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Henneguya (Cnidaria: Myxobolidae) species infecting *Oligosarcus jenynsii* (Characiformes: Characidae) in a Neotropical shallow lake from Argentina: morphological and molecular characterisation

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Abstract: Two previously undescribed myxozoan species, *Henneguya sardellae* sp. n. and *H. margaritae* sp. n., found infecting connective tissues of the Neotropical characid fish *Oligosarcus jenynsii* (Günther) from Argentina are morphologically and molecularly characterised. Mature spores of *H. sardellae* sp. n. are ellipsoid, with two, straight and visibly fused caudal appendages cleaved at its blunt terminal end; measuring 33.5 ± 1.2 (30.9–35.5) µm in total length, spore body 17.5 ± 0.6 (16.3–18.6) µm, 7.8 ± 0.4 (7.0–8.8) µm wide and 6.9 ± 0.2 (6.6–7.2) µm thick, with two elongated, unequally-sized polar capsules situated at anterior end, and 11–13 turns of polar tubules. Mature spores of *H. margaritae* sp. n. are pyriform, with two caudal appendages visible fused together and much longer than spore body, with unequal endings; measuring 35.9 ± 2.8 (29.2–40.7) µm in total length, spore body 11.5 ± 0.9 (9.2–13.0) µm long, 5.8 ± 0.4 (5.1–6.7) µm wide and 5.5 ± 0.2 (5.1–5.8) µm thick, with two polar capsules similar in size, pyriform polar capsules containing polar tubules with 4–5 coils. Both species showed a membraneous sheath surrounding the spore body and caudal appendages; in *H. sardellae* sp. n. this feature can deploy laterally. Phylogenetic analyses based on SSU rDNA sequences showed that *H. sardellae* sp. n. and *H. margaritae* sp. n. clustered with other myxobolids parasitising Characiformes in Brazil, Cichliformes in Mexico and Cyprinodontiformes in Mexico and the United States. The description of these two new species of *Henneguya* as the first described species of the genus that parasitise freshwater fish in Argentina highlights the importance of further research on the diversity and distribution of myxozoans in this region.

Keywords: Myxozoa, fish parasite, fresh water, South America

Myxozoa Grassé, 1970 is a highly diverse and widely distributed group of cnidarian endoparasites with more than 2,600 species described to date (Okamura et al. 2018), mainly from freshwater and marine fish (Kent et al. 2001, Lom and Dyková 2006). Members of the Myxobolidae Thélohan, 1892 comprise nearly half of all known myxozoan species diversity (Liu et al. 2019), and stand out for having been studied due to their association with diseases in economically important cultured and wild fish species (Lom and Dyková 2006).

This family includes *Henneguya* Thélohan, 1892 and *Myxobolus* Bütschli, 1882 as the most comprehensively studied genera, and 11 others less diversified genera, namely *Dicauda* Hoffman et Walker, 1978; *Hennegoides* Lom, Tonguthai et Dyková, 1991; *Laterocaudata* Chen et Hsieh, 1984; *Neohenneguya* Tripathi, 1953; *Neothelohanellus* Das et Haldar, 1986; *Phlogospora* Qadri, 1962; *Spirosuturia* Chen et Hsieh, 1984; *Tetrauronema* Wu, Wang et Jiang, 1988; *Thelohanellus* Kudo, 1933; *Trigonosporus* Hoshina, 1952; and *Unicauda* Davis, 1944 (Fiala et al. 2015). Myxobolid genera are largely distinguished by the number of polar capsules, shape of the sutural line, and the presence, number and nature of myxospore caudal projection(s) (Lom and Dyková 2006, Fiala et al. 2015). However, the classical spore morphology-based taxonomic classification of Myxobolidae is not supported by DNA sequence-based phylogenies and has led to a discussion on the validity of some of its genera resolved as non-mono-

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phyletic (Kent et al. 2001, Liu et al. 2019, Zhang et al. 2019). Nonetheless, genera within the family Myxobolidae remain valid until molecular data are available for their type species (Liu et al. 2019).

The genus *Henneguya* includes myxobolid species with ellipsoid, spindle-shaped or rounded spores in valvular view and biconvex in sutural view, with a caudal projection as an extension of each smooth shell valve, and two polar capsules typically elongated (Lom and Dyková 2006). Currently, it encompasses more than 250 nominal species (Rangel et al. 2023), mainly as histozoic parasites of the gills of freshwater fish (Lom and Dyková 2006).

In the Neotropical realm, including freshwater habitats of South America, Central America, the Caribbean islands, and southern North America, species of *Henneguya* are among the most frequently encountered and thoroughly studied myxozoans (Müller et al. 2023). Notably, among the 79 Neotropical species of *Henneguya* described to date (Figueredo et al. 2023, Müller et al. 2023, Rangel et al. 2023), 77 have been registered as parasites of Brazilian fish (Eiras 2002, Eiras and Adriano 2012, Range et al. 2023), and nearly 56% of these records are associated with fish of the order Characiformes.

Within this fish order, the endemic family Characidae includes key components of Neotropical freshwater ecosystems (Oliveira et al. 2011). One of the most common and widely distributed characid fish in this region is *Oligosarcus jenynsii* (Günther), commonly known as 'dientudo', a generalist carnivorous fish which lives in rivers, streams and ponds from Rio Grande do Sul, Brazil to the Rio Colorado River, Argentina (Liotta 2005, Wendt et al. 2019).

Based on biological, morphological and molecular characterisation of the partial sequences of the SSU rDNA gene, the present study describes two new species of *Henneguya*, parasites of *O. jenynsii* (Characidae), from a shallow eutrophic lake in the Pampasic region of Argentina.

MATERIALS AND METHODS

Fish and parasite collection and processing

A total of 158 specimens of *Oligosarcus jenynsii* were collected in the freshwater shallow lake Nahuel Rucá, Buenos Aires Province, Argentina (37.6200S, 57.4300W) between March 2010 and October 2012. Fish sampling was performed using beach seine net (20 m). Fish captured were euthanised by an overdose of benzocaine solution as suggested by international guidelines (Barker et al. 2002). Fish were kept fresh on ice until dissected and examined using a stereoscope microscope. Any tissue lesion or cyst observed, as well as gills filaments and fins, smears of brain, liver and kidney, and contents of gall and urinary bladders were examined with the aid of a light microscope (LM) equipped with differential interference contrast (DIC). Samples containing myxosporeans were studied under light microscope for morphological characterisation and then fixed in 96% ethanol for molecular characterisation or 10% formaldehyde solution for subsequent histological analyses.

Morphological analysis

Digital microphotographs of fresh myxospores observed under differential interference contrast (DIC) were taken at 100× magnification using the Leica DM2500 stereoscopic microscope equipped with a Leica DFC295 camera. Myxospores were measured in ImageJ v.1.45 s (Rueden et al. 2017) following the guidelines proposed by Lom and Arthur (1989) for species descriptions of. All measurements are given in micrometres (µm) as a mean ± standard deviation (SD), followed by range in parentheses.

