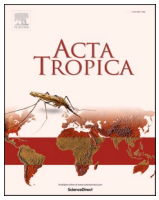
Acta Tropica 266 (2025) 107642

Contents lists available at ScienceDirect

Acta Tropica

journal homepage: www.elsevier.com/locate/actatropica



Ortholinea paraensis n. sp. (Myxosporea: Ortholineidae) infecting the urinary bladder of *Ageneiosus ucayalensis* Castelnau, 1855 (Siluriformes: Auchenipteridae) in the Amazon region of Brazil

Camila Maria Barbosa Pereira [a,b], Jhonata Eduard [a,c], José Francisco Berrêdo Reis da Silva [d], Maria do Perpétuo Socorro Progene Vilhena [e], José Ledamir Sindeaux Neto [a,f], Michele Velasco [a,g,*]

[a] *Morpho-Molecular Integration Laboratory and Technologies (LIMT), Institute of Animal Health and Production (ISPA), Federal Rural University of the Amazon (UFRA), Belém, Pará, Brazil*
[b] *Postgraduate Program Biodiversity and Biotechnology (PPG-BIONORTE), Federal University of Pará (UFPA), Belém, Pará, Brazil*
[c] *Postgraduate Program in the Biology of Infectious and Parasitic Agents (BAIP), Federal University of Pará (UFPA), Belém, Pará, Brazil*
[d] *Emílio Goeldi Museum of Para, Belém, PA, Brazil*
[e] *Food Science and Technology (CTA), Federal Rural University of the Amazon – UFRA, Belém, PA, Brazil*
[f] *Postgraduate Program in Animal Reproduction in the Amazon (REPROAMAZON), Federal Rural University of Amazonia (UFRA), Belém, Pará, Brazil*
[g] *Postgraduate Program in Animal Health and Production (PPGSPAA), Federal Rural University of the Amazon (UFRA), Belém, Pará, Brazil*

ARTICLE INFO

Keywords:
Urinary system
Amazon
Phylogeny
Myxozoa

ABSTRACT

The present study describes a new parasite species of the myxozoan genus *Ortholinea*, based on the interpretation of morphological and molecular parameters. This species was found infecting the urinary bladder of the driftwood catfish *Ageneiosus ucayalensis*, captured in the region of Santo Antônio and Guajará bays, in the Amazonian state of Pará, Brazil. Plasmodia and myxospores were observed in pairs in the urinary bladder, either floating freely or adhered to the mucosa. The myxospores are spherical in the frontal view and valvular, with two equal, sub-spherical polar capsules, oriented divergently, containing 6–7 coils of the polar tubule. Scanning electron microscopy revealed ridges on the surface of the spore, which confer it with the appearance of a ball of wool, covering the entire surface of the valve, a slightly undulating suture line, and the presence of discharge pores for the polar tubule on opposite sides of the suture, that permit the extrusion of the polar tubule. The new species presents morphological characteristics typical of the genus *Ortholinea*. In the phylogenetic analysis, *Ortholinea paraensis* n. sp. occupied a basal position within a clade of species from the Amazon region. The sum of the morphological and molecular evidence clearly supports the description of a new species, denominated *Ortholinea paraensis* n. sp., which is the first *Ortholinea* species reported from Brazil.

1. Introduction

The myxozoans are a diverse group of microscopic aquatic parasites that belong to the phylum Cnidaria. These spore-forming organisms have a worldwide distribution, and are found in a range of different organs and tissues, with a complex life cycle alternating between vertebrate hosts, typically fish from marine, freshwater, and brackish environments, and invertebrate hosts, such as annelids (Lom and Dyková, 2006; Fiala et al., 2015; Freeman and Kristmundsson, 2015).

The genus *Ortholinea* Shulman (1962) includes more than 20 recognized species, most of which have been described from marine fish. These parasites are predominantly coelozoic, and typically infect the excretory system of their hosts, being found in the urinary bladder, kidney, and ureter, and, more rarely in the gallbladder and visceral peritoneum (Padma Dorothy and Kalavati, 1993; Lom et al., 1992; Lom and Dyková, 1995; Abdel-Baki et al., 2015; Chandran et al., 2020; Shin et al., 2023; Okkay et al., 2024; Rangel et al., 2024). Only two species of *Ortholinea* have been described from South American hosts – *O. lauquen*, recorded in the Common galaxias, *Galaxias maculatus*, and *O. concentrica*, found in the sea bass, *Acanthistius patachonicus*

* Corresponding author at: Morpho-Molecular Integration Laboratory and Technologies 16 (LIMT), Avenida Presidente Tancredo Neves, N° 2501 Neighborhood, Montese, City, Belém, Pará. CEP: 66.077-901, Brazil.
E-mail address: michele.velasco@ufra.edu.br (M. Velasco).

https://doi.org/10.1016/j.actatropica.2025.107642
Received 30 January 2025; Received in revised form 30 April 2025; Accepted 4 May 2025
Available online 6 May 2025

(Alama-Bermejo and Hernández-Orts, 2018; Alama-Bermejo et al., 2019) The morphology of these myxospores is spherical to sub-spherical, with a prominent sutural ridge, two sub-spherical to pyriform polar capsules, and binucleate sporoplasm (Lom and Dyková, 2006).

Ageneiosus ucayalensis Castelnau, 1855 is a species of catfish, order Siluriformes, which is widely distributed in the Amazon basin. This fish is an important subsistence resource for the region's riverside communities, although few data have been published on its parasitology (Hahn et al., 2004; Batista et al., 2012; Sá-Oliveira et al., 2014; Ribeiro et al., 2017; De Oliveira Ferreira and Tavares-Dias, 2017).

The present study describes a new species of *Ortholinea*, which was found infecting the urinary bladder of *A. ucayalensis*, based on morphological and molecular analyses. This is the first species of the genus to be described from Brazil.

2. Materials and methods

2.1. Sample collection

A total of 65 *A. ucayalensis* specimens were analyzed in the present study. These fish were captured between October 2023 and May 2024 in the region of Santo Antônio and Guajará bays (01°15′0″ S; 48°30′0″ W), in the southern arm of the estuary of the Amazon River, off the city of Belém, in the state of Pará, Brazil. The fish were frozen in cooler boxes and transported to the Laboratory of Morpho-Molecular Integration and Technologies at the Belém campus of the Federal Rural University of Amazonia (UFRA). All ethical guidelines were followed in this study as per the UFRA Committee for Ethics in the Experimental Use of Animals, CEUA–UFRA (no. 8323,110,522, dated May 11th, 2022).

2.2. Morphological analysis

The specimens were necropsied under a light stereomicroscope to detect lesions, with the organs of the coelomic cavity being dissected in search of potential focuses of infection by myxozoans. Fragments of the urinary bladder were removed for examination under a light microscope, to confirm the presence of parasites. The parasites were photographed using a differential interference contrast (DIC) microscope attached to an AxiocaCam ERC 5 camera with AxioVision LE software. A total of 30 fresh myxospores were measured, referring to six fish specimens, with the mean values of each parameter being calculated based on the guidelines of Lom and Arthur (1989).

For the histological analysis, a urinary bladder was first fixed in Davidson's solution (ethanol, formaldehyde, acetic acid, and distilled water) for 24 hours. The bladder was then dehydrated in a graded ethanol series, clarified in xylene, and embedded in paraffin. Sections 5 μm thick were excised from the paraffin blocks and stained with Giemsa for the examination of the tissue structure.

