

A new species of *Myxidium* (Myxozoa) infecting the gallbladder of siluriform fish *Pimelodus pantaneiro* from the Brazilian Pantanal wetland

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ABSTRACT

This study describes a new species of myxozoan, *Myxidium pantanalense* n. sp., parasitizing the gallbladder of the freshwater fish *Pimelodus pantaneiro* Souza-Filho and Shibatta, 2007, collected in the Brazilian Pantanal wetland, Mato Grosso do Sul State. The identification was based on morphological and molecular analyses. Myxospores exhibited a fusiform shape, 7–8 striations on the valvular surface, measuring 16.5 µm in length and 4.4 µm in width, with equally sized pyriform nematocysts measuring 5.5 µm in length and 2.8 µm in width, each containing a tubule making 4 to 5 turns. Phylogenetic analysis, based on small subunit ribosomal DNA sequences, positioned *M. pantanalense* n. sp. as the sister species to *Myxidium amazonense*. Morphological, genetic, and phylogenetic data support the designation of *M. pantanalense* n. sp. as a new taxon and expand the known diversity and geographic distribution of the genus *Myxidium* in South America.

1. Introduction

Myxozoa comprise a diverse group of microscopic cnidarians that are widely distributed and known to infect a broad range of hosts. They primarily parasitize fish, but can also infect other vertebrates, including amphibians and reptiles, and, more rarely, aquatic birds and small mammals. Invertebrate hosts include annelids and bryozoans (Eszterbauer et al., 2015; Lom and Dykoyá, 2006; Okamura et al., 2015).

Myxidium Bütschli, 1882 is a polyphyletic genus of myxozoans whose species are characterized by fusiform myxospores, straight or curved, with pointed ends containing the nematocysts. The shell valves may be smooth or striated, and the sutural line bisects the myxospore (Lom and Dykoyá, 2006). The species are generally coelozoic, infecting primarily fish gallbladder, but also have been found parasitizing turtles, and one species was described in ducks (Bartholomew et al., 2008; Eiras et al., 2011).

While nearly 300 species of the genus *Myxidium* are known worldwide, only a little more than a dozen have been reported from South America (Eiras et al., 2011; Oliveira et al., 2025; Whipps et al., 2025a). In this context, based on morphological characteristics and small subunit ribosomal DNA (SSU rDNA) sequence data, we describe a new species infecting the gallbladder of *Pimelodus pantaneiro* (Souza-Filho

and de and Shibatta, 2007), a South American freshwater siluriform of the family Pimelodidae, commonly known in Brazil as “Mandi”. This fish species occurs in rivers and bays of the Pantanal plain, as well as in watercourses of the plateau, and has potential for the aquarium trade. Its diet consists primarily of terrestrial and aquatic insects, fish, and reproductive fragments of higher plants (Catella and Petrere, 1996; Gimênes and Rech, 2022).

2. Materials and methods

During field work carried out in September 2022 at the Pantanal wetland, six specimens of *P. pantaneiro* were caught in the regions where waters of the Miranda and Paraguay Rivers merge, in the district of Albuquerque, municipality of Corumbá, state of Mato Grosso do Sul, Brazil (19°24'41"S 57°20'01"W [distance variation of 3 km]). The fish were captured using cast nets and/or throw nets and transported alive to a field laboratory set up near the collection site, where they were euthanized and examined. The authorizations for collection and access to genetic data were obtained from the Brazilian Ministry of the Environment SISBIO n° 67,616 and SisGen n° A33CB83. The euthanasia method was approved by the Ethics Committee of the Universidade Federal de São Paulo - UNIFESP (CEUA n° 8244,281,222) and the Ethics

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Committee of Faculdade de Zootecnia e Engenharia de Alimentos - FZEA (n° 4550,201,223).

After obtaining the measurements (total length), external examinations were conducted to detect lesions and/or parasite plasmodia. Necropsies were then performed, exposing the gills and viscera to observe, with the aid of a stereomicroscope (Zeiss Stemi, Oberkochen, Germany), any alterations in organ morphology and the presence or absence of parasites or plasmodia. When positive for myxosporeans, the collected material was fixed in 100 % ethanol for molecular analysis and in 10 % buffered formalin for morphological analysis.