Histological section and Giemsa stain

Histological sections were made from tissues containing myxosporidian cysts, fixed in formalin and dehydrated for embedding in paraffin blocks. Histological sections were made according to standard histological techniques and stained with haematoxylin-eosin (Biopack, Buenos Aires, Argentina). Myxospores were air-dried, stained with Giemsa (Biopack), and deposited in the Other Invertebrate Collection, Museo de La Plata, La Plata, Argentina.

Molecular analysis

DNA extraction, PCR amplification and sequencing

Selected samples which were visually positive for myxosporeans were fixed in 96% ethanol and preserved at 4 °C for molecular characterisation by sequencing of the SSU rDNA. Each sample was pelleted at 3,000 rpm for 3 min and washed with DNAse-free water twice to remove ethanol. Total genomic DNA was extracted from the infected tissues (fins, stomach wall, visceral adipose tissue, and kidney) using the commercial DNeasy Blood and Tissue Kit (Qiagen Inc., Hilden, Germany) following the manufacturer's specifications. Partial SSU rDNA gene sequences were obtained by assembling overlapping parts amplified with both universal eukaryote and myxozoan-specific primers. Thereby, the reaction with 18e (Hillis and Dixon 1991) and 18R (Whipps et al. 2003) primers in the first PCR was followed by nested PCRs with Myxgp2f (Kent et al. 1998) and ACT1r (Hallett and Diamant 2001), MyxospecF and MyxospecR (both Fiala 2006) or with Myxgen4F (Diamant et al. 2004) and 18R for the second round of amplifications.

Polymerase chain reactions (PCRs) of the SSU rDNA were conducted in a 20 µl reaction volume comprising: 1 µl template DNA, 20 pmol of each primer, 200 µM of dNTPs, 1x EasyTaq® Buffer (Transgen Biotech, China) with a final $MgCl_2$ concentration of 1.5 mM, 1 unit of EasyTaq® DNA Polymerase (Transgen Biotech, China) in ultrapure water. Reactions were performed in a programmable thermal cycler (Techne ^{3}Prime thermal cycler, UK) with PCR cycling parameters used for the primary/nested PCR set as follows: initial denaturation at 95 °C for 3 min, followed by 30 cycles of amplification at 95 °C for 1 min, 62 °C/58 °C for 1 min, 72 °C for 2 or 1 min and followed by a terminal extension at 72 °C for 10 min. All amplified PCR products were visualised by 1% agarose gel electrophoresis, purified using QIAquick PCR Purification Kit (Qiagen Inc.) following the manufacturer's protocol and sent to Macrogen Inc. (Seoul, South Korea) for DNA sequencing using ACT1r, MyxospecF and 18R primers.

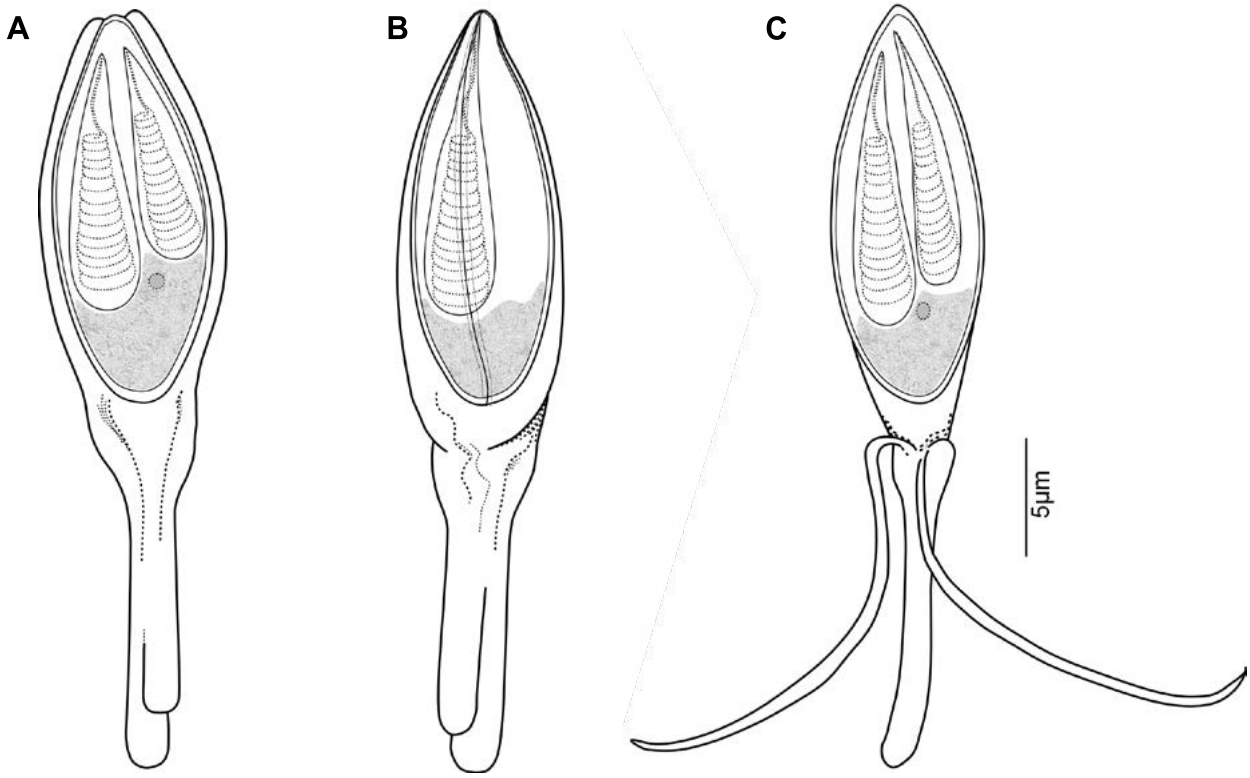

Fig. 1. *Henneguya sardellae* sp. n. parasitising the fins of *Oligosarcus jenynsii* (Günther) from Argentina. **A** – valvular view; **B** – sutural view; **C** – valvular view, membraneous sheath deployed laterally.

Sequence assembly, alignment and phylogenetic analyses

The overlapping partial sequences of the SSU rDNA were assembled into contigs in SeqMan II v5.05 (DNASTAR Inc., Madison, Wisconsin, USA). An alignment based on SSU rDNA sequences was created in the MAFFT v7.49 (Katoh et al. 2002) using the E-INS-i strategy and default parameters (gap opening penalty: 1.53 and gap extension penalty 0.0) implemented in Geneious Prime 2019.0.4 (Kearse et al. 2012). The alignment contained newly obtained sequences, almost all sequences of taxa of the subclade I in the phylogeny of Myxobolidae (Liu et al. 2019), and other closely related sequences retrieved from GenBank selected by using Basic Local Alignment Search Tool (BLAST) of the National Center for Biotechnology Information (NCBI). *Myxidium lieberkuehni* Bütschli, 1882 (Acc. No. X76638) and *Zschokkela nova* Klokacewa, 1914 (Acc. No. DQ377690) were set as the outgroup. The alignment was edited manually by removal of ambiguous aligned regions.

