234-9>
- 408 [38] M.M. Carriero, E.A. Adriano, M.R.M. Silva, P.S. Ceccarelli, A.A.M. Maia,  
 409 Molecular phylogeny of the *Myxobolus* and *Henneguya* genera with several new South  
 410 American species, PLoS One 8 (9) (2013) 73713.  
 411 <https://doi.org/10.1371/journal.pone.0073713>.
- 412 [39] Y. Liu, A. Lövy, Z. Gu, I. Fiala, Phylogeny of Myxobolidae (Myxozoa) and the  
 413 evolution of myxospore appendages in the *Myxobolus* clade, Int. J. Parasitol. 49 (2019)  
 414 523-530. <https://doi.org/10.1016/j.ijpara.2019.02.009>
- 415 [40] N.L. Gunter, R.D. Adlard, Seven new species of *Ceratomyxa* Thélohan, 1892  
 416 (Myxozoa) from the gall-bladders of serranid fishes from the Great Barrier Reef,  
 417 Australia, Syst. Parasitol. 73 (2009) 1–11. <https://doi.org/10.1007/s11230-008-9162-6>
- 418 [41] M. Velasco, M. Videira, L.C.S. Nascimento, P. Matos, E.C. Gonçalves, E. Matos,  
 419 *Henneguya paraensis* n. sp. (Myxozoa; Myxosporea), a new gill parasite of the  
 420 Amazonian fish *Cichla temensis* (Teleostei: Cichlidae): morphological and molecular  
 421 aspects, Parasitol. Res. 115 (2016) 177–91787. <https://doi.org/10.1007/s00436-016-4916-6>
- 422 [42] P.D. Mathews, A.A. Maia, E.A. Adriano EA, *Henneguya melini* n. sp.  
 423 (Myxosporea: Myxobolidae), a parasite of *Corydoras melini* (Teleostei: Siluriformes) in  
 424 the Amazon region: morphological and ultrastructural aspects, Parasitol. Res. 115  
 425 (2016) 3599–3604.
- 426 [43] M. Videira, M. Velasco, R. Azevedo, R. Silva, G.P. Matos, E. Matos,  
 427 Morphological aspects of *Henneguya aequidens* n. sp. (Myxozoa: Myxobolidae) in  
 428 *Aequidens plagiozonatus* Kullander, 1984 (Teleostei: Cichlidae) in the Amazon region,

- 429 Brazil, Parasitol. Res. 114 (2015) 1159–1162. <https://doi.org/10.1007/s00436-014->  
 430 4295-9
- 431 [44] M.M. Feijo, S. Arana, P.S. Ceccarelli, E.A. Adriano, Light and scanning electron  
 432 microscopy of *Henneguya arapaima* n. sp. (Myxozoa: Myxobolidae) and histology of  
 433 infected sites in pirarucu (*Arapaima gigas*: Pisces: Arapaimidae) from the Araguaia  
 434 River, Brazil, Vet. Parasitol. 157 (2008) 59–64.  
 435 <https://doi.org/10.1016/j.vetpar.2008.06.009>
- 436 [45] C. Azevedo, G. Casal, P. Matos, E. Matos, (2008) A new species of Myxozoa,  
 437 *Henneguya rondoni* n. sp. (Myxozoa), from the peripheral nervous system of the  
 438 Amazonian fish, *Gymnorhamphichthys rondoni* (Teleostei), J. Eukaryot. Microbiol. 55  
 439 (2008) 229–234. <https://doi.org/10.1111/j.1550-7408.2008.00317.x>
- 440 [46] E. Matos, J. Tajdari, C. Azevedo, Ultrastructural studies of *Henneguya rhamdia* n.  
 441 sp. (Myxozoa) a parasite from the Amazon teleost fish, *Rhamdia quelen* (Pimelodidae),  
 442 J. Eukaryot. Microbiol. 52 (2005) 532–537.
- 443 [47] J.C. Eiras, J.C. Malta, A. Varela, G.C. Pavanelli, *Henneguya schizodon* n. sp.  
 444 (Myxozoa, Myxobolidae), a parasite of the Amazonian teleost fish *Schizodon fasciatus*  
 445 (Characiformes, Anostomidae), Parasite 11(2004) 169–173.
- 446 [48] G. Casal, E. Matos, C. Azevedo, Light and electron microscopic study of the  
 447 myxosporean, *Henneguya friderici* n. sp. from the Amazonian teleostean fish,  
 448 *Leporinus friderici*, Parasitology 126 (2003) 313–319.
- 449 [49] P. Vital, L. Corral, E. Matos, C. Azevedo, Ultrastructural aspects of the  
 450 myxosporean *Henneguya astyanax* n. Sp. (Myxozoa: Myxobolidae), a parasite of the  
 451 Amazonian teleost *Astyanax keithi* (Characidae), Dis. Aquat. Org. 53 (2003) 55–60.