For scanning electron microscopy (SEM), small fragments of parasitized tissue were fixed in 5 % glutaraldehyde buffered in sodium cacodylate (pH 7.2) for 24 h, washed in the same buffer solution for 24 h, and then post-fixed in 2 % osmium tetroxide buffer for 3 h. The samples were then dehydrated in a graded ethanol series, dried to the critical point, and metalized. Photomicrographs were obtained at the scanning electron microscopy Laboratory on the research campus of the Goeldi Museum in Belém.

2.3. Molecular and phylogenetic analysis

For the molecular analyses, samples of the parasitized tissue were fixed in absolute alcohol (P.A.) and stored at −4 °C. The DNA of these samples was extracted using a DNeasy Blood & Tissue kit (Qiagen, Hilden, Germany), following the manufacturer's instructions. Immediately following its extraction, the DNA was processed by Polymerase Chain Reaction (PCR) to obtain sequences of the small subunit ribosomal RNA (SSU rDNA). The samples were first amplified using the primers Erib 1 and Erib 10 (Barta et al., 1997), followed by a semi-nested PCR using the primers MyxospecF-ERIB10 and MyxospecR-ERIB1 (Barta et al., 1997; Fiala, 2006). Both PCRs were run in a final volume of 25 μl, containing 20 mM of Tris (pH 8.4), 50 mM of KCl, 4 mM of dNTP (Invitrogen), 2 mM of $MgCl_2$, 5 pmol of each primer and 1.2 units of Taq DNA polymerase (Invitrogen®), with 5–10 ng of the DNA.

The protocol for the first PCR with the primers Erib1 and Erib10 consisted of an initial denaturation at 95 °C for 2 min, followed by 35 cycles at 95 °C for 30 s, 48 °C for 30 s (annealing), and 72 °C for 2 min, with a final extension at 72 °C for 7 min. The same protocol was followed in the semi-nested PCR, except for the annealing temperature, which was increased to 50 °C. The PCR products were stained with 6x Safer dye (KASVI) and then electrophoresed in 1.5 % agarose gel in TAE buffer. The PCR products were then purified, and sequenced in an AB 3.500 DNA automatic sequencer (Applied Biosystems ™, Carlsbad, CA, USA), using a Big Dye Terminator v3.1 cycle sequencing kit (Applied Biosystems, USA), in accordance with the manufacturer's instructions.

The partial SSU rDNA sequences were assembled into a consensus sequence using Geneious 7.1.3 (Kearse et al., 2012) and then compared with other myxozoan sequences available in the GenBank database, which were identified by the Basic Local Alignment Search Tool (BLAST) for inclusion in this analysis, based on a genetic identity of at least 80 % with the consensus sequence, occurrence in the same geographic region and sequences of species used in phylogenetic analyses in the study of Shin et al. (2023), Alama-Bermejo and Hernández-Orts (2018). The final dataset consisted of sequences from 31 species of coelozoic myxozoans with a mean length of 1800 bp, which were aligned in MUSCLE, with the ambiguous regions being edited in AliView, version 1.28 (Larsson, 2014).

A Bayesian Inference (BI) was run in MrBayes v. 3.0 (Huelsenbeck and Ronquist, 2001; Ronquist and Huelsenbeck, 2003) using Markov Chain Monte Carlo (MCMC) searches, with two independent runs of four simultaneous algorithms for five million generations. During these runs, the first 1000 trees being discarded as burn-in, and one tree in every 250 was saved. The GTR+I + G nucleotide substitution model was selected for the dataset by J-modelTest v. 2.1 (Darriba et al., 2012). The phylogenetic tree was visualized in FigTree v.1.4.3 (Rambaut, 2016) and edited in Inkscape, version 1.2.2. The genetic distances p between sequences were estimated using the PAUP* software, 4.0 (Wilgenbusch and Swofford, 2003).

3. Results

3.1. Description

Plasmodia were observed floating in the contents of the urinary bladder, which contained numerous refractory granules and developing myxospores, with peripheral, stereociliary-type projections in parts of the membrane (Fig. 1A). The myxospores were either floating freely in pairs or adhered to the mucosa of the organ, and were spherical in the frontal view and valvular, 11.2 ± 0.5 μm in length and 11.7 ± 0.5 μm in width (Fig. 1B and C). The spores contain two equal-sized, sub-spherical polar capsules, 5.0 ± 0.2 μm in length and 4.5 ± 0.4 μm in width, oriented divergently, with a polar tubule that has 6–7 coils (Fig. 1D) (Table 1). They have a visible suture line and ornamentation (Fig. 1E) The histological analysis revealed a slight morphological alteration in the wall of the epithelium at the attachment point of the myxospores, with cuboid-shaped cells (Fig. 1F).

The scanning electron microscopy highlighted the ridges on the spore surface, which cover the entire surface of the valve and give it the appearance of a ball of wool. These ridges are spaced regularly, with occasional branching, and 7–9 ridges on each valve (Fig. 2A). Two valves joined by a slightly wavy suture line with polar tubule discharge pores in each valve located on opposite sides of the suture line, between the first and second ridges, revealing the extrusion of the polar tubule