Phylogenetic analyses were performed using maximum likelihood (ML) and Bayesian inference (BI). ML was done in the RAxML v7.0.3. (Stamatakis 2006) implemented in Geneious Prime 2019.0.4 (Kearse et al. 2012) with GTR Γ model of evolution selected in jModelTest2 (Posada 2008) and clade supports were assessed with bootstrapping of 1,000 replicates with random sequences additions. BI was conducted in MrBayes v3.0 (Ronquist and Huelsenbeck 2003) implemented in Geneious Prime 2019.0.4 (Kearse et al. 2012) using the GTR Γ model of evolution. Posterior probabilities were estimated over 1,000,000 generations via two independent runs of four simultaneous Markov chain Monte Carlo chains with every 100th tree saved.

RESULTS

Polysporic plasmodia and mature myxospores consistent with the morphological diagnosis of the genus *Henneguya* were observed infecting the fins, visceral adipose tissue, stomach wall and kidneys of fish examined. Morphological and molecular analyses revealed the presence of two new species of *Henneguya* parasitising *Oligosarcus jenynsii*.

Henneguya sardellae Rossin et Cantatore sp. n.

Figs. 1, 2, 5

ZooBank number for species:
urn:lsid:zoobank.org:act:CD3CF578-DDBB-48ED-BC8B-849F30CB9AC0

Vegetative stages (based on 3 plasmodia) (Fig. 2A,B): Plasmodia spherical to oval, 283–351 long. In histological section, cysts show thin wall and numerous mature and developing spores inside. No significant inflammatory response present.

Mature ospores (Figs. 1A–C, 2C–F, 5A): Typical mature spore biconvex, ellipsoid, with two, straight caudal appendages, visibly fused together and cleaved at its blunt terminal end, arising terminally at posterior end of spore body. Shell valves symmetrical, compressed parallel to sutural plane. Suture line straight, inconspicuous, running in the same plane as polar capsules. In valvular view, membraneous sheath surrounds spore body and caudal appendages that can be deployed laterally at level of spore body.

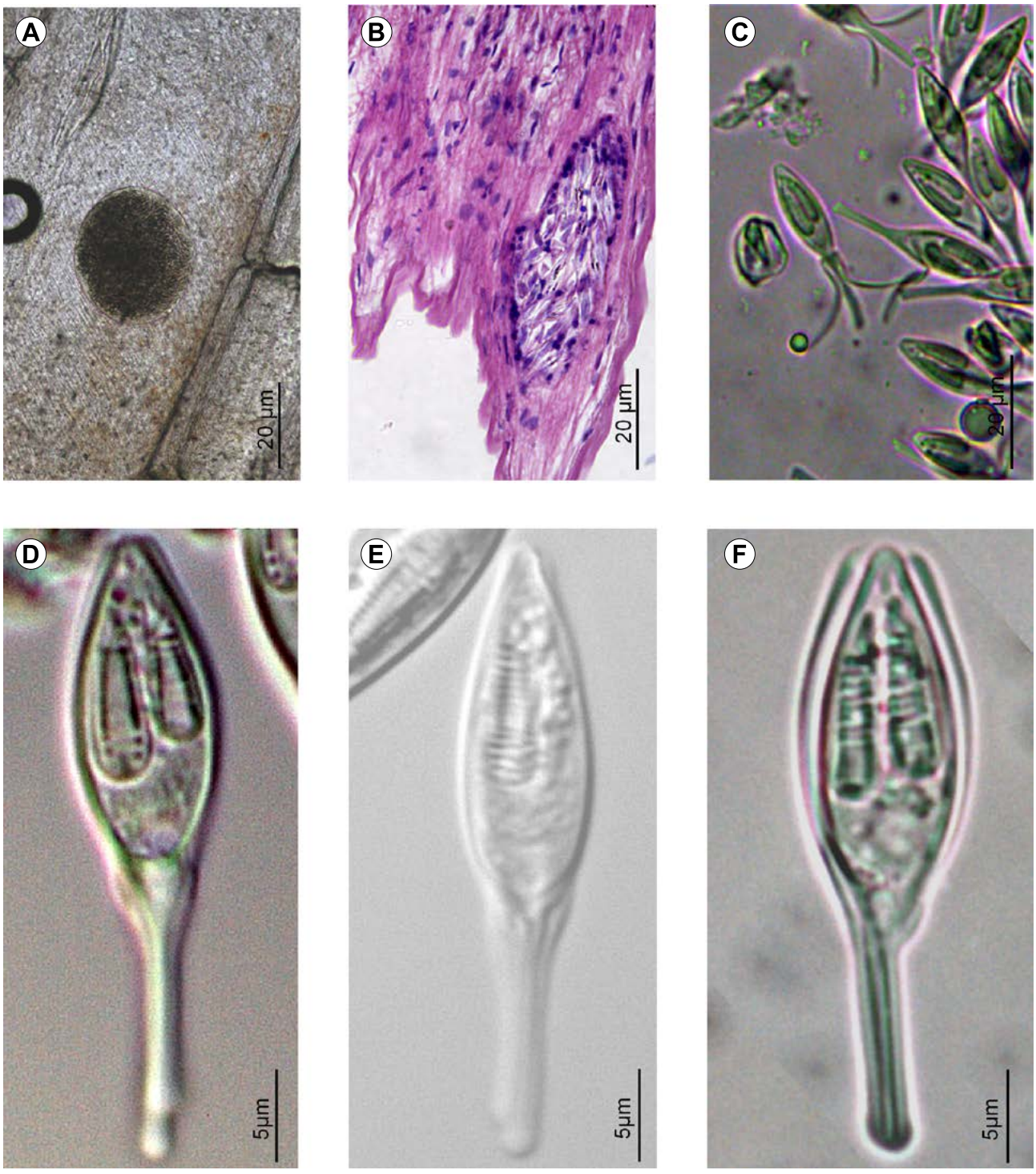

Fig. 2. *Henneguya sardellae* sp. n. parasitising *Oligosarcus jenynsii* (Günther) from Argentina. **A** – plasmodia; **B** – histological section of plasmodia; **C** – mature spore with membraneous sheath deployed laterally; **D** – mature spore, valvular view; **E** – mature spore, sutural view; **F** – mature spore with visible membraneous sheath.

Two elongated, unequally-sized polar capsules situated at anterior end. Polar tubules coiled perpendicular to longitudinal axis of polar capsules. Sporoplasm occupying almost 1/3 of spore body with only one nucleus observed.