2.1. Morphological characterization

Myxozoan species were identified and described based on the morphological criteria proposed by Lom and Arthur (1989). For morphological characterization, bile containing myxospores, fixed in 10 % buffered formalin, was examined using a Leica DM500 light microscope equipped with a Leica ICC50 W camera (Leica Microsystems Limited, Switzerland). Recorded images were used for morphological analysis, and the measurements of 25 myxospores were obtained with LAS EZ 3.4.0 image capture software (Leica Microsystems Limited, Switzerland). Data were expressed as mean $\pm$ standard deviation in micrometers. After examination, a slide was air-dried, fixed with methyl alcohol, stained with Giemsa, and incorporated into the collection of the Museu de Diversidade Biológica do Instituto de Biologia da Universidade de Campinas (UNICAMP), São Paulo, Brazil.

2.2. Molecular analysis

Myxospores preserved in 100 % ethanol were washed with ultrapure water (DNase/RNase-free) and transferred to sterile 1.5 mL microtubes for DNA extraction, which was performed using the DNeasy® Blood and Tissue Kit (Qiagen Inc., California, USA), following the manufacturer's instructions. The extracted DNA was quantified using a NanoDrop 2000 spectrophotometer (Thermo Scientific, Wilmington, USA), with absorbance measured at 260 nm.

SSU rDNA and internal transcribed space (ITS-1) regions were amplified using a two-round polymerase chain reaction (PCR), resulting in two amplified fragments. For the first fragment (~1100 bp), the initial PCR round was performed with the primer pair ERIB1 (Barta et al., 1997) and MC3 (Molnár et al., 2002), followed by a semi-nested PCR using primers MC5 (Molnár et al., 2002) and MC3 (Molnár et al., 2002). For the second fragment (~1500 bp), the first PCR was performed with the primer pair ERIB1 (Barta et al., 1997) and NC13R (Zhu et al., 1998), followed by a semi-nested PCR using primers MilF (forward) 5' – ATTTGGCAGCGAGAGGTGAA – 3' (Milanin et al., personal communications) and NC13R (Zhu et al., 1998).

Polymerase chain reactions (PCR) were prepared in a final volume of 25 μ L, containing: 12.5 μ L of DreamTaq Green PCR Master Mix (2x) (Thermo Scientific – Carlsbad, California, USA), 0.5 μ M of each primer, 2 μ L of DNA extracted and 9.5 μ L nuclease-free water (Thermo Scientific – Carlsbad, California, USA). The amplification was performed in an AG 22,331 thermocycler (Eppendorf, Hamburg, Germany). The PCR of the first fragment was programmed as follows: initial denaturation at 95 °C for 5 min, followed by 35 cycles of denaturation at 95 °C for 60 s, annealing at 61 °C for 60 s (63 °C for semi-nested), and extension at 72 °C for 120 s (90 for semi-nested), with a final extension at 72 °C for 5 min. For the second fragment, the PCR was defined as follows: initial denaturation at 95 °C for 5 min, followed by 35 cycles of denaturation at 95 °C for 60 s, annealing at 56 °C for 60 s (54 °C for semi-nested), and extension at 72 °C for 120 s, with a final extension at 72 °C for 5 min.

The amplified products were subjected to electrophoresis on a 1.5 % agarose gel in TAE buffer (40 mM Tris, 20 mM acetic acid, and 1 mM EDTA), stained with SYBR Safe DNA Gel Stain (Invitrogen, Thermo Fisher Scientific, Waltham, USA), and visualized using an LED trans-illuminator (Kasvi, Paraná, Brazil). Fragment size was estimated by

comparison with the 1 Kb Plus DNA Ladder marker (Invitrogen, Thermo Fisher Scientific, USA). PCR products were purified using the QIAquick PCR Purification Kit (Qiagen Inc., California, USA), according to the manufacturer's protocol. Purified DNA was quantified by electrophoresis on a 2 % agarose gel using the Low DNA Mass Ladder (Thermo Fisher Scientific, Vilnius, Lithuania) as a marker.

Purified products were sent for sequencing to the Centro de Recursos Biológicos e Biologia Genômica (CREBIO) da Faculdade de Ciências Agrárias e Veterinárias, Universidade Estadual Paulista “Júlio de Mesquita Filho” – UNESP, Jaboticabal campus. Sequencing was performed using the four of the primers employed in PCR (MC5, MC3, MilF, and NC13R), together with the additional primers ERIB10 (Barta et al., 1997), MilR2 (reverse) 5' – CCCGGTCTCGGCATAGTTTAC – 3' (Milanin et al., personal communication), and ERTSF (forward) 5' – CCGTAGGTGAACCTGCGGAAG – 3' (designed in this study), to ensure overlap between fragments. Sequencing reactions were carried out using an ABI 3730 DNA Analyzer (Applied Biosystems™ Inc., California, USA), with the BigDye® Terminator v3.1 Cycle Sequencing Kit.