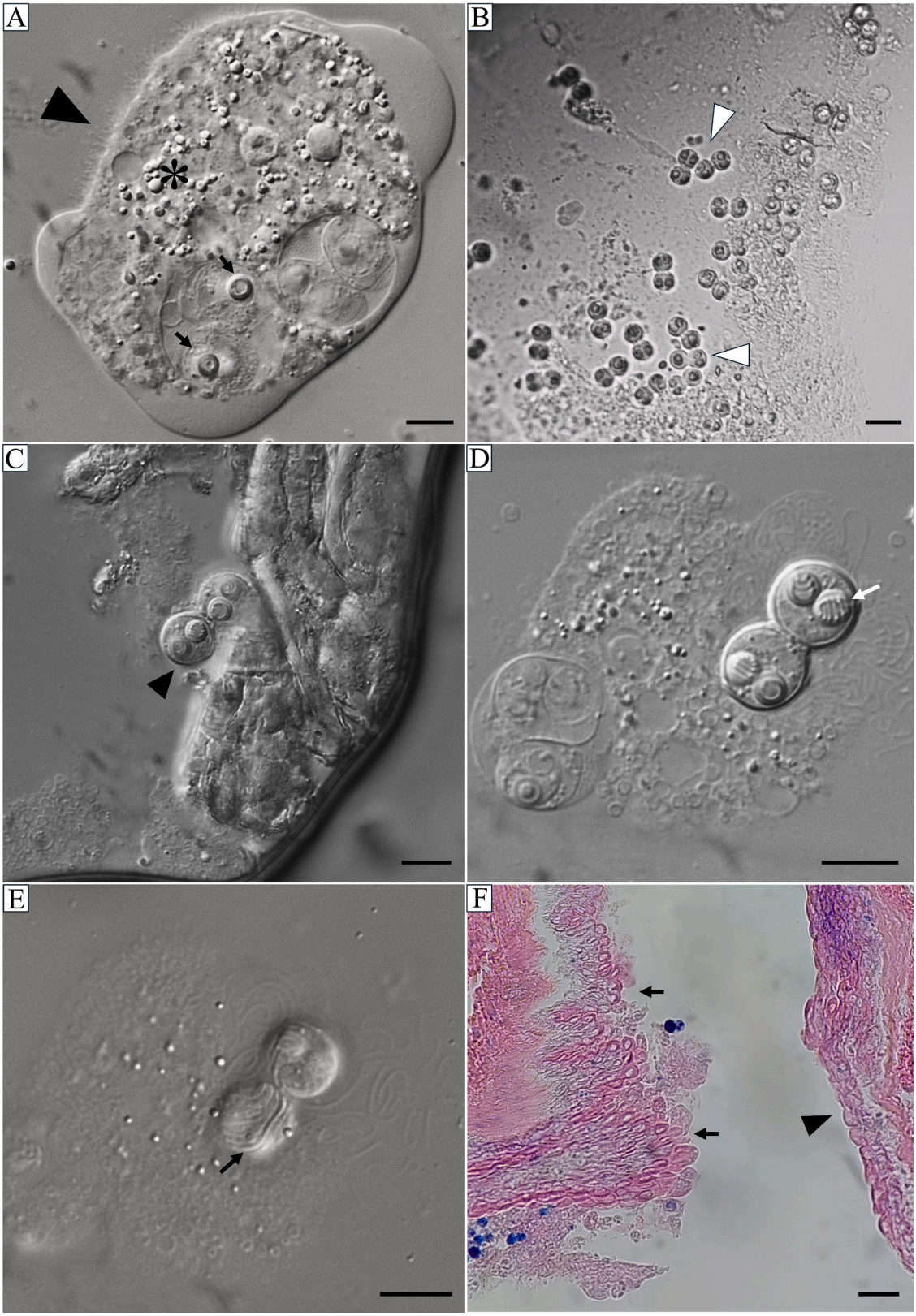


Fig. 1. *Ortholinea paraensis* n. sp. from urinary bladder of *Ageneiosus ucayalensis*. A: A plasmodium with peripheral projections (arrowhead), containing refractory granules (*) and developing myxospores (arrow), scale bar = 20 μm; B: Pairs of myxospores floating freely in the urinary bladder (arrowhead), scale bar = 20 μm; C: Pairs of myxospores in the apical view (arrowhead), scale bar = 10 μm; D: Divergent polar capsules, with 6–7 coils of the polar tubule (arrow), scale bar = 10 μm; E: Suture line (arrow) and ornamentation, scale bar = 10 μm; F: Histological section of the urinary bladder of the host, stained with Giemsa, showing a slight alteration in the mucosa (arrow), associated with the attached myxospores, and the flatter cells (arrowhead) in the rest of the epithelium, without attached myxospores, scale bar = 30 μm.

Table 1
Comparison of spore measurements of *Ortholinea paraensis* n. sp. with the other related species. N: number of polar tubule coils.

Species	Host	Site of infection	Spore (μm)		Polar capsule (μm)			Prevalence	Locality	References
			Long	Wide	Long	Wide	N	(%)		
Ortholinea paraensis n. sp.	*Ageneiosus ucayalensis*	Urinary bladder	11.2 ± 0.5 (10.8–11.9)	11.6 ± 0.5 (11.1–12.4)	5.0 ± 0.2 (4.7–5.4)	4.5 ± 0.4 (4.0–4.9)	6–7	47.0	Brazil	This study
O. hamsiensis	*Engraulis encrasicolus*	Urinary bladder	9.1 ± 0.25 (8.8–9.9)	8.4 ± 0.33 (8.2–9.1)	3.1 ± 0.11 (3.0–3.3)	2.7 ± 0.11 (2.6–2.9)	3–4	1.4	Türkiye	(Okkay et al., 2024)
O. gobiusi	*Neogobius melanostomus*	kidney	8.6 ± 0.15 (8.3–8.8)	7.5 ± 0.18 (7.3–7.9)	2.7 ± 0.16 (2.5–3.3)	2.1 ± 0.09 (2.0–2.3)	–	4.8	Türkiye	(Okkay et al., 2024)
O. nupchi	*Paralichthys olivaceus*	Urinary bladder	7.6 ± 0.5 (6.4–9.0)	7.3 ± 0.5 (6.2–8.5)	3.1 ± 0.2 (2.6–3.4)	2.1 ± 0.2 (1.5–2.4)	3–4	50.0	Republic of Korea	(Shin et al., 2023).
O. divergens	*Symphotus cinereus*	Kidney	9.1 (8.2–9.6)	9.3 (8.5–9.8)	2.0 (1.8–2.2)	2.1 (1.8–2.3)		33.3	Türkiye	(Okkay and Özer, 2020)
O. scatophagi	*Scatophagus argus*	Urinary bladder and Ureters	7.34 ± 0.67 (6.22–8.71)	6.90 ± 0.71 (5.9–8.21)	2.59±0.42 (1.66–3.23)	2.24 ± 0.35 (1.27–2.98)	4–5	70.14	India	(Chandran et al., 2020)
O. lauquen	*Galaxias maculatus*	kidney tubule	7.3 ± 0.4 (6.5–8.3)	7.6 ± 0.4 (6.6–8.8)	3.3 ± 0.3 (2.2–4.0)	2.4 ± 0.3 (1.8–3.1)	3–4	7.0	Argentina	(Alama-Bermejo et al., 2019).
O. concêntrica	*Acanthistius patachonicus*	Urinary bladder, kidney and Ureters	8.9 ± 0.6 (8.2–11.0)	8.7 ± 0.6 (7,9 - 11,0)	3.1 ± 0.3 (2,4 – 3,8)	2.7 ± 0.2 (2,3 - 3.6)	4–5	30.0	Argentina	(Alama-Bermejo and Hernández-Orts, 2018)
O. mullusi	*Mullus barbatus*	Urinary bladder, Kidney	9.3 (9.0–9.7)	8.7 (8.2–9.3)	3.1 (3.0–3.2)	2.5 (2.4–2.6)	3–4	24.5	Türkiye	(Gürkanli et al., 2018)
O. labracis	*Dicentrarchus labrax*	Urinary bladder, Kidney	7.6 (6.8–8.7)	7.2 (6.7–7.7)	3.0 (2.6–3.4)	2.4 (2.0–2.9)	4–5	11.0	Portugal	(Rangel et al., 2017)
O. saudii	*Siganus rivulatus*	kidney tubule	10 (9–11)	12 (11–13)	4.5 ± 0.3 (4.0–5.0)	4.5 ± 0.3 (4.0–5.0)	3	5.0	Saudi Arabia	(Abdel-Baki et al., 2015)
O. auratae	*Sparus aurata*	Urinary bladder, Kidney	9.0 ± 0.3 (8.2–10.1)	8.3 ± 0.4 (7.5–9.1)	3.2 ± 0.1 (2.9–3.6)	2.7 ± 0.1 (2.4–2.9)	3–4	51.6	Portugal	(Rangel et al., 2014)
O. orientalis	*Clupea harengus sprattus*	Ureter, kidney tubule	9.0 (8.5–9.2)	7.9 (7.7–8.0)	2.7 (2.3–2.9)	2.7 (2.3–2.9)	–	11.0	Denmark	(Karlsbakk and Køie, 2011)
O. africanus	*Oreochromis niloticus*	Urinary bladder	7.71±0.21 (6.93–.47)	7.67±0.25 (6.93–8.47)	2.87±0.24 (2.31–3.85)	2.87±0.24 (2.31–3.85)	4–5	44.7	Egypt	(Abdel-Ghaffar et al., 2008)
O. basma	*Clinus agilis*	Urinary bladder	13.5 ± 1.0 (12.0–15.0)	12.3 ± 0.5 (11.8–13.0)	4.3 ± 0.3 (4.0–4.8)	3.5 ± 0.5 (3.0–4.3)	4–5	16,6	South Africa	(Ali, 2000)
O. gadusiae	*Gudusia chapra*	Urinary bladder	10.8 (9.0–11.7)	9.2 (9.0–9.9)	2.8 (1.8–3.0)	2.0 (1.0–2.5)	4–5	3.6	India	(Sarkar, 1999a)
O. indica	*Macrospinosa cuja*	Urinary bladder, Kidney	7.4 ± 0.8 (6.5–9.0)	6.2 ± 0.5 (5.5–8.0)	1.7 ± 0.2 (1.5–2.0)	–	3–5	18.8	India	(Sarkar, 1999b)
O. fluviatilis	*Dichotomyctere fluviatilis*	kidney tubule and ducts	8.3 (7.9–8.4)	7.8 (7.3–8.0)	3.1 (2.8–3.3)	3.1 (2.8–3.3)	4–6	100	South Asia	(Lom and Dyková, 1995)
O. striateculus	*Leptatherina presbyteroides*	Ureter	10.1 (9.1–10.5)	10.0 (8.9–10.4)	3.5 (3.4–3.6)	2.9 (2.8–3.1)	5–7	0.3	Australia	(Su and White, 1994)
O. macrouri	*Coelorinchus fasciatus*	Urinary bladder	9.3–10.6	8.0–9.0	3.3–3.9	2.6	–	–	Namibia	(Kovaleva et al., 1993)
O. visakhapatnamensis	*Planiliza macrolepis*	Visceral peritoneum	5.9 (5.2–6.0)	5.9 (5.2–6.0)	3.0 (2.6–3.5)	2.2 (1.7–2.6)	5–6	20.3	India	(Padma Dorothy and Kalavati, 1993)
O. asymmétrica	*Caranx rhonchus*	Gall bladder	8.0–10.0	7.5–9.3	3.3–4.0	2.0–3.3	–	13.3	Africa	(Kovaleva et al., 1993)
O. australis	*Acanthopagrus australis, Rhabdosargus sarba*	Gall bladder	8.7 (7.8–10.4)	8.0 (7.3–9.5)	3.7 (2.8–4.4)	2.9 (2.3–3.2)	3–4	16.6 25	Australia	(Lom et al., 1992)
O. polymorpha	*Opsanus tau*	Urinary bladder	8.0 (7.0–10.0)	8.0 (7.0–10.0)	4.0–5.0	2.0–2.5	–	81.8	USA	(Davis, 1917)