Measurements of mature myxospores (based on 30 fresh spores otherwise stated; from interlepidotrichial region of fins): Total length 33.5 ± 1.2 (30.9–35.5). Spore body 18.5 ± 1.1 (16.5–21.0) long, 7.8 ± 0.4 (7.0–8.8) wide and 6.9 ± 0.2 (6.6–7.2, n = 4) in thickness, representing 55% of total length. Caudal appendage 15.1 ± 1.6 (10.8–17.2) long and 2.3 ± 0.2 (2.0–2.8, n = 6) maximum width. Larger polar capsule 10.4 ± 1.0 (9.0–13.2) long and 2.8 ± 0.5 (2.2–3.7, n = 16) wide, smaller polar capsule 9.5 ± 1.0 (7.6–11.5, n = 29) long and 2.6 ± 0.4 (2.1–3.4) width. Number of turns of polar tubule 11–13 (n = 7).

Measurements of mature spores (based on 30 fresh spores unless otherwise stated; from connective tissue of stomach wall): Total length 32.2 ± 1.4 (30.5–35.4). Spore body 17.5 ± 0.6 (16.3–18.6) long, 7.8 ± 0.5 (6.7–8.7) wide and 6.5 (5.7–7.6, n=7) in thickness, representing 54% of total length. Caudal appendage 14.6 ± 0.8 (12.9–16.5) long and 1.7 (1.4–2.2, n = 7) maximum width. Larger polar capsule 9.5 ± 0.5 (8.7–10.7) long and 2.5 ± 0.2 (2.1–3.0) width, smaller polar capsule 9.3 ± 0.41 (8.4–10.1) long and 2.4 ± 0.2 (2.0–2.9) wide. Number of turns of polar tubule 10–12 (n = 8).

Type host: Characin *Oligosarcus jenynsii* (Günther) (Characiformes: Characidae); vernacular name 'dientudo'.

Type locality: Nahuel Rucá shallow lake (37.6200S, 57.4300W), Buenos Aires Province, Argentina.

Site of infection: Interlepidotrichial region of fins, connective tissue of stomach wall, visceral adipose tissue.

Prevalence: 18.4% (29 infected out of 158 examined fish).

Type material: Syntype MLP Oi-4421 (Giemsa-stained slide) and voucher MLP Oi-4422 (myxospores in 96% ethanol) deposited in the Invertebrate Collection, Museo de La Plata, La Plata, Argentina.

GenBank accession numbers: SSU rDNA sequences available in the GenBank database under the accession numbers OQ822167 (1,696 bp), OQ822168 (1,710 bp), OQ822169 (889 bp), OQ822170 (898 bp) and OQ822171 (893 bp).

Etymology: The specific epithet is dedicated to Norma H. Sardella, a passionate university professor and pioneering Argentine female parasitologist who began the studies of myxozoans in the South Atlantic Ocean.

Remarks. Among myxobolids that have been described so far, the morphology of the spores, particularly the presence of a sheath surrounding the body capsules and appendages, as well as the visibly fused distinct spore appendages, spore metrics (i.e., length, width and thickness whenever available), and molecular characterisation, reveal that *Henneguya sardellae* sp. n. is most closely related to *H. polarislonga* Jorge, Dias Vieira, Zago, Franceschini et da Silva, 2022, a parasite found on the gills of *Astyanax lacustris* (Lütken) (Characiformes: Characidae) from streams of the Middle Parana River, Brazil (Jorge et al. 2022).

However, the new species can be distinguished from *H. polarislonga* by having larger and wider spore bodies (16.5–21.0 µm vs. 13.3–18.1 µm in length, 7.0–8.8 µm vs. 5.8–7.9 µm in width), unequal and larger polar capsules (with larger polar capsule measuring: 9.0–13.2 µm in length and 7.6–11.5 µm in width, and smaller polar capsule measuring: 2.2–3.7 µm in length and 2.1–3.4 µm in wide vs. 5.7–12.1 µm in length and 1.2–1.9 µm in width), and shorter caudal appendages (10.8–17.2 µm vs. 10.9–19.2 µm) (Table 1).

In contrast, *H. testicularis* Azevedo, Corral et Matos, 1997, a parasite found in the testes of *Moenkhausia oligolepis* (Günther) (Characiformes: Characidae) in the Amazon River, Brazil exhibits ellipsoidal asymmetrical valves and a tail enveloped by a homogeneous sheath consisting of two electron-light layers (Azevedo et al. 1997). This structural feature bears a resemblance to that observed in *H. sardellae* sp. n.. Unfortunately, no DNA sequences are available for *H. testicularis*. However, based on spore body metrics, both species can be clearly distinguished.

In this regard, *H. sardellae* sp. n. differs from *H. testicularis* by having a larger total length, wider and thicker spore body (30.9–35.5 µm vs. 27.0–28.5 µm in length, 16.5–21.0 µm vs. 14.0–14.5 µm in wide; 7.0–8.8 µm vs. 6.0–6.5 µm in thickness), and larger polar capsules (larger polar capsule: 9.0–13.2 × 2.2–3.7 µm, and smaller polar capsule: 7.6–11.5 × 2.1–3.4 µm vs. 8.5–9.5 × 2.0–2.5 µm) (Table 1). Moreover, *H. sardellae* sp. n. can be differentiated from the previously mentioned species based on the specific host tissues it infects.

Henneguya margaritae Rossin et Cantatore sp. n.

Figs. 3–5

ZooBank number for species:
urn:lsid:zoobank.org:act:8BB7CF7A-CACB-4E93-8276-D7C72B49FDBC

Vegetative stages: Not observed.

Mature spores (Figs. 3A,B, 4A,B, 5B): Typical mature spore pyriform with two caudal appendages visibly fused together, extending posteriorly from fully developed spore. Caudal appendages much longer than spore body, with cleaved distal end of unequal ending. Suture line straight, running in same plane as polar capsules. In valvular view, membraneous sheath surrounding spore body. Two pyriform polar capsules, similar in size, situated in anterior end of spore body, containing polar tubule coiled perpendicular to longitudinal axis. Sporoplasm occupying almost half of spore body, with only one nucleus observed.

Measurements of mature spores (based on 30 fresh spores unless otherwise stated): Total length 35.9 ± 2.8 (29.2–40.7). Spore body 11.5 ± 0.9 (9.2–13.0) long, 5.8 ± 0.4 (5.1–6.7) wide and 5.5 (5.1–5.8, n=12) in thickness. Caudal appendages 24.5 ± 2.8 (19.0–30.0) long and 2.7 (2.3–3.2, n = 18) maximum width. Polar capsules 5.3 ± 0.5 (4.9–6.5) long and 2.2 ± 0.2 (1.8–2.8) wide. Number of turns of polar tubule 4–5 (n = 8).

Type host: Characin *Oligosarcus jenynsii* (Günther) (Characiformes: Characidae); vernacular name 'dientudo'.

Type locality: Nahuel Rucá shallow lake (37.6200S, 57.4300W), Buenos Aires Province, Argentina.

Site of infection: Connective tissue of kidney.

Prevalence: 37.9% (60 infected out of 158 examined fish).