The resulting sequences were visualized and the contigs generated were edited using BioEdit 7.1.3.0 (Hall, 1999), employing the ClustalW algorithm (Thompson et al., 1994). Subsequently, the nucleotide basic local alignment search tool (BLASTn) was conducted to assess the similarity of the obtained sequences with reference sequences available in National Center for Biotechnology Information (NCBI) database.

2.3. Phylogenetic analysis

Phylogenetic analysis was performed using SSU rDNA sequence fragments of the new species here sequenced plus 36 myxosporean species available in the GenBank. *Tetracapsuloides bryosalmonae* and *Buddenbrockia plumatellae* were included as outgroup taxa. GenBank accession numbers for each species are indicated following their names in the phylogenetic tree.

To determine the phylogenetic position of the parasites, sequences were first aligned using the ClustalW algorithm (Thompson et al., 1994). Phylogenetic reconstruction was conducted using the Maximum Likelihood method in PhyML 3.0 (Guindon et al., 2010) via the ATGC: Montpellier Bioinformatics Platform (Guindon et al., 2010), applying the best-fit evolutionary model determined by Smart Model Selection – SMS (Lefort et al., 2017), based on the Akaike Information Criterion (AIC). Statistical support for the tree branches was assessed using a bootstrap analysis with 1000 replicates. The results were visualized using FigTree v1.4.5-pre (Rambaut, 2018). Another alignment, including the most closely related myxosporeans to the new species in the phylogenetic tree, was performed for use in the pairwise dissimilarity matrix using the *p*-distance model matrix in MEGA v.12.0.11 (Kumar et al., 2024).

3. Results

Bile analysis revealed free myxospores with characteristics of the genus *Myxidium* in one out of six examined specimens (16.6 %) of *P. pantaneiro*. Morphological and SSU rDNA sequence data indicate that this parasite represents an undescribed species. No other myxosporean species were detected in the examined hosts.

3.1. Taxonomic summary

Phylum: Cnidaria Verrill, 1865.

Subphylum: Endocnidozoa Schuchert, 1996.

Class: Myxozoa Grassé, 1970.

Subclass: Myxosporea Bütschli, 1881.

Genus: *Myxidium* Bütschli, 1882.

Species: *Myxidium pantanalense* n. sp.

Type host: *Pimelodus pantaneiro* Souza-Filho and Shibatta, 2007 (Siluriformes: Pimelodidae).

Site of infection: Gallbladder (myxospores floating free in bile).

Type locality: Brazilian Pantanal wetland, district of Albuquerque, municipality of Corumbá, state of Mato Grosso do Sul, Brazil.

Type material: glass slides with Giemsa stained myxospores were deposited in the collection of the Museu de Diversidade Biológica do Instituto de Biologia da Universidade de Campinas (UNICAMP), São Paulo, Brazil, under the accession number ZUEC MYX 121.

Molecular data: A partial SSU rDNA and ITS-1 sequence (2012 bp) was deposited in the GenBank under accession number PX630363.

Etymology: The specific epithet *pantanalense* refers to the Portuguese name of the extensive Brazilian wetland region where the type material was collected.

ZooBank registration: The Life Science Identifier for *Myxidium pantanalense* n. sp. is urn:lsid:zoobank.org:act:29F154A6-FC13-4DD5-9552-5DBD43D26CE2.

3.2. Morphological and morphometric data

Mature myxospores were fusiform, slightly curved with rounded ends and 7–8 striations on the valvular surface. The myxospores contained two pyriform nematocysts of equal size, located at the ends of the body (Fig. 1). Measurements of the myxospores showed an average body length of 16.5 ± 0.9 (15.6–17.4) μm and an average width of 4.4 ± 0.4 (4.0–4.8) μm . The nematocysts measured 5.5 ± 0.4 (5.1–5.9) μm in length and 2.8 ± 0.3 (2.5–3.1) μm in width. The nematocyst tubule contained 4 to 5 turns (Table 1).