(Fig. 2B and 2C).

3.2. Taxonomic summary

Species: *Ortholinea paraensis* n. sp. (Fig. 3)
Host: *Ageneiosus ucayalensis* Castelnau, 1855
Site of infection: Urinary bladder.
Prevalence: 28 (43.1 %) of the 65 specimens examined.
Type locality: Santo Antônio and Guajará Bays (01°15′0″ S; 48°30′0″ W), in the municipality of Belém, Pará state, Brazil.

Etymology: The species epithet alludes to the geographical origin of the species, that is, the Brazilian state of Pará.

Type specimen: Glass slide of a histological section, stained with Giemsa, containing a syntype of the new species, was deposited in the Zoology Museum of the National Institute for Amazonian Research (INPA) in Manaus, Amazonas, Brazil – Number: INPA-CND 000,107.

Molecular data: A partial rDNA SSU sequence of 1669 base pairs was deposited in GenBank, under accession number PQ816784.

Observed myxozoan co-infections: Infection by *Ellipsomyxa matosi* Pereira et al. (2025) was observed in the gallbladder of all (100 %) of the

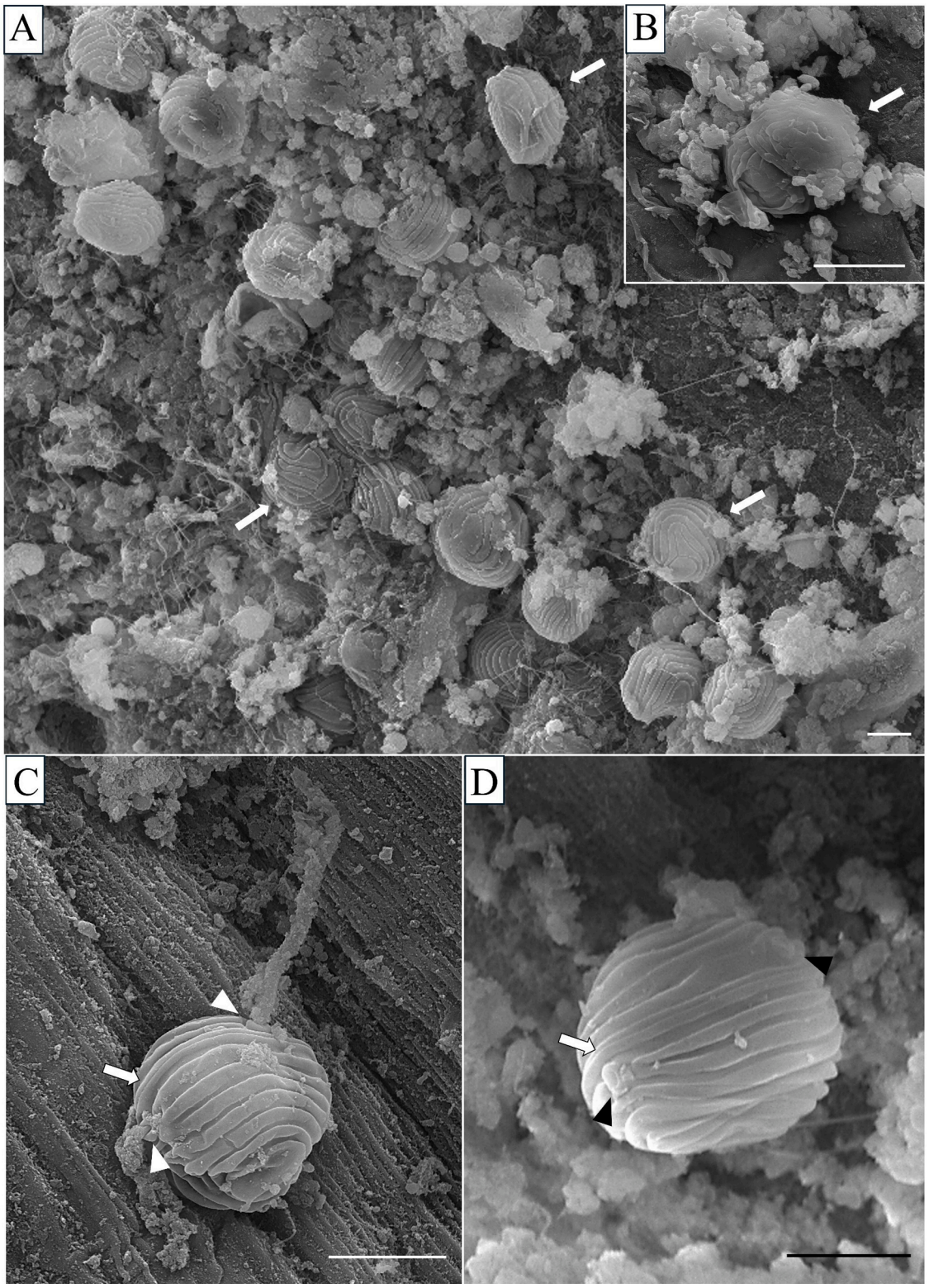


Fig. 2. Scanning electron microscopy of myxospores of *Ortholinea paraensis* n. sp. A: Myxospores in the apical and valvular views, showing ornamentation organized in crests (arrow), scale bar = 5 μm. B: Pairs of myxospores (arrow), scale bar = 10 μm. C: Myxospore showing the suture line (arrow) and discharge pore of the polar tubule, with the extrusion of the polar tubule (arrowhead), scale bar = 5 μm. D: Polar tubule discharge pores of each valve in the apical view (arrowhead) and a slightly undulating suture line (arrow), scale bar = 5 μm.

host specimens examined.