[50] C. Azevedo, E. Matos, Fine structure of the myxosporean, *Henneguya curimata* n. sp., parasite of the Amazonian fish, *Curimata inornata* (Teleostei, Curimatidae), J. Eukaryot. Microbiol. 49 (2002) 197–200.

[51] C. Azevedo, E. Matos, *Henneguya malabarica* sp. nov. (Myxozoa, Myxobolidae) in the Amazonian fish *Hoplias malabaricus*. Parasitol. Res. 82 (1996) 222–224.

[52] C. Azevedo, E. Matos, *Henneguya adherens* n. sp. (Myxozoa, Myxosporea), parasite of the Amazonian fish, *Acestrorhynchus falcatus*. J. Eukaryot. Microbiol. 42 (1995) 515–518.

[53] E. Rocha, E. Matos, C. Azevedo, (1992) *Henneguya amazonica* n. sp. (Myxozoa, Myxobolidae), parasitizing the gills of *Crenicichla lepidota* Heckel, 1840 (Teleostei, Cichlidae) from Amazon river, Eur. J. Protistol. 28 (1992) 273–278.

## Legends

**Table 1.** Primers used in the amplification and sequencing of the 18S rDNA gene of *Henneguya multiradiatus* n. sp.

**Table 2.** Comparative data of *Henneguya multiradiatus* n. sp. with other *Henneguya* species parasites of Amazon fish. Spore dimensions, infection sites, and fish host are given. TL: total length; BL: body length; APCL: caudal appendage length; SW: spore width; ST: spore thickness; PCL: polar capsule length; PCW: polar capsule width; NCT: number of coils of polar tubules; –: no data. All measurements are range in  $\mu\text{m}$  and/or means  $\pm$  SD.

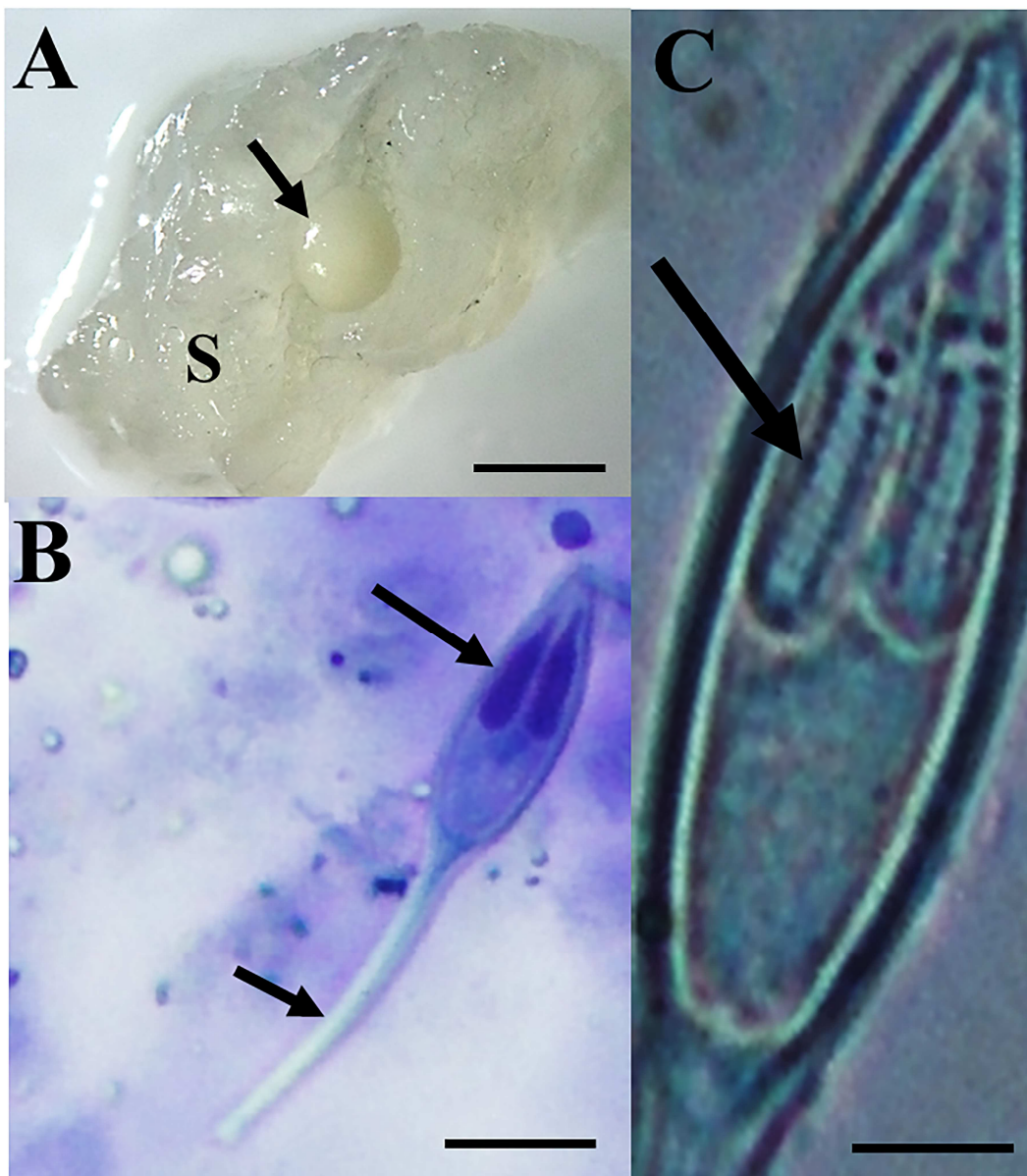
**Fig. 1.** Plasmodium and myxospores of *Henneguya multiradiatus* n. sp. from *Brochis multiradiatus*. A- Whitish plasmodium macroscopically visible (black arrow) in the serosa of the visceral cavity (S). Scale bar= 3 mm. B- Mature myxospore stained with