3.3. Sequencing, phylogenetic, and genetic distance data

Sequencing of *M. pantanalense* n. sp. (GenBank accession PX630363) yielded a fragment of 2012 bp, including the SSU rDNA and ITS-1 regions. BLASTn analysis revealed no identical matches with any other myxozoan sequence available in the NCBI database. The highest sequence identity (91.4 %) was with *Myxidium amazonense* Mathews et al., 2015 (GenBank accession KT625442), a parasite of *Corydoras melini* (Lönnberg and Rendahl, 1930), an Amazonian siluriform of the family Callichthyidae. In the phylogenetic analysis, based on the SSU

rDNA sequences, *M. pantanalense* n. sp. emerged as a sister species to *M. amazonense*, with strong bootstrap support (Fig. 2). *P*-distance analysis also revealed that the smallest genetic distance to the new species (6.5 %) was with *M. amazonense*. (Table 2).

4. Discussion and conclusions

Several pimelodid fish species have been reported as hosts of parasitic cnidarians (Rocha et al., 2019; Vieira et al., 2025), but none have been found to be infected by species of the genus *Myxidium*. In this study, *M. pantanalense* n. sp. is described from the gallbladder of *P. pantaneiro*, and the morphology of its myxospores is compared with those of freshwater *Myxidium* species previously described from South America and other regions worldwide (Eiras et al., 2011; Whipps et al., 2025b).

The South American species most morphologically similar to *M. pantanalense* n. sp. is *M. amazonense*, a parasite of the Amazonian *C. melini*, another siluriform that belongs to the family Callichthyidae. However, the new species differs from *M. amazonense* by having narrower nematocysts ($2.8 \times 3.4 \mu\text{m}$), slightly less curved myxospores, and a 6.5 % genetic divergence in the SSU rDNA sequence.

Considering *Myxidium* species from other geographical regions, *M. pantanalense* n. sp. shows the greatest morphological and morphometric resemblance to *Myxidium sarcocheilichthysi* Feng and Wang, 1990, described from the cypriniform *Sarcocheilichthys nigripinnis* Günther, 1873 in China. However, the myxospores of the new species are slightly shorter and narrower ($16.5 \times 4.4 \mu\text{m}$) than those of the Chinese species ($17.2 \times 5.7 \mu\text{m}$). The nematocysts of *M. pantanalense* n. sp. are also narrower (2.8 μm) than those of *M. sarcocheilichthysi* (3.6 μm). No SSU rDNA sequence of *M. sarcocheilichthysi* is currently available in the NCBI database. Thus, morphological and SSU rDNA data support the establishment of this new myxozoan taxon in the Brazilian Pantanal wetland.

In the phylogenetic analysis, *M. pantanalense* n. sp., emerged with strong bootstrap support as a sister species to *M. amazonense*, which also parasitizes a siluriform fish, but in this case one belonging to the family Callichthyidae (Mathews et al., 2015).

The description of *M. pantanalense* n. sp. expands the current knowledge of the diversity of the genus *Myxidium* in South American