Type material: Syntype MLP Oi-4423 (Giemsa-stained slide) deposited in the Invertebrate Collection, Museo de La Plata, La Plata, Argentina.

GenBank accession numbers: SSU rRNA gene sequences available in the GenBank database under the accession numbers OQ822164 (879 bp), OQ822165 (881 bp), OQ822166 (858 bp).

Etymology: The specific epithet is named in honour to the late Margarita Ostrowski de Núñez, in recognition of her significant contributions to the knowledge of freshwater parasites, and for her pioneering role in the development of parasitology in Argentina.

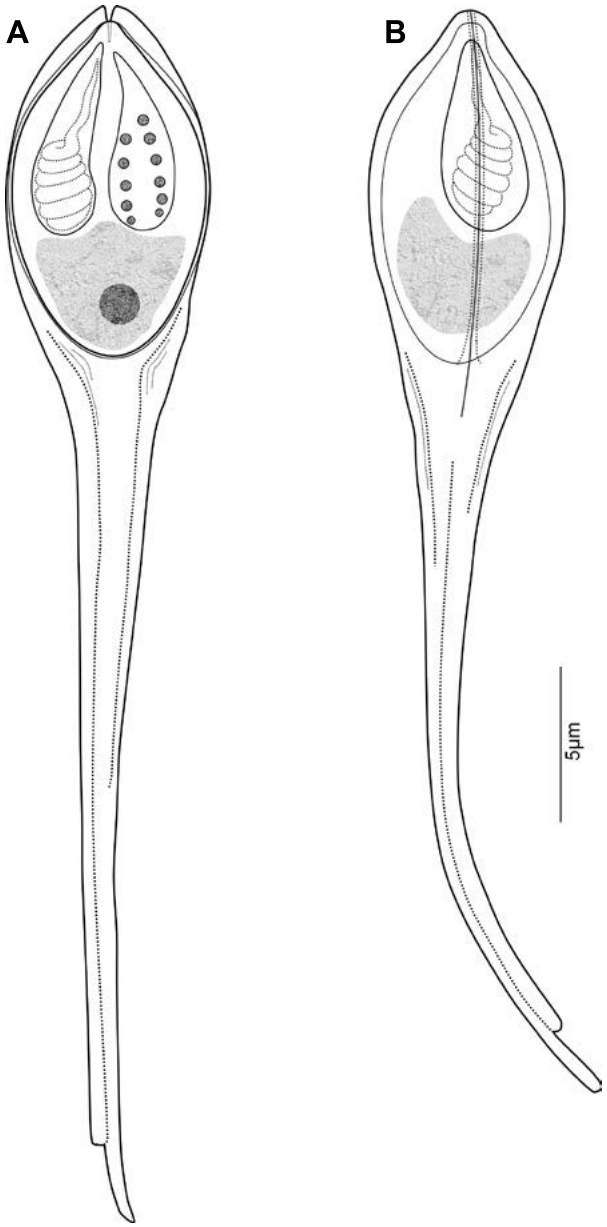

Fig. 3. *Henneguya margaritae* sp. n. parasite of kidneys of *Oligosarcus jenynsii* (Günther) from Argentina: **A** – valvular view; **B** – sutural view.

Remarks. Among the described myxobolids, similarities in the general morphology of spores, which includes the observation of apparent fused caudal appendages and the presence of sheath surrounded body capsules, as well as spore measurements encompassing length, width and thickness whenever available, the new species most closely resembles three previously described species, *Henneguya adherens* Azevedo et Matos, 1995, *H. malabarica* Azevedo et Matos, 1996 and *H. pellucida* Adriano, Arana et Cordeiro 2005, parasites of gill filaments of the Amazonian fishes *Acestrorhynchus falcatus* (Bloch) (Characiformes: Characidae) and *Hoplias malabaricus* (Bloch) (Characiformes: Erythrinidae), and the serous membrane of the viscera of *Piaractus mesopotamicus* (Holmberg) (Characiformes: Serrasalmidae), respectively.

However, *Henneguya margaritae* sp. n. can be differentiated from the above mentioned species by presenting a larger caudal appendage (19.0–30.0 µm vs. 18.0–21.7 µm in *H. adherens* and 16.2–18.9 µm in *H. malabarica*), wider spore body (5.1–6.7 µm vs. 4.1 ± 0.4 µm in *H. pellucida*) and fewer filaments coils (4–5 vs. 6–7 in both *H. malabarica* and *H. pellucida*). In contrast to *H. adherens*, which possesses unequal polar capsules, the newly described species exhibits polar capsules of equal size, resembling *H. malabarica*. In addition, *H. margaritae* sp. n. has the largest polar capsules (Table 1).

Based to the phylogenetic results obtained and the observed morphological similarity, *H. margaritae* sp. n. most closely resembles two Brazilian, one-tailed myxobolid species, namely *Unicauda whippsi* Vidal, McIntosh et Luque, 2018, a parasite of the kidney of *Astyanax altiparanae* Garutti et Britski (Characiformes: Characidae), and *U. tavaresii* da Silva, Maciel, da Silva, Matos Guerreiro, Matos et Hamoy, 2020, a parasite found in the circumorbital region of the ocular conjunctiva of *Moenkhausia grandisquamis* (Müller et Troschel) (Characiformes: Characidae) and *Triportheus angulatus* (Spix et Agassiz) (Characiformes: Triportheidae) (Vidal et al. 2018, da Silva et al. 2020).

Henneguya margaritae sp. n. is characterised by having equal polar capsules instead of unequal polar capsule like *U. whippsi* and by having fewer coils of polar fila-

Table 1. Morphometric comparison of *Henneguya sardellae* n. sp. and *H. margaritae* with spores from different species of the genus *Henneguya* with a fused caudal appendages and a sheat surrounded body capsule and species of *Unicauda* closely in the phylogenetic analysis.

Species	TL	BL	BW	TaL	PCL	PCW	FC	VT
Henneguya adherens	32.3	12.4	5.8	20.5	3.1	1.2	3–4	unequal
H. malabarica	28.3	12.6	4.8	17.1	3.7	1.8	6–7	equal
H. pellucida	33.3 ± 1.5	11.4 ± 0.3	4.1 ± 0.4	24.1 ± 1.5	4.0 ± 0.4	1.6 ± 0.2	6–7	equal
Unicauda tavaresii	–	13.2–16.5	4.5–5.5	47–57	4.2–5.8	1.1–1.8	5–7	equals
U. whippsi	26.8–44.0	10.0–12.0	4.7–7.2	16.2–26.2	3.4–6.7	1.4 –2.7	7–9	unequals
H. margaritae sp. n.	29.2–40.7	9.2–13.0	5.1–6.7	19.0–30.0	4.9–6.5	1.8–2.8	4–5	equal
H. testicularis	27.5	14.0	6.5	13.5	9.0	2.0	12–13	unequal
H. polarislonga	27.5–37.2	13.3–18.1	5.8 –7.9	10.9–19.2	5.7–12.1	1.2–1.9	9–11	equal
H. sardellae sp. n.	30.9–35.5	16.5–21.0	7.0–8.8	10.8–17.2	9.0 –13.2	2.2–3.7	11–13	unequal

Abbreviations: TL, total length; BL, body length; BW, body width; TaL, tail length; PCL, polar capsule length; PCW, polar capsule width; FC, number of polar filament coils; VT, valve types.

