

New species of *Ellipsomyxa* (Bivalvulida: Ceratomyxidae) parasitizing the gallbladder of *Ageneiosus ucayalensis* (Siluriformes: Auchenipteridae) in the Brazilian Amazon region

Camila Maria Barbosa Pereira^a, Jhonata Eduard Farias de Oliveira^b,
Marcia de Nazaré Sacco dos Santos^b, Lana Priscila Barbosa Pereira^c, Igor Guerreiro Hamoy^d,
Marcelo Francisco da Silva^e, José Ledamir Sindeaux-Neto^f, Michele Velasco Oliveira da Silva^{f,*}

^a Amazon Biodiversity and Biotechnology Network (BIONORTE), Federal University of Pará (UFPA), Belém, Pará, Brazil

^b Biology of Infectious and Parasitic Agents (BAIP), Federal University of Pará (UFPA), Belém, Pará, Brazil

^c Supreme Redeemer faculty (FACSUR), Pinheiro, Maranhão, Brazil

^d Socio-Environmental and Water Resources Institute (ISARH), Federal Rural University of Amazonia (UFRA), Belém, Pará, Brazil

^e State University of the Tocantina Region of Maranhão (UEMASUL), Imperatriz, Maranhão, Brazil

^f Morpho-molecular Integration and Technologies Laboratory (LIMT), Institute of Animal Health and Production (ISPA), Federal Rural University of Amazonia (UFRA), Belém, Pará, Brazil

ARTICLE INFO

Keywords:

Fish
Myxozoa
Morphology
Molecular description

ABSTRACT

The present study describes a new myxozoan species, *Ellipsomyxa matosi* n. sp. infecting the gallbladder of the catfish *Ageneiosus ucayalensis*, on Jutuba Island, municipality of Belém, state of Pará, Brazil. The new species was diagnosed based on morphological and molecular analyses. 33 specimens were examined between February and May 2023, and all (100 %) presented disporic plasmodia in the bile fluid, with ellipsoidal, slightly elongated mature myxospores, with a subtle valve projection in the apical region and a curved suture line, typical morphological characteristics of the genus *Ellipsomyxa*. The polar capsules were pyriform and of equal size, with a subterminal opening and 6–7 polar tubule coils. No histopathological changes, lesions, or inflammatory responses were observed in the epithelial layer or any part of the tissue. PCA identified the proximity in spore length (SL) of the new species to *E. amazonensis* and *E. papantla*. The partial SSU rDNA sequence obtained was distinct from all other available sequences from species of this genus. The phylogenetic analysis obtained high nodal support, grouping the new species as an ancestor of the well-defined clade of *Ellipsomyxa* species described in the Amazon region.

1. Introduction

Myxozoans constitute a group of prominent parasites in fish, comprising a heterogeneous and widely distributed collection of endoparasites with pathogenic potential, with a considerable variety of forms, reported in different organs or tissues [1–4]. They belong to the Phylum Cnidaria, with more than 2600 species described worldwide in marine and freshwater environments, classified into 64 genera [1,5–7].

The myxosporean of the genus *Ellipsomyxa* Kōie, 2003, a member of the family Ceratomyxidae Doflein, 1899, in the order Bivalvulida [8]. However, phylogenetic aspects show greater proximity to marine

Myxidium than to *Ceratomyxa* species [2,8,9]. *Ellipsomyxa* species form plasmodia, monosporic or disporic, elongated myxospores, with polar capsules located at opposite ends, have a well-defined suture line in the transversal plane, which may be straight or sinuous, and show tropism for fish gallbladders [5,8–12]. At present, only seven species have been identified in the Amazon region based on morphological and phylogenetic traits, except *E. gobioides* [4,14–18].

In the Amazon region, the catfish *Ageneiosus ucayalensis* Castelnau, 1855, from the order Siluriformes, has a wide distribution in the river Brazilian Amazon basin, with wide spatial distribution in the water column, carrying out annual reproductive migrations, being an

* Corresponding author at: Morpho-Molecular Integration Laboratory and Technologies 16 (LIMT), Avenida Presidente Tancredo Neves, N° 2501 Neighborhood, Montese, City, Belém, Pará 66.077-901, Brazil.

E-mail address: michele.velasco@ufra.edu.br (M.V.O. da Silva).

<https://doi.org/10.1016/j.parint.2025.103036>

Received 23 October 2024; Received in revised form 21 December 2024; Accepted 16 January 2025

Available online 17 January 2025

1383-5769/© 2025 Elsevier B.V. All rights are reserved, including those for text and data mining, AI training, and similar technologies.

important source of subsistence for riverside communities [19–21].