475 Ziehl-Neelsen showing two elongated equal polar capsules (black large arrow) and  
476 caudal appendage not bifurcated (black small arrow). Scale bar= 10  $\mu$ m. C: Myxospore  
477 showing polar coiled tubules (black arrow) perpendicular to the long axis of the polar  
478 capsule. Scale bar= 3  $\mu$ m.

479 **Fig. 2.** Schematic representation of myxospore of *Henneguya multiradiatus* n. sp. from  
480 *Brochis multiradiatus*. Scale bar= 7  $\mu$ m.

481 **Fig. 3.** Maximum likelihood phylogenetic tree based on partial 18S rDNA sequences  
482 containing *Henneguya multiradiatus* n. sp. and closely related myxozoans based on  
483 BLAST. GenBank accession numbers and host family are given in front of species.  
484 Bootstrap values above 50 are indicated at the nodes.

485

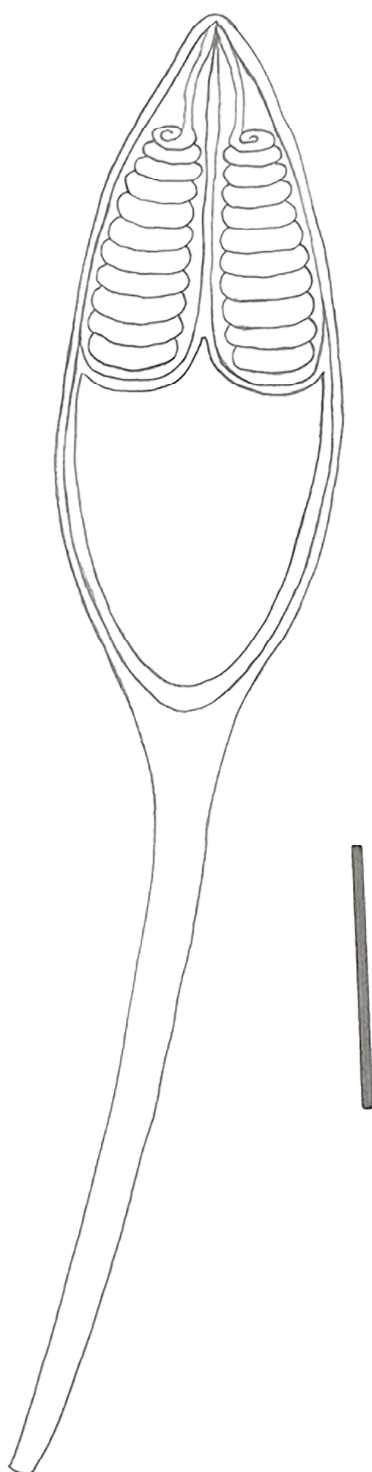


486

487

488

489

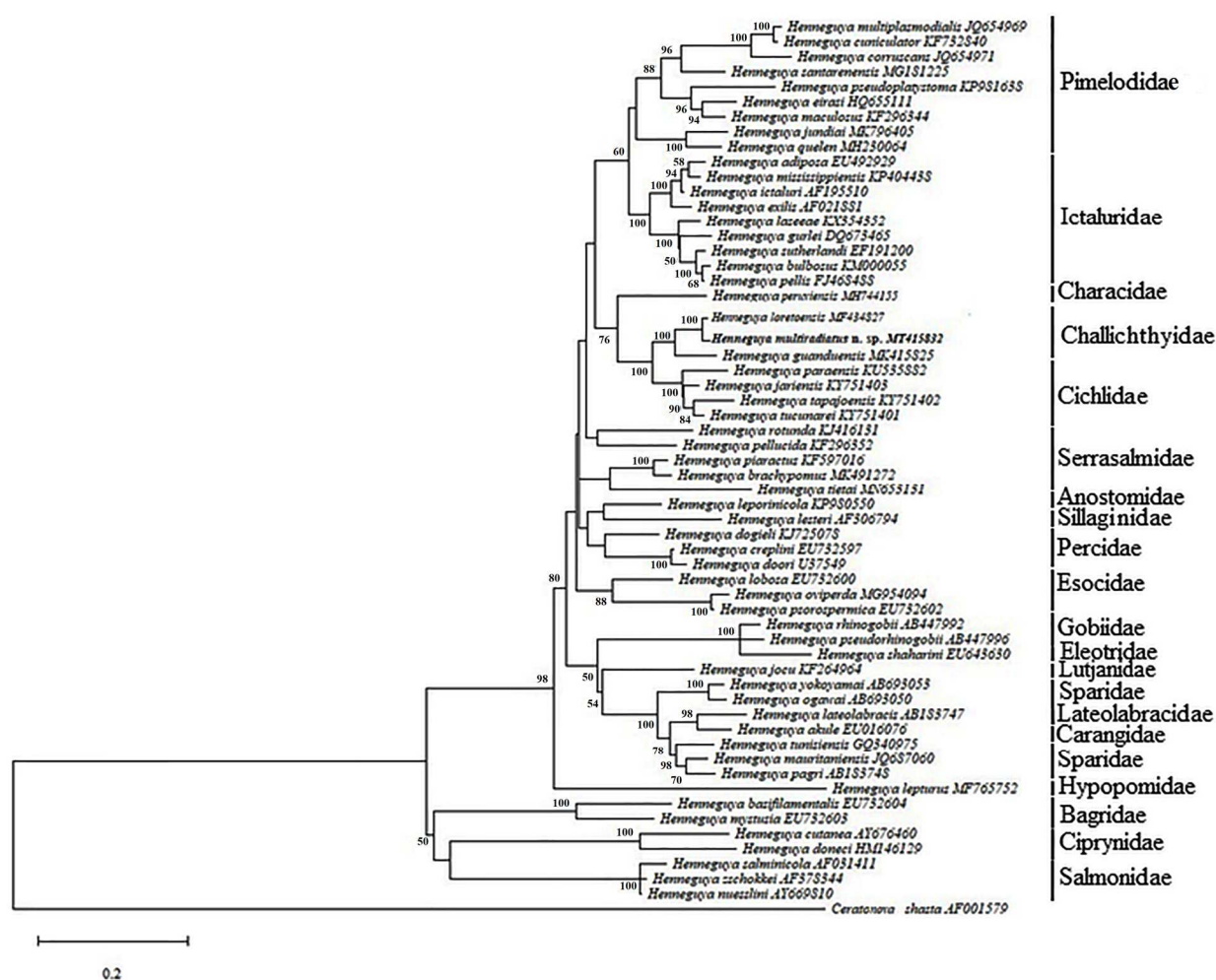


490

491

492





493

494

<b>Primers</b>	<b>Sequences (5'-3')</b>	<b>References</b>
ACT1r	AATTTACCTCTCGCTGCCA	Hallett and Diamant [20]
ERIB1	ACCTGGTTGATCCTGCCAG	Barta et al. [19]
ERIB10	CTTCCGCAGGTTACCTACGG	Barta et al. [19]
Myxgen4F	GTGCCTTGAATAAATCAGAG	Diamant et al. [21]
MC5	CCTGAGAAACGGCTACCACATCCA	Molnár et al. [22]
MC3	GATTAGCCTGACAGATCACTCCACGA	Molnár et al. [22]