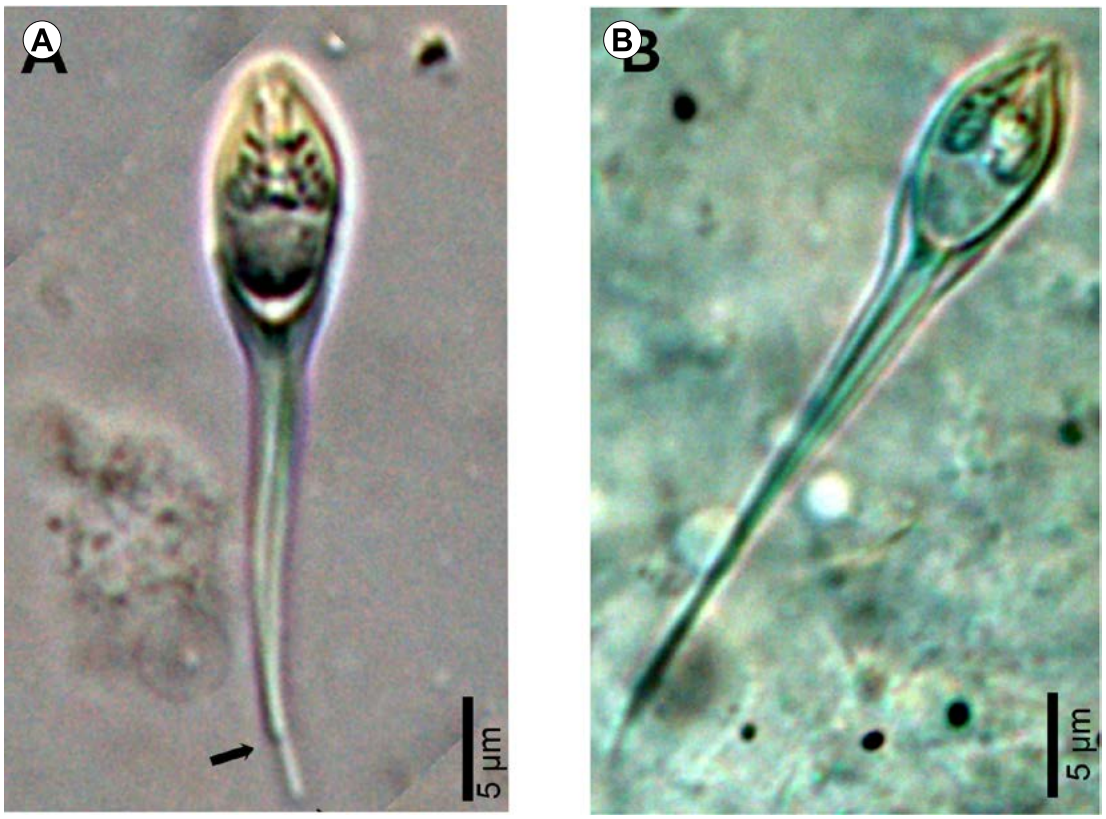

Fig. 4. *Henneguya margaritae* sp. n. parasitising *Oligosarcus jenynsii* (Günther) from Argentina. **A**, **B** – mature spore, arrow: cleaved distal end and unequal ending.

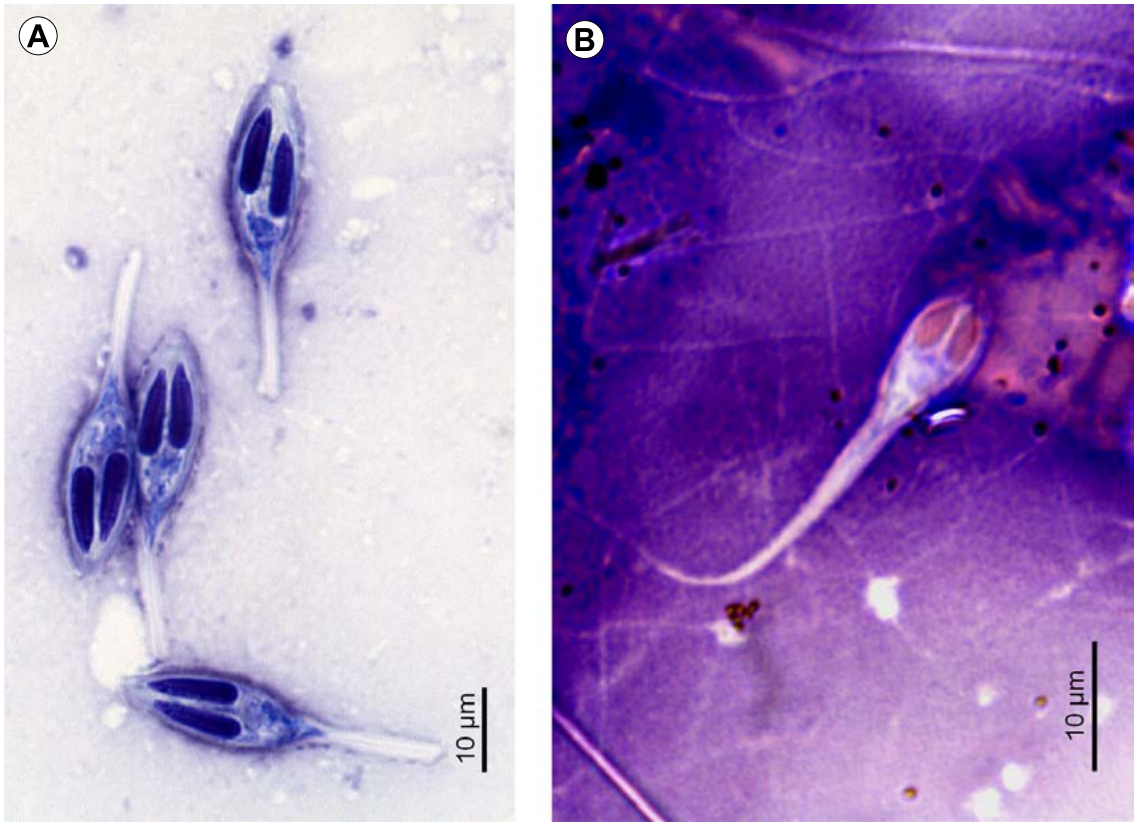

Fig. 5. Mature spores staining with Giemsa staining **A** – *Henneguya sardellae* sp. n. from *Oligosarcus jenynsii* (Günther); **B** – *Henneguya margaritae* sp. n. from *O. jenynsii*.