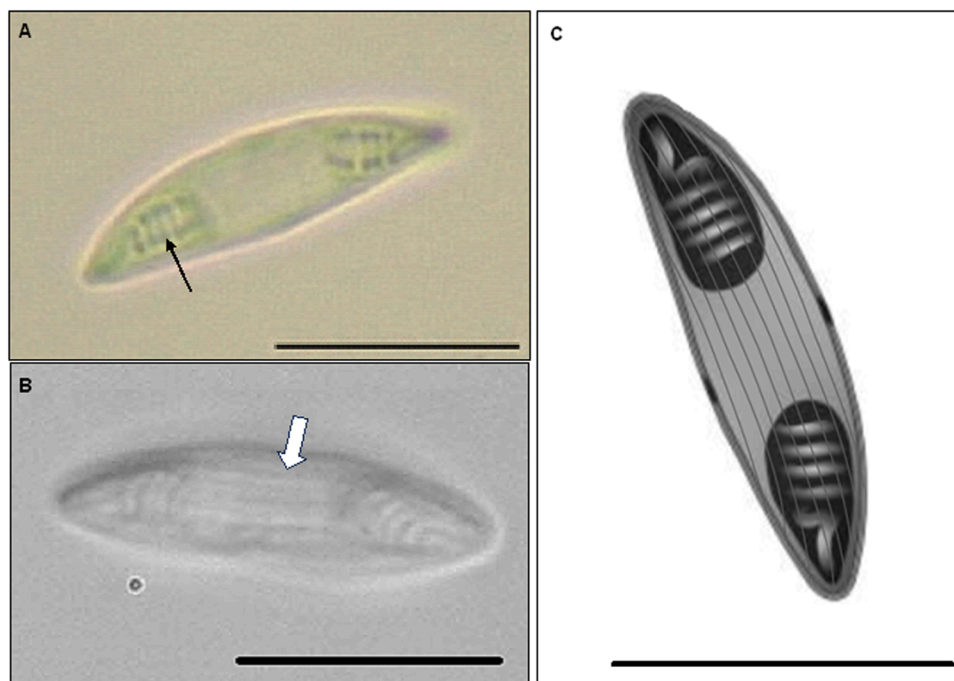


Fig. 1. *Myxidium pantanalense* n. sp. parasite of the gallbladder of *Pimelodus pantaneiro*. A – B: Photomicrographs of mature myxospore. Note the turns of the tube in nematocyst (black arrow) and the striations on the valvular surface (white arrow). C – Schematic drawing. Scale bar: 10 μm .

Table 1

Comparative morphological data of *Myxidium pantanalense* n. sp. with other closely related species according to the morphology and phylogenetic tree.

Species	Myxospore length	Myxospore width	NL	NW	NT	Infection site and host	Locality	References
1 <i>Myxidium pantanalense</i> n. sp.	16.5 ± 0.9	4.4 ± 0.4	5.5 ± 0.4	2.8 ± 0.3	4–5	Gallbladder of <i>Pimelodus pantaneiro</i>	Pantanal, Brazil	In this study
2 <i>Myxidium amazonense</i>	17.0 ± 0.9	3.7 ± 0.7	5.4 ± 0.5	3.4 ± 0.6	4–5	Gallbladder of <i>Corydoras melini</i>	Amazon Basin, Brazil	Mathews et al., 2015
3 <i>Myxidium horatioense</i>	12.2 ± 0.8	4.7 ± 0.4	3.0 ± 0.3	2.9 ± 0.3	3–4	Gallbladder of <i>Ameiurus natalis</i>	EUA	McAllister et al., 2025
4 <i>Myxidium cuneiforme</i>	12.2 ± 0.3	5.4 ± 0.3	3.9 ± 0.2	2.6 ± 0.1	5–6	Gallbladder of <i>Cyprinus carpio haematopterus</i>	China	Jones et al., 2011
5 <i>Myxidium truttae</i>	14.0 – 16.0	6.0 – 8.0	-	-	-	Urinary bladder of <i>Salmo trutta</i>	United Kingdom	Kent et al., 2001
6 <i>Myxidium whippsi</i>	8.7	5.1	2.5	2.4	3–5	Gallbladder of <i>Esox niger</i> and <i>Esox americanus vermiculatus</i>	EUA	McAllister et al., 2022
7 <i>Myxidium fonti</i>	13.7	6.5	4.3	3.6	4–6	Gallbladder of <i>Heterandria formosa</i>	EUA	Whipps, 2025b
8 <i>Myxidium sarcocheilichthysi</i>	17.2 (16.0–18.5)	5.7 (5.1–6.0)	5.0 (4.0–6.0)	3.6 (3.2–4.0)	4–5	<i>Sarcocheilichthys nigripinnis</i>	China	Feng and Wang, 1990

NL: Nematocyst Length; NW: Nematocyst Width; NT: Number of turns of the tubule; dash: no data. All measurements are means ± standard deviation, in µm.