3.3. Phylogenetic analysis

The BLAST analysis revealed that the *Ortholinea paraensis* n. sp. sequence was most similar 93.8 % to that of *Hoferellus jutubensis*

Fig. 3. Diagram of *Ortholinea paraensis* n. sp., in the valvular view, Scale bar = 10 μm.

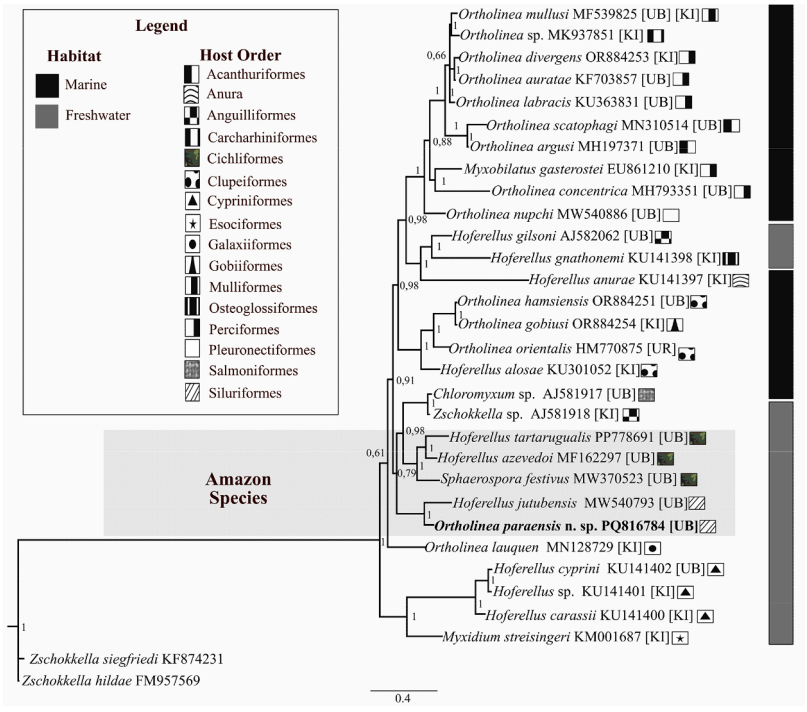


Fig. 4. Phylogenetic tree produced by Bayesian Inference (BI), based on the alignment of the partial SSU rDNA sequence of *Ortholinea paraensis* n. sp. with those of closely-related myxozoan species, highlighting the host habitat, infection site (UB = Urinary Bladder, UB = Ureter, and KI = Kidney), and the taxonomic order of the host. The number on each branch is the posterior probability of the BI. The new species is highlighted in bold script. The outgroup includes the myxosporeans *Zschokkella siegfriedi* (KF874231) and *Zschokkella hildae* (FM957569).

(MW540793), followed by *Ortholinea auratae* (KF703857), with a similarity of 88.8 %. Comparisons with other *Ortholinea* species also revealed a similarity of more than 88 %, including 88.7 %, in the case of *O. lauquen* (MN128729), 88.4 % for *O. divergens* (OR884253), 88.3 % for *Ortholinea* sp. (MK937851), 88.2 % for *O. argusi* (MH197371), and 88.1 % for *O. mullusi* (MF539825).

The phylogenetic analysis of the SSU rDNA sequences revealed a polyphyletic group of freshwater and marine *Ortholinea* species. *Ortholinea paraensis* n. sp. was identified as part of a group of species that infect the urinary bladder of fishes from the Brazilian Amazon, including *Hoferellus azevedoi* (host: *Chaetobranchus flavescens*), *H. tartarugualis* and *Sphaerospora festivus* (host: *Mesonauta festivus*), and *H. jutubensis*, a parasite of the driftwood catfish *Ageneiosus inermis* (Fig. 4). The smallest genetic distance *p* found between the *Ortholinea paraensis* n. sp. sequence and those of other myxozoans (Table 2) was 10.01 %, in the case of *H. jutubensis*, while the largest distance was 17.84 %, in the case of *O. labracis* (KU363831).

4. Discussion

The new species described here has morphological characteristics typical of the genus *Ortholinea*, including spherical myxospores, divergent polar capsules, superficial crests, and a suture line (Lom and Dyková, 2006). While the morphometric parameters of *Ortholinea paraensis* n. sp. are approximately similar to those of *O. saudii*, which infects primarily the renal tubules (Abdel-Baki et al., 2015), the morphology of the myxospore is distinct, given its sub-spherical shape and spherical polar capsules, which occupy half of the spore, in addition to differences in the number of coils of the polar tubule, the tissue parasitized, the host species, and geographic region. *O. saudii* also has smooth valves and an indistinct suture line.

The surface ridges of *Ortholinea paraensis* n. sp. resemble a ball of wool, similar to the widely-spaced ridges observed in *O. nupchi* (host: *Paralichthys olivaceus*) from South Korea, which has five to seven ridges, although they are more prominent, deeper, and intricate than those observed in the new species described here (Shin et al., 2023). Most of the *Ortholinea* species described up to now have external striations or ridges (Ali, 2000; Rangel et al., 2014; Alama-Bermejo and Hernández-Orts, 2018).

The presence of peripheral projections in the plasmodia, with the appearance of stereocilia, may be related to an enhanced capacity to adhere to the mucosa of the host's organ. These projections likely contribute to the nutritional flow of the plasmodia, enhancing their adherence, and the uptake of particles that contribute to the pinocytic activity of the plasmodium surface, as observed in many coelozoic myxozoans (Lom and Dyková, 1996; Uspenskaya, 1982; Rocha et al., 2011). Similar projections have also been observed in *O. basma*, a parasite of the agile klipfish, *Clinus agilis* (Ali, 2000), *O. africanus*, which infects the Nile tilapia, *Oreochromis niloticus* (Ali, 2009), *O. auratae*, a parasite of the fish *Sparus aurata* (Rangel et al., 2014), *O. labracis* – host, *Dicentrarchus labrax* (Rangel et al., 2017), and in *O. scatophagi*, a parasite of *Scatophagus argus* (Chandran et al. 2020). It is pertinent to note here that the urinary bladder has a transitional epithelium, whose tension varies considerably, which implies that the stereocilia may be important to guarantee the adhesion of the myxospore to the mucosa of this organ.

In the present study, the urinary bladder presented a slight morphological alteration at the attachment point of the myxospore, which did not appear to be pathological, given that the cell structure was apparently unaltered. However, the tension of the mucosa in the region of the attachment site altered the shape of the epithelium. It is important to emphasize here that, while the transitional epithelium is fluid in shape, it usually varies homogeneously throughout the mucosa and not in localized areas, as observed here. Few data are available on the patterns of pathogenicity in *Ortholinea* species, and pathological alterations have only been observed in the kidney, including cell necrosis, disintegration of the tubular epithelium, and obstruction of the renal tubules (Alama-Bermejo et al., 2019; Abdel-Baki et al., 2015). However, Lom et al. (1992) found that *O. australis* caused stagnation of the flow of bile and liver disorder when infecting the gallbladders of two fish hosts – *Acanthopagrus australis* and *Rhabdosargus sarba*.