Species	TL	BL	APCL	SW	ST	PCL	PCW	NCT	Site of infection	Fish species
<i>Henneguya multiradiatus</i> n. sp. [This study]	44.5 ± 0.6 (43.9–45.1)	18.7 ± 0.9 (16.8–19.6)	25.8 ± 0.6 (24.7–26.5)	7.1 ± 0.2 (6.6–7.4)	5.5 ± 0.3 (4.9–5.6)	9.1 ± 0.1 (8.8–9.4)	1.7 ± 0.1 (1.6–1.8)	10–11	Abdominal cavity serosa	<i>Brochis multiradiatus</i>
<i>Henneguya peruviansis</i> [30]	24.2 ± 1.3 (22.9–25.5)	13.4 ± 0.9 (12.5–14.3)	10.7 ± 1.2 (9.5–11.9)	3.9 ± 0.1 (3.8–4.0)	–	3.3 ± 0.2 (3.1–3.5)	1.6 ± 0.2 (1.4–1.8)	4–5	Gill filaments	<i>Hyphessobrycon loretoensis</i>
<i>Henneguya loretoensis</i> [29]	36.2 ± 0.2 (36.1–36.3)	14.3 ± 0.1 (14.2–14.4)	21.9 ± 0.1 (21.8–22)	5.1 ± 0.2 (4.9–5.3)	–	5.1 ± 0.2 (4.9–5.3)	2.4 ± 0.3 (2.1–2.7)	5	Gill filaments	<i>Corydoras leucomelas</i>
<i>Henneguya tucunareii</i> [32]	43.8 ± 4.1 (36.1–49.6)	14 ± 0.8 (12.1–15.7)	28.1 ± 4.3 (19.6–35.6)	6.1 ± 0.7 (4.9–7.8)	–	3.4 ± 0.5 (2.5–4.6)	1.98 ± 0.3 (1.3–2.6)	3–4	Gill filaments	<i>Cichla monoculus</i>
<i>Henneguya tapajoensis</i> [32]	54.6 ± 3.9 (47.2–62.2)	16.4 ± 1.2 (14.5–19.1)	39 ± 3.9 (31.7–46.5)	7 ± 0.4 (5.7–9.3)	5 ± 0.1 (4.8–5.1)	4.2 ± 0.5 (2.9–5.0)	2.1 ± 0.4 (1.5–2.8)	4–5	Gill filaments	<i>Cichla pinima</i>
<i>Henneguya jariensis</i> [32]	46.7 ± 1.5 (43.9–49.2)	13.4 ± 0.7 (11.9–14.6)	33.1 ± 1.7 (30.2–37.0)	6.5 ± 0.5 (4.9–7.3)	–	4 ± 0.3 (3.4–4.3)	2 ± 0.1 (1.7–2.4)	4	Fins	<i>Cichla monoculus</i>
<i>Henneguya paraensis</i> [41]	42.3 ± 0.3 (41.6–42.9)	12.8 ± 0.42 (12.3–13.2)	29.5 ± 0.73 (28.7–30.2)	8.6 ± 0.32 (8.18–8.92)	–	7.4 ± 0.16 (6.67–7.5)	2.6 ± 0.1 (2.52–2.68)	5–7	Gill filaments	<i>Cichla temensis</i>
<i>Henneguya melini</i> [42]	40.8 ± 0.3 (40.3–41.1)	15.5 ± 0.2 (15.3–15.7)	25.3 ± 0.1 (25.2–25.4)	4.7 ± 0.1 (4.6–4.8)	–	4.8 ± 0.5 (4.3–5.3)	1.7 ± 0.3 (1.4–2)	5–6	Gill filaments	<i>Corydoras melini</i>
<i>Henneguya aequidens</i> [43]	41 ± 1.5	15 ± 0.9	27 ± 0.6	6 ± 0.8	–	3 ± 0.3	3 ± 0.3	4–6	Gill filaments	<i>Aequidens plagiozonatus</i>