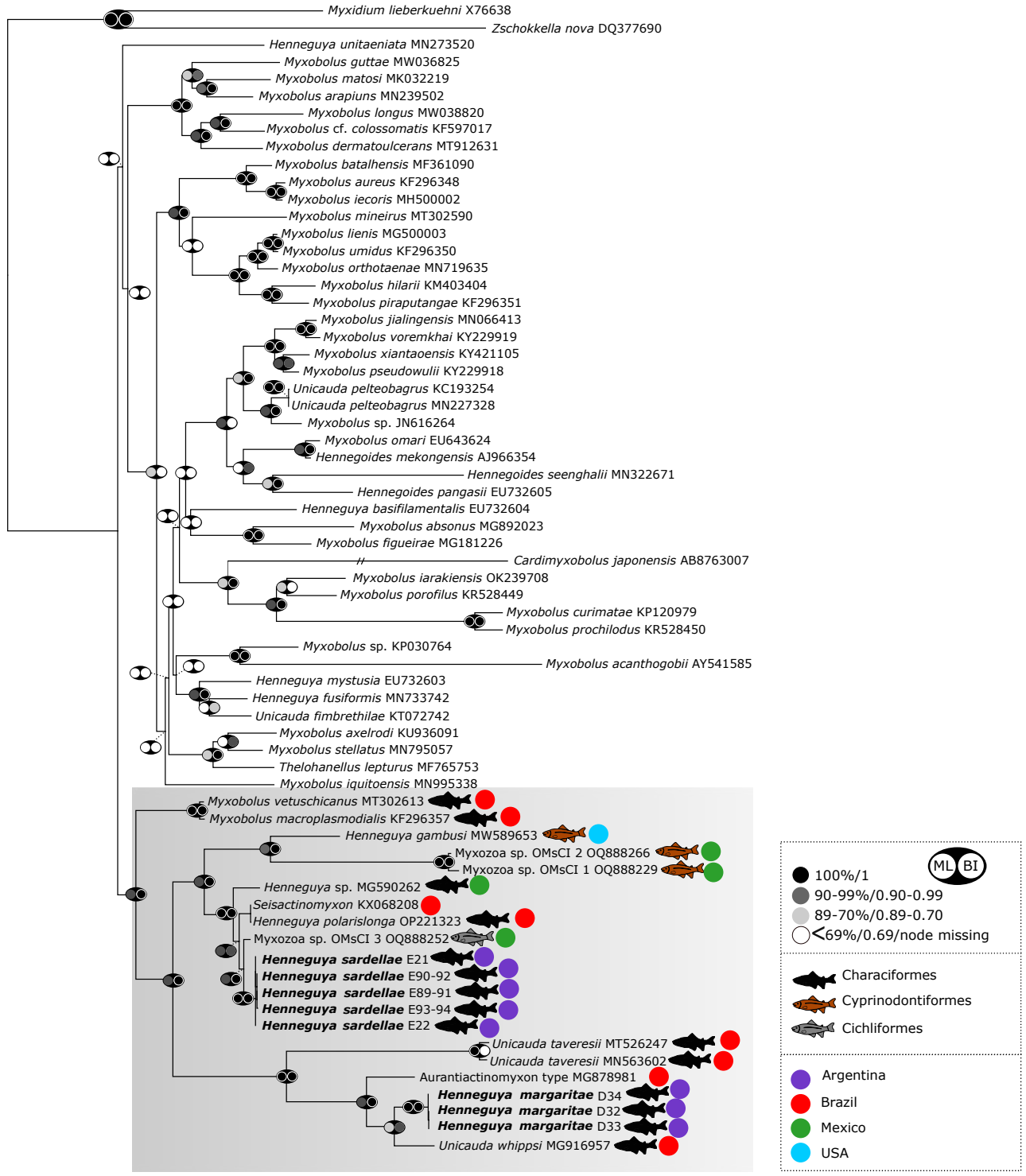

Fig. 6. The maximum likelihood tree showing the phylogenetic position of *Henneguya sardellae* sp. n. and *Henneguya margaritae* sp. n. parasitising *Oligosarcus jenynsii* (Günther) (Characiformes: Characidae) among related myxobolids. *Myxidium lieberkuehni* Bütschli, 1882 and *Zschokkella nova* Klokacewa, 1914 were used as the outgroup. Maximum likelihood/Bayesian inference nodal supports are shown at each node by the coloured circle with scaling as shown in the legend. Newly generated sequences are in bold. Species names are supplemented with corresponding GenBank accession numbers. Colour icons (according to legend in the right) indicate the host group order and geographic area.

ments compared to the Brazilian species (4–5 vs. 7–9 in *U. whippsi* and 5–6 in *U. tavaresii*); also for having smaller (9.2–13.0 µm vs. 13.23–16.5 µm) and wider spore body (5.1–6.7 µm vs. 4.5–5.5 µm) and shorter caudal processes (19.0–30.0 µm vs. 47.0–57.0 µm) than myxospores identified as *U. tavaresii* (Table 1).

Henneguya margaritae sp. n. is distinguished by the presence of equal-sized polar capsules, contrasting to the unequal polar capsules observed in *U. whippsi*.

Furthermore, it displays a reduced number of coils in the polar filaments when compared to the Brazilian species, with 4–5 coils as opposed to 7–9 in *U. whippsi* and 5–6 in *U. tavaresii*. Moreover, *H. margaritae* sp. n. exhibits smaller spore bodies (9.2–13.0 µm compared to 13.2–16.5 µm), wider spore bodies (5.1–6.7 µm compared to 4.5–5.5 µm), and shorter caudal processes (19.0–30.0 µm compared to 47.0–57.0 µm) when contrasted with the myxospores identified as *U. tavaresii* (Table 1).

Phylogenetic analyses

The assemblages of eight amplified samples resulted in consensus of almost complete and partial SSU rDNA gene sequences of *Henneguya sardellae* sp. n. of 1,696 bp, 1,710 bp, 889 bp, 898 bp and 893 bp, and *H. margaritae* sp. n. of 879 bp, 881 bp and 858 bp. These sequences were compared with each other and with other myxozoan sequences available in Genbank, and BLAST search of the NCBI dataset demonstrated that they were not identical to any of them.

The resulting trimmed alignment consists of 1,062 positions. Phylogenetic analyses based on 18S rDNA sequences, including newly obtained sequences from *Henneguya* spp. specimens parasitising *O. jenynsii*, resulted in similar ML and BI topologies, particularly in terms of the well-supported clade that included them. Both species clustered with other myxobolids parasitising freshwater fish of the order Characiformes in Brazil (*H. polarislonga* [Acc. No. OP221323], *Myxobolus macroplasmodialis* Molnár, Ranzani-Paiva, Eiras et Rodrigues, 1998 [Acc. No. KF296357], *M. vetuschicans* Naldoni, Carriero, Moreira, da Silva, Maia et Adriano, 2020 [Acc. No. MT302613], *Unicauda tavaresii* [Acc. No. MT526247-MN563602], and *U. whippsi* [Acc. No. MG916957] and Mexico (unpublished sequences of *Henneguya* sp. [Acc. No. MG590262]).