The phylogenetic analysis revealed a number of polyphyletic groups, including species that present tropism to the urinary system of their hosts. The freshwater *Ortholinea* species (*O. lauquen* and *Ortholinea paraensis* n. sp.) form a taxonomically heterogeneous group, together with species of the genera *Hoferellus* and *Sphaerospora*, rather than a distinct marine clade. This arrangement may be related to evolutionary shifts in the characteristics of the myxozoans, as they adapted to different aquatic habitats (Fiala and Bartosova, 2010; Bartosova et al., 2011; Fiala et al., 2015). The results of previous studies indicate that the definitive hosts of *Ortholinea* species influence this phylogenetic arrangement; however, the number of species with the complete life cycle is still limited, with only actinospores of two species being observed in marine oligochaetes, *O. auratae* in *Limnodriloides agne* and *O. labracis* in hosts of the genus *Tectidrilus* (Rangel et al., 2015, 2017; Fiala et al., 2015; Holzer et al., 2018). To confirm this relationship with freshwater fish hosts, it will be necessary to describe the complete life cycle of *Ortholinea paraensis* n. sp. including its definitive host, which is probably a freshwater oligochaete.

In this analysis, the host of *Hoferellus jutubensis*, a sister species of *Ortholinea paraensis* n. sp., is the driftwood catfish *Ageneiosus inermis* (order Siluriformes), a member of the same genus as the host of the new species described here (Pereira et al., 2022). This indicates that, in addition to tissue tropism, the type of host may also influence the phylogenetic relationships among the parasites, as observed in other groups of histozoic myxozoans, such as *Myxobolus* and *Henneguya* (Carriero et al. 2013; Ferguson et al. 2008; Liu et al. 2019; Velasco et al. 2024). These relationships may be further clarified as the diversity of the coelozoic myxozoans is better defined in future studies.

Many fish undergo extensive migrations over the course of their life cycle, which may have influenced the grouping of these myxozoans into freshwater lineages (Kent et al., 2001; Rangel et al., 2017). *A. ucayalensis* is known to have a seasonal migration cycle, first reproducing in estuaries during the dry season and then migrating toward the headwaters of the rivers during the rainy season, to develop into the adults, which

Table 2
Genetic distance p (%) of *Ortholinea paraensis* n. sp. compared to species of *Ortholinea* and *Hoferellus*.

Species	(1)	(2)	(3)	(4)	(5)	(6)	(7)	(8)	(9)	(10)
(1) *Ortholinea paraensis* n. sp. (PQ816784)	–									
(2) *Hoferellus jutubensis* (MW540793)	10.01	–								
(3) *Ortholinea auratae* (KF703858)	16.64	21.47	–							
(4) *Ortholinea mullusi* (MF539825)	16.96	21.22	4.93	–						
(5) *Ortholinea divergens* (OR884253)	17.19	20.81	2.23	5.38	–					
(6) *Ortholinea nupchi* (MW540886)	17.32	20.60	11.56	11.18	11.63	–				
(7) *Ortholinea argusi* (MH197371)	17.54	21.15	9.43	8.61	9.14	12.74	–			
(8) *Ortholinea hamsiensis* (OR884251)	17.73	21.46	18.45	17.92	17.59	17.68	18.81	–		
(9) *Ortholinea gobiusi* (OR884254)	17.80	21.49	18.67	18.00	17.79	17.63	18.66	1.24	–	
(10) *Ortholinea labracis* (KU363831)	17.84	21.26	4.54	4.07	4.50	11.45	7.99	18.60	18.61	–

spend most of their life cycle in this fluvial environment (Röpke et al. 2016). This would explain why *Ortholinea paraensis* n. sp. groups with the freshwater species.

Overall, then, the molecular and morphological evidence presented here supports the description of *Ortholinea paraensis* n. sp. This is the first species of *Ortholinea* reported from Brazil.

Funding

This study received no specific grant from any funding agency in either the public, commercial or not-for-profit sectors.

CRediT authorship contribution statement

Camila Maria Barbosa Pereira: Writing – review & editing, Writing – original draft, Methodology, Investigation, Conceptualization. **Jhonata Eduard:** Writing – review & editing, Methodology. **José Francisco Berrêdo Reis da Silva:** Methodology. **Maria do Perpétuo Socorro Progene Vilhena:** Methodology. **José Ledamir Sindeaux Neto:** Writing – review & editing, Supervision, Methodology. **Michele Velasco:** Writing – review & editing, Writing – original draft, Supervision, Methodology, Conceptualization.

Declaration of competing interest

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

Acknowledgments

We dedicate this study to the memory of Professor Dr. Edilson Matos, an exceptional researcher in the field of parasitology, who was a fundamental inspiration to the research group that developed this analysis.

Data availability

Data will be made available on request.

References

Abdel-Baki, A.A.S., Soliman, H., Saleh, M., Al-Quraishy, S., El-Matbouli, M., 2015. *Ortholinea saudii* sp. nov. (Myxosporea: ortholineidae) in the kidney of the marine fsh *Siganus rivulatus* (Teleostei) from the Red Sea, Saudi Arabia. Dis. Aquat. Organ. 113, 25–32. https://doi.org/10.3354/dao02821.

Abdel-Ghafar, F., El-Toukhy, A., Al-Quraishy, S., Al-Rasheid, K., Abdel-Baki, A., Hegazy, A., Bashtar, A.R., 2008. Five new 5-orean species (Myxozoa: myxosporea) infecting the Nile tilapia *Oreochromis niloticus* in Bahr Shebin, Nile Tributary, Nile Delta, Egypt. Parasitol. Res. 103, 1197–1205. https://doi.org/10.1007/s00436-008-1116-z.

Alama-Bermejo, G., Hernández-Orts, J.S., 2018. *Ortholinea concentrica* n. sp. (Cnidaria: myxozoa) from the Patagonian seabass *Acanthistius patachonicus* (Jenyns, 1840) (Perciformes: serranidae) of Patagonia, Argentina. Parasitol. Res. 117, 3953–3963. https://doi.org/10.1007/s00436-018-6105-2.

Ali, M.A., 2000. *Ortholinea basma* n. sp. (Myxozoa: myxosporea) from agile klipfsh *Clinus agilis* (Teleostei: clinidae), light and scanning electron microscopy. Eur. J. Protistol. 36, 100–102. https://doi.org/10.1016/S0932-4739(00)80026-7.

Ali, M.A., 2009. Light and scanning electron microscopy (SEM) of *Ortholinea africanus* Abdel-Ghafar et al., 2008 (Myxozoa: myxosporea) infecting tilapia fsh *Oreochromis niloticus* (Osteichthyes: cichlidae) with description of preparation of coelozoic myxosporea for SEM. Acta protozool 48, 185–190.

Alama-Bermejo, G., Viozzi, G.P., Waicheim, M.A., Flores, V.R., Atkinson, S.D., 2019. Host-parasite relationship of *Ortholine lauquen* sp. nov. (Cnidaria: myxozoa) and the fish *Galaxias maculatus* in northwestern Patagonia. Argentina. Dis. Aquat. Organ 136, 163–174. https://doi.org/10.3354/dao03400.

Barta, J.R., Martin, D.S., Liberator, P.A., Dashkevicz, M., Anderson, J.W., Feighner, S.D., Elbrecht, A., Perkins-Barrow, A., Jenkins, M.C., Danforth, H.D., Ruff, M.D., Profous-Juchelka, H., 1997. Phylogenetic relationships among eight *Eimeria* species infecting domestic fowl inferred using complete small subunit ribosomal DNA sequences. J. Parasitol. 83, 262–271.

Bartosova, P., Freeman, M.A., Yokoyama, H., Caffara, M., Fiala, I., 2011. Phylogenetic position of *Sphaerospora testicularis* and *Latyspora scomberomori* n. gen. n. sp. (Myxozoa) within the marine urinary clade. Parasitology 138, 381–393.

Batista, V.S., Isaac, V.J., Fabré, N.N., Gonzalez, J.C.A., Almeida, O.T., Rivero, S., Júnior, J.N.O., Ruffino, M.L., Silva, C.O., Saint-Paul, U., 2012. Peixes e Pesca No Solimões Amazonas: Uma Avaliação Integrada. Ibama/PróVárzea, Brasília.