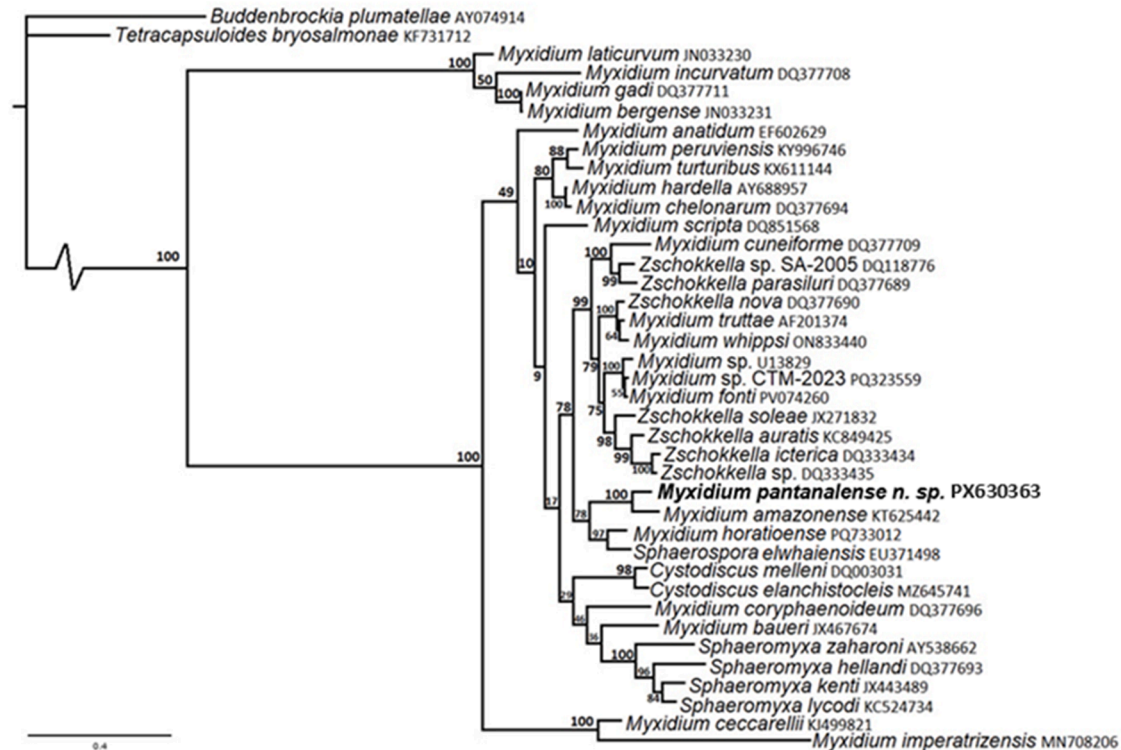


Fig. 2. Maximum likelihood tree inferring the phylogenetic relationship between *M. pantanalense* n. sp. and other myxozoans, based on SSU rDNA sequences available in GenBank. Bootstrap support values are indicated at the nodes.

freshwater environments, corroborates the importance of the Brazilian Pantanal wetland as a hotspot for myxozoan biodiversity (Adriano et al., 2009; 2012; Carriero et al., 2013) and highlights the need for broader studies on the parasitic of native fauna fish species of the region, many of the which have large importance for aquaculture.

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CRediT authorship contribution statement

Tatiane Carolina Ponzetto: Writing – original draft, Visualization, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Edson A Adriano:** Writing – review & editing, Visualization, Validation, Resources, Investigation, Funding acquisition. **Antonio Augusto Mendes Maia:** Writing – review & editing, Visualization, Validation, Supervision, Resources, Investigation, Funding acquisition.

Table 2

Dissimilarity matrix, based on the SSU rDNA sequences of *Myxidium* and *Sphaerospora* species grouped into a clade of phylogenetic tree. The upper triangle corresponds to the number of bases that differ between the species, and the lower triangle corresponds to the percentage genetic difference between the species. .

Species	1	2	3	4	5	6	7	8	9	10
1 <i>M. pantanalense</i> n. sp. PX630363	-	100	145	103	181	155	164	189	183	191
2 <i>Myxidium amazonense</i> KT625442	6.5	-	150	145	215	190	204	219	205	206
3 <i>Myxidium horatioense</i> PQ733012	9.0	8.6	-	96	199	169	156	166	173	169
4 <i>Sphaerospora elwhaiensis</i> EU371498	8.2	9.2	6.6	-	193	175	181	188	179	175
5 <i>Myxidium cuneiforme</i> DQ377709	11.2	11.3	10.9	12.2	-	205	214	220	218	216
6 <i>Myxidium truttae</i> AF201374	10.7	10.6	10.1	11.0	11.0	-	59	160	158	156
7 <i>Myxidium whippsi</i> ON833440	10.2	10.7	8.6	11.4	10.6	3.2	-	174	154	150
8 <i>Myxidium</i> sp. U13829	13.1	12.3	10.0	12.0	11.8	8.6	9.4	-	66	63
9 <i>Myxidium</i> sp. CTM-2023 PQ353559	11.3	10.8	17.3	11.3	10.7	8.5	7.6	3.5	-	34
10 <i>Myxidium fonti</i> PV074260	12.0	10.8	9.4	11.0	10.8	8.3	7.5	3.4	1.7	-

Declaration of competing interest

All authors declare no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Data availability

Data will be made available on request.

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