Moreover, sequences from unidentified myxozoan species obtained from freshwater fish of the order Cyprinodontiformes [Acc. No. OQ888266 and OQ888229] and Cichliformes [Acc. No. OQ888252] from Mexico, and *H. gambusi* [Acc. No. MW589653] from a cyprinodontiformes fish of the USA also clustered within this clade. In addition, two sequences of actinospores parasitising oligochaetes collected from a fish farm in Brazil (Aurantiactinomyxon [Acc. No. MG878981] and Seisactinomyxon [Acc. No. KX068208]) clustered with the newly obtained *Henneguya* sequences (Fig. 6).

DISCUSSION

In the present paper, two new species of *Henneguya* were described based on biological, morphological and molecular data from spores found in *Oligosarcus jenynsii*, a characiform fish inhabiting a shallow lake from Pampasic region of Argentina. These species, named *Henneguya sardellae* sp. n. and *Henneguya margaritae* sp. n., were found in connective tissues of fins and stomach wall, and kidneys, respectively. In the freshwater ecosystems of Argentina, unidentified *Henneguya* spp. have been reported from other freshwater fish, namely *Gymnotus carapo* Linnaeus (Gymnotiformes: Gymnotidae) (Domitrovich et al. 1991), *Serrasalmus* sp. (Characidae: Characiformes) (Flores Quintana et al. 1992, Chemes and Takemoto 2011), *Hoplosternum littorale* (Hancock) (Callichthyidae: Siluriformes) (Eiras et al. 2008), and *Percichthys trucha* (Centrarchiformes: Percichthyidae) (Viozzi 1996). Therefore, the present work represents the first described *Henneguya* species infecting a freshwater fish in Argentina.

The non-monophyly of the genus *Henneguya* has been reported in several studies, with species clustering together with those of the genera *Unicauda*, *Hennegoides*, *Myxobolus* and *Thelohanellus* (e.g., Liu et al. 2019, da Silva et al. 2020). This is significant because the presence/absence and nature of the caudal appendage(s) is one of the main taxonomic characters used to distinguish genera in Myxobolidae family, particularly the four genera mentioned above and their distinction from *Henneguya*. Interestingly, independent evolutionary origins of spore appendage(s), or secondary losses have been found in myxobolid phylogeny, and the presence of caudal appendages has been reported in aberrant spores of 'untailed' *Myxobolus* spp. in several previous studies (Bahri 2008, Liu et al. 2010, 2014, 2019, Zhang et al. 2017), suggesting the potential ability to form the caudal appendages on the myxospore.

These findings raise questions about the reliability of the caudal appendages as a valid taxonomic character for this group. It is noteworthy to mention that in both newly described species the presence of a membraneous sheath surrounding the body and the caudal appendages of spores was observed, which can cause confusion by resembling a fused or single caudal appendages.

A membraneous sheath has previously been observed in other six *Henneguya* species, i.e. *H. adherens*, *H. malabarica*, *H. pellucida*, *H. polarislonga*, *H. testicularis*, and *H. theca* Kent et Hoffman, 1984 (Adriano et al. 2005, Azevedo and Matos 1995, 1996, Azevedo et al. 1997, Kent and Hoffman 1984, Jorge et al. 2022). This structure was described as a thin 'sheath-like' membrane that involved the valve walls and formed the junction of the two tails giving the impression that there was only one caudal process for *H. pellucida* (Adriano et al. 2005). The ultrastructure of this feature has been described as a homogeneous sheath that consisted of two electron-light layers in *H. adherens* and *H. testicularis* (Azevedo and Matos 1995, Azevedo et al. 1997) and as a homogeneous sheath that consisted of a single electron-light layer in *H. malabarica* (Azevedo and Matos 1996).

In other myxobolids such as *Thelohanellus wuhanensis* Xiao et Chen, 1993, *T. macrovacuolaris* Liu, Zhai et Gu, 2016, *Myxobolus pseudowulli* Zhang, Zhai, Liu et Gu, 2017, and *M. jialingensis* Gao, Zhang, Yang et Zhao, 2020 a membraneous sheath surrounding the spores were also observed (Xiao and Chen 1993, Liu et al. 2014, 2016, Zhang et al. 2017, Gao et al. 2020). In *M. pseudowulli* the existence of a membrane surrounding spores is related to spore maturity (Zhang et al. 2017). In *M. jialingensis* the presence of a membraneous sheath appears to be dependent on the tissue or organ that is infected. In fact, this sheath was observed only in spores within the urinary blad-

der, and not in those infecting the hepatopancreas (Gao et al. 2020).

In contrast to these other species, the presence of a membraneous sheath in *H. sardellae* sp. n. was consistently observed across all spores, regardless of maturity or infected tissue. It is worth noting that this inconsistency may be due to the proximity of the sheath to the valves, which makes it difficult to observe under a light microscope (Liu et al. 2014). The membraneous sheath of *H. sardellae* sp. n. demonstrated the ability to undergo lateral deployment. This is noteworthy, as the size, shape, and surface structure of myxozoan spores are key factors that influence their capacity for flotation and dispersion in aquatic environments upon being released from their host (Okamura et al. 2015). Understanding these factors can shed light on the ecology of these organisms and their dispersal capabilities and their ability to infect definitive hosts.

It is important to note that taxonomic decisions should not be based solely on morphological data, as this may result in inaccurate species identification and classification. Therefore, a combination of morphological, molecular and ecological data should be used to determine the taxonomic status of *Henneguya* species and their relationship to other myxobolids. However, until the type species *Henneguya psorospermica* Thélohan, 1892, is genetically analysed using the same rDNA region and its evolutionary relationships are clarified, a definitive taxonomic placement of *Henneguya* cannot be made.

Several factors have been reported to influence species clustering within phylogenetic reconstructions in myxozoans, including phylogenetic proximity of the host, preference for a particular site of development, geographic distribution and morphological characteristics (Okamura et al. 2015, Holzer et al. 2018). In the case of myxobolids, there is a correlation between the clustering patterns of myxozoans and taxonomic classification of fish at the order or family level (Carriero et al. 2013, Liu et al. 2019).

In our phylogenetic reconstruction, neither geographical nor host association was evident, at least for closely related species within the highly supported subclade that included both the newly sequenced species. Specifically, fish hosts belong to the orders Cichliformes in Mexico, Cyprinodontiformes in Mexico and the USA, and Characiformes in Brazil and Argentina (Albert et al. 2011).

In conclusion, this study provides new insights into the diversity and distribution of myxosporean parasites in South American freshwater fish, particularly within the genus *Henneguya*. The identification and description of *H. sardellae* sp. n. and *H. margaritae* sp. n. as the first described species of the genus that parasitise freshwater fish in Argentina highlights the importance of further research on the diversity and distribution of myxozoans in this region.

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