Carriero, M.M., Adriano, E.A., Silva, M.R.M., Ceccarelli, P.S., Maia, A.A.M., 2013. Molecular phylogeny of the *Myxobolus* and *Henneguya* genera with several new south american species. PLoS ONE 8, 73713. https://doi.org/10.1371/journal.pone.0073713. –73713.

Chandran, A., Zacharia, P.U., Sanil, N.K., 2020. *Ortholinea scatophagi* (Myxosporea: ortholineidae), a novel myxosporean infecting the spotted scat, *Scatophagus argus* (Linnaeus 1766) from southwest coast of India. Parasitol. Int. 75, 102020. https://doi.org/10.1016/j.parint.2019.102020.

Darriba, D., Taboada, G.L., Doallo, R., Posada, D., 2012. jModelTest 2: more models, new heuristics and parallel computing. Nat. Methods. 9, 772. https://doi.org/10.1038/nmeth.2109.

Davis, H.S., 1917. The Myxosporidia of the Beaufort region, a systematic and biological study. Bull. Bur. Fish. 35, 203–243.

De Oliveira Ferreira, D., Tavares-Dias, M., 2017. Ectoparasites and endoparasites community of *Ageneiosus ucayalensis* (Siluriformes: auchenipteridae), catfish from Amazon River system in northern Brazil. J. Parasit. Dis. 41, 639–646. https://doi.org/10.1007/s12639-016-0857-3.

Ferguson, J.A., Atkinson, S.D., Whipps, C.M., Kent, M.L., 2008. Molecular and Morphological Analysis of *Myxobolus* Spp. of Salmonid Fishes with the Description of a New *Myxobolus* Species. J. Parasitol. 94, 1322–1334. https://doi.org/10.1645/GE-1606.1.

Fiala, I., 2006. The phylogeny of myxosporea (myxozoa) based on small subunit ribosomal RNA gene analysis. Int. J. Parasitol. 36, 1521–1534.

Fiala, I., Bartosova, P., 2010. History of myxozoan character evolution on the basis of rDNA and EF-2 data. BMC Evol. Biol. 10, 228. https://doi.org/10.1186/1471-2148-10-228.

Fiala, I., Bartošová-Sojková, P., Whipps, C.M., 2015. Classification and phylogenetics of Myxozoa. In: Okamura, B., Gruhl, A., Bartholomew, J.L. (Eds.), Myxozoan Evolution, Ecology and Development. Springer, Cham, pp. 85–110. https://doi.org/10.1007/978-3-319-14753-6_5.

Freeman, M.A., Kristmundsson, Á., 2015. Histozoic myxosporeans infecting the stomach wall of elopiform fishes represent a novel lineage, the Gastromyxidae. Parasit. Vectors. 8, 1–13. https://doi.org/10.1186/s13071-015-1140-7.

Gürkanlı, C.T., Okkay, S., Çiftçi, Y., Yurakhno, V., Özer, A., 2018. Morphology and molecular phylogeny of *Ortholinea mullusi* sp. nov. (Myxozoa) in *Mullus barbatus* from the Black Sea. Dis. Aquat. Organ. 127, 117–124. https://doi.org/10.3354/dao03192.

Hahn, N.S., Fugi, R., Andrian, I.F., 2004. Trophic ecology of the fish assemblages. In: Thomaz, S.M., Agostinho, A.A., Hahn, N.S. (Eds.), The Upper Paraná River and Its Floodplain: Physical Aspects, Ecology and Conservation. Backhuys Publishers, Leiden, pp. 247–259.

Holzer, A.S., Bartošová-Sojková, P., Born-Torrijos, A., Lovy, A., Hartigan, A., Fiala, I., 2018. The joint evolution of the Myxozoa and their alternate hosts: a cnidarian recipe for success and vast biodiversity. Mol. Ecol. 27, 1651–1666. https://doi.org/10.1111/mec.14558.

Huelsenbeck, J.P., Ronquist, F., 2001. MrBayes: bayesian inference of phylogenetic trees. Bioinformatics 17, 754–755. https://doi.org/10.1093/bioinformatics/17.8.754.

Karlsbakk, E., Køie, M., 2011. Morphology and SSU rDNA sequences of *Ortholinea orientalis* (Shul'man and Shul'man-Albova, 1953) (Myxozoa, Ortholineidae) from *Clupea harengus* and *Sprattus sprattus* (Clupeidae) from Denmark. Parasitol. Res. 109, 139–145. https://doi.org/10.1007/s00436-010-2237-8.

Kearse, M., Moir, R., Wilson, A., Sones-Havas, S., Cheung, M., Sturrock, S., Buxton, S., Cooper, A., Markowitz, S., Duran, C., Thierer, T., Ashton, B., Meintjes, P., Drummond, A., 2012. Geneious basic: an integrated and extendacle desktop platform for the organization and analysis of sequence data. Bioinformatics 28, 1647–1649. https://doi.org/10.1093/bioinformatics/bts199.

Kent, M.L., Andree, K.B., Bartholomew, J.L., El-Matbouli, M., Desser, S.S., Devlin, R.H., Feist, S.W., Hedrick, R.P., Hoffmann, R.W., Khattra, J., Hallett, S.L., Lester, R.J.G., Longshaw, M., Palenzeula, O., Siddall, M.E., Xiao, C., 2001. Recent advances in our knowledge of the Myxozoa. J. Eukaryot. Microbiol. 48, 395–413.

Kovaleva, A.A., Velev, P., Vladev, P., 1993. New data on myxosporidians (Cnidospora: myxosporea) fauna from commercial fishes of the Atlantic coast of Africa. In: Bukatin, P.A. (Ed.), Ecology and Resources of Commercial Fishes of the Eastern Atlantic. AtlantNIRO, Russian, pp. 174–194.

Larsson, A., 2014. AliView: a fast and lightweight alignment viewer and editor for large datasets. Bioinformatics 30, 3276–3278. https://doi.org/10.1093/bioinformatics/btu531.

Liu, Y., Lövy, A., Gu, Z., Fiala, I., 2019. Phylogeny of Myxobolidae (Myxozoa) and the evolution of myxospore appendages in the *Myxobolus* clade. Int. J. Parasitol. 49, 523–530. https://doi.org/10.1016/j.ijpara.2019.02.009.

Lom, J., Arthur, J.R., 1989. A Guideline for the Preparation of Species Descriptions in Myxosporea. J. Fish Dis. 12, 151–156. https://doi.org/10.1111/j.1365-2761.1989.tb00287.x.

Lom, J., Rohde, K., Dyková, I., 1992. Studies on protozoan parasites of Australian fishes. 1. New species of the genera *Coccomyxa* Leger et Hesse, 1907, *Ortholinea* Shulman, 1962 and *Kudoa* Meglitsch, 1947 (Myxozoa, Myxosporea). Folia. Parasitol 39, 289–306.

Lom, J., Dyková, I., 1995. New species of the genera *Zschokkella* and *Ortholinea* (Myxozoa) from the Southeast Asian teleost fish, *Tetraodon fuviatilis*. Folia Parasitol 42, 161. –16.