<i>Henneguya torpedo</i> [36]	48.62 ± 0.51 (48.3–48.9)	28.53 ± 0.36 (28.3–30.1)	19.64 ± 0.44 (19.2–19.9)	7.25 ± 0.31 (7–7.5)	3.06 ± 0.2 (2.9–3.1)	6.41 ± 0.26 (6.3–6.6)	1.84 ± 0.19 (1.7–1.9)	5–6	Brain and spinal cord	<i>Brachyhypopomus pinnicaudatus</i>
<i>Henneguya arapaima</i> [44]	51.6 ± 3.4 (48.4–53.1)	14.2 ± 0.8 (13.5–15.2)	38.3 ± 2.9 (38–41.2)	5.7 ± 0.5 (5.1–6.1)	4.9 ± 0.2 (4.7–5.3)	6.5 ± 0.2 (6.3–6.8)	6.3 ± 0.1 (6.3–6.8)	5	Gill arch	<i>Arapaima gigas</i>
<i>Henneguya rondoni</i> [45]	17.7 (16.9–18.1)	7 (6.8–7.3)	10.7 (10.3–11)	3.6 (3–3.9)	2.5 (2.2–2.8)	2.5 (2.2–2.8)	0.85 (0.79–0.88)	6–7	Lateral nerves	<i>Gymnorhamphichthys rondoni</i>
<i>Henneguya rhamdia</i> [46]	50 ± 1.8	13.1 ± 1.1	36.9 ± 1.6	5.2 ± 0.5	–	4.7 ± 0.4	1.1 ± 0.2	10–11	Gill filaments	<i>Rhamdia quelen</i>
<i>Henneguya schtzodon</i> [47]	28.9 (27–30)	13.1 (12–14)	16.3 (15–17)	3.3 (3–4)	–	5.4 (5–6)	1.3 (1–1.5)	8–10	Kidney	<i>Schtzodon fasciatum</i>
<i>Henneguya friderici</i> [48]	33.8 (28.7–39.3)	10.4 (9.6–11.8)	23.3 (19.1–28.7)	5.7 (4.8–6.6)	4.9	4.9 (4.25–5.9)	2.1 (1.59–2.62)	7–8	Gut, gill, kidney and liver	<i>Leporinus friderici</i>
<i>Henneguya astyanax</i> [49]	47.8 ± 0.71	15.2 ± 0.77	32.6 ± 1.11	5.7 ± 0.71	4.2 ± 0.31	5.0 ± 0.13	1.5 ± 0.07	8–9	Gill filaments	<i>Astyanax bimaculatus</i>
<i>Henneguya curimata</i> [50]	35.4 (4.2–36)	16.6 (16–17.4)	19.1 (18.3–19.9)	6.2 (5.8–6.6)	–	3.3 ± 0.02 (2.7–3.6)	1.5 ± 0.04 (1.1–1.9)	10–11	Kidney	<i>Curimata inornata</i>
<i>Henneguya testicularis</i> [35]	27.5 (27–28.5)	14 (14–14.5)	13.5 (13–14.5)	6.5 (6–6.5)	–	9 (8.5–9.5)	2 (2–2.5)	12–13	Testicle	<i>Moenkhausia oligolepis</i>
<i>Henneguya malabarica</i> [51]	28.3 (26.6–29.8)	12.6 (11.8–13.1)	17.1 (16.2–18.9)	4.8	–	3.7 (3.0–4.3)	1.8 (1.6–2.2)	6–7	Gill filaments	<i>Hoplias malabaricus</i>

<i>Henneguya adherens</i> [52]	32.3 (30.7–35.1)	12.4 (10.5–13.8)	20.5 (18–21.7)	5.8 (5.1–6.5)	–	3.1 (2.8–3.5)	1.2 (1–1.6)	3–4	Gill filaments	<i>Acestrorhynchus falcatus</i>
<i>Henneguya amazonica</i> [53]	59.3 ± 0.56 (55–65.9)	13.9 ± 0.16 (11.5–14.9)	45.4 ± 0.61 (41.7–52.1)	5.7 ± 0.06 (5.2–6.3)	–	3.3 ± 0.02 (2.7–3.6)	1.5 ± 0.04 (1.1–1.9)	6	Gill lamellae	<i>Crenicichla leplota</i>

---