Lom, J., Dyková, I., 1996. Notes on the ultrastructure of two myxosporean (Myxozoa) species, *Zschokkella pleomorpha* and *Ortholinea fluviatilis*. Folia Parasitol 43, 189–202.
Lom, J., Dyková, I., 2006. Myxozoan genera: definition and notes on taxonomy, life-cycle terminology and pathogenic species. Folia. Parasitol 53, 1–36. https://doi.org/10.14411/fp.2006.001.
Okkay, S., Özer, A., 2020. New locality and host record of some myxozoan parasite species (Cnidaria) off Turkish coast of the Black Sea. Acta. Zoo. Bulg. 72, 123–130.
Okkay, S., Gürkanlı, C.T., Çiftçi, Y., Özer, A., 2024. New molecular evidence on the members of the genus *Ortholinea* (Cnidaria, Myxozoa) and the description of *Ortholinea hamsiensis* n. sp. infecting the urinary bladder of European anchovy *Engraulis engrasicolus* in the Black Sea. Parasitology 151, 485–494. https://doi.org/10.1017/S0031182024000325.
Padma Dorothy, K., Kalavati, C., 1993. A new myxosporean parasite, *Ortholinea visakhapatnamensis* n.sp from the mullet, *Liza macrolepis* from Visakhapatnam Harbour. India. Riv. Parassitol. 54, 461–465.
Pereira, C.M.B., Guerreiro, S.L.M., Silva, D.T., Azevedo, R.K., Matos, E.R., Hamoy, I.G., 2022. Morphology and molecular phylogeny of *Hoferellus jutubensis* n. sp. (Cnidaria: myxozoa) found parasitising *Ageneiosus inermis* (Siluriformes: auchenipteridae), in the Brazilian Amazon region. Parasitol. Int. 86, 102445. https://doi.org/10.1016/j.parint.2021.102445.
Pereira, C.M.B., Oliveira, J.E.F., Santos, M.N.S., Pereira, L.P.B., Hamoy, I.G., Silva, M.F., Sindeaux-Neto, J.L., Velasco, M., 2025. New species of *Ellipsomyxa* (Bivalvulida: Ceratomyxidae) parasitizing the gallbladder of *Ageneiosus ucayalensis* (Siluriformes: Auchenipteridae) in the Brazilian Amazon region. Parasitol. Int. 106, 103036. https://doi.org/10.1016/j.parint.2025.103036.
Rambaut, A., 2016. FigTree v1.4.3: tree Figure Drawing Tool. Available at: http://tree.bio.ed.ac.uk/software/figtree/.
Rangel, L.F., Rocha, S., Borkhanuddin, M.H., Cech, G., Castro, R., Casal, G., Azevedo, C., Severino, R., Székely, C., Santos, M.J., 2014. *Ortholinea auratae* n. sp. (Myxozoa, Ortholineidae) infecting the urinary bladder of the gilthead seabream *Sparus aurata* (Teleostei, Sparidae), in a Portuguese fish farm. Parasitol. Res. 113, 3427–3437. https://doi.org/10.1007/s00436-014-4008-4.
Rangel, L.F., Rocha, S., Castro, R., Severino, R., Casal, G., Azevedo, C., Cavaleiro, F., Santos, M.J., 2015. The life cycle of *Ortholinea auratae* (Myxozoa: ortholineidae) involves an actinospore of the triactinomyxon morphotype infecting a marine oligochaete. Parasitol. Res. 114, 2671–2678. https://doi.org/10.1007/s00436-015-4472-5.
Rangel, L.F., Rocha, S., Casal, G., Castro, R., Severino, R., Azevedo, C., Cavaleiro, F., Santos, M.J., 2017. Life cycle inference and phylogeny of *Ortholinea labracis* n. sp. (Myxosporea: ortholineidae), a parasite of the European seabass *Dicentrarchus labrax* (Teleostei: moronidae), in a Portuguese fish farm. J. Fish Dis. 40, 243–262. https://doi.org/10.1111/jfd.12508.
Rangel, L.F., Rocha, S., Santos, M.J., 2024. Synopsis of the species of *Ortholinea* Shulman, 1962 (Cnidaria: myxosporea: ortholineidae). Syst. Parasitol. 101, 37. https://doi.org/10.1007/s11230-024-10155-2.
Ribeiro, F.R., Rapp Py-Daniel, L.H., Walsh, S.J., 2017. Taxonomic revision of the South American catfish genus *Ageneiosus* (Siluriformes: auchenipteridae) with the description of four new species. J. fish bio. 90, 1388–1478. https://doi.org/10.1111/jfb.13246.
Rocha, S., Casal, G., Matos, P., Dkhil, M., Azevedo, C., 2011. Descrição de *Triangulamyxa psittaca* sp. nov. (Myxozoa: myxosporea), um novo parasita da bexiga urinária de *Colomesus psittacus* (Teleostei) do Rio Amazonas, com ênfase na ultraestrutura dos estágios plasmodiais. Acta Protozool 50, 327–338. https://doi.org/10.4467/16890027AP.11.030.0067.
Ronquist, F., Huelsenbeck, J.P., 2003. Mr Bayes 3: bayesian phylogenetic inference under mixed models. Bioinformatics 19, 1572–1574.
Röpke, C.P., Amadio, S.A., Winemiller, K.O., Zuanon, J., 2016. Seasonal dynamics of the fish assemblage in a floodplain lake at the confluence of the Negro and Amazon Rivers. J. Fish Biol. 89, 194–212. https://doi.org/10.1111/JFB.12791.
Sarkar, N.K., 1999a. *Ortholinea gadusiae* sp. n. and *Sphaeromyxa opisthopterae* sp. n. (Myxozoa: myxosporea) from the clupeid fish of the Bay of Bengal, West Bengal, India. Acta Protozool 38, 145–153.
Sarkar, N.K., 1999b. Some new Myxosporidia (Myxozoa: myxosporea) of the genera *Myxobolus* Butschli, 1882 *Unicapsula* Davis, 1942 *Kudoa* Meglitsch, 1947 *Ortholinea* Shulman, 1962 and *Neoparvicapsula* Gaevskaya, Kovaleva and Shulman, 1982. Proc. Zool. Soc. Lond. 52, 38–48.
Sá-Oliveira, J.C., Maciel, A.G.P., Araújo, A.S., Isaac-Nahum, V.J., 2014. Dieta do mandubé, *Ageneiosus ucayalensis* (Castelnau, 1855) (Osteichthyes: auchenipteridae) do Reservatório da Usina Hidrelétrica Coaracy Nunes, Ferreira Gomes-Amapá, Brasil. Biota Amazon. 4, 73–82. https://doi.org/10.18561/2179-5746/biotaamazonia.v4n3p73-82.
Shin, S.P., Jin, C.N., Sohn, H., Kim, J., Lee, J., 2023. *Ortholinea nupchi* n. sp. (Myxosporea: ortholineidae) from the urinary bladder of the cultured olive founder *Paralichthys olivaceus*, South Korea. Parasitol. Int. 94, 102734. https://doi.org/10.1016/j.parint.2019.102020.
Shulman, S.S., 1962. Myxosporidia. In: Pavlovskii, E.N. (Ed.), Key to parasites of freshwater fish of USSR. Publ. House of the Academy of Sciences of the USSR, pp. 47–130 (In Russian).
Su, X., White, R.W.G., 1994. New Myxosporeans (Myxozoa: myxosporea) from Marine Fishes of Tasmania, Australia. Acta Protozool 33, 251. –25.
Uspenskaya, A.V., 1982. New Data on the Life Cycle and Biology of Myxosporidia. Archiv. Protistenkd. 126, 309–338. https://doi.org/10.1016/s0003-9365(82)80041-9.
Velasco, M., Neto, J.L.S., Eduard, J., Gonçalves, E.C., Videira, M., Oliveira, E., Matos, E., 2024. New species of *Myxobolus* in potamodromous catfish from the eastern Amazon. Brazil. Parasitol. Int. 103, 102939. https://doi.org/10.1016/J.PARINT.2024.102939.