The present study describes a new species of myxozoan, *Ellipsomyxa matosi* n. sp., which was found in the gall bladder of specimens of catfish, *A. ucayalensis*, collected from Jutuba Island, in the municipality of Belém, in Pará state, Brazil, based on morphological and molecular analyses.

2. Materials and methods

2.1. Sample collection

A total of 33 *A. ucayalensis* specimens were collected from Jutuba Island (01°15' S, 48°30' W), in the northern Brazilian state of Pará, between February and May 2023. This island is located between Santo Antônio and Guajará bays, in the southeastern extreme of the estuary of the Amazon River.

The specimens were transported alive to the Carlos Azevedo Research Laboratory - LPCA, located on the Belém campus of the Federal Rural University of Amazonia- UFRA, in Pará state. In the laboratory, the fish were anaesthetized with 50 mg/L of tricaine (MS 222) and necropsied under a light stereomicroscope for the detection of myxozoans on the surface of the body and in the internal organs.

The analysis of the specimens presented here was authorized by the UFRA Ethics Committee for the Use of Animals in Research (CEUA 8323110522) and by a license from the Brazilian Institute for the Environment and Renewable Natural Resources, IBAMA (SISBIO/ICM-Bio license number 27119–1).

2.2. Morphological analysis

As myxospores were observed in the gall bladder, the organ was removed for histological analysis, for which it was fixed in Davidson solution (ethanol, formaldehyde, acetic acid, and distilled water) for 24 h. They were subsequently dehydrated in an increasing ethanol series, diaphanized in xylol, and included in paraffin. Then, 5 µm thick sections were obtained using a microtome and stained with special Ziehl-Neelsen technique [22].

The fresh myxospores and the stained slides were photographed under a Zeiss Primo Star Differential Interference Contrast (DIC) microscope attached to an AxioCamErc 5 camera equipped with AxioVision LE software. The fresh myxospores ($n = 32$) were measured (µm) following the protocol of [23], with the mean values being calculated for each parameter.

2.3. Phylogenetic analysis

For the molecular analysis, myxospores were fixed in 80 % ethanol for the extraction of the DNA using the PureLink Genomic kit (Invitrogen, USA), following the protocol provided by the manufacturer. The amplification of the Small Subunit of the ribosomal DNA (SSU rDNA) by Polymerase Chain Reaction (PCR) using the standard primers 18E and 18R in the first round of amplification [24,25]. The second amplification uses the primers MC5 and MC3 [25,26].

The reaction protocol for the 18E/18R primers consisted of an initial extension at 95 °C for 5 min, followed by 35 cycles of 94 °C for 50 s, 52 °C for 50 s, and 68 °C for 1 min and 30 s, with a final extension at 68 °C for 10 min. The protocol for the second sequencing reaction, with the MC3/MC5 primers, consisted of an initial extension at 95 °C for 5 min, followed by 35 cycles of 95 °C for 30 s, 56 °C for 30 s, and 72 °C for 1 min, with a final extension at 72 °C for 10 min. Following these procedures, 5 µL of the amplicons was electrophoresed in 1 % agarose gel with Tris-borate-EDTA (TBE) and viewed under blue light. The PCR products were purified and sequenced using the Big Dye Terminator v3.1 sequence cycling kit (Applied Biosystems, USA), following the manufacturer's instructions.

The resulting sequences were aligned in BioEdit [27], with

ambiguous bases being resolved using the respective chromatograms. The SSU rDNA sequences of the myxozoans that are most closely related to the new taxon were identified based on the highest similarity scores recovered using the Basic Local Alignment Search Tool (BLAST). These sequences were used for the subsequent phylogenetic analyses. The best nucleotide substitution model indicated for the data set, indicated in the jModelTest software, version 0.1.1, was GTR + G [28,29]. Phylogenetic analyzes by Bayesian inference analysis were performed in the multi-platform software BEAST v.1.8.4 [30], using a relaxed, uncorrelated lognormal model [31] based on the birth-death speciation process [32], with a principal tree being derived from the unweighted pair group method with arithmetic mean (UPGMA). The Markov Chain Monte Carlo (MCMC) was run for 10,000,000 generations and sampled every 10,000 steps [33]. The software Tracer [34], TreeAnnotator v1.8.4 [35], and FigTree v.1.4.3 [36] were used to verify the convergence of analysis results and generate the maximum redibility of the clad tree, with 10 % burn-in.

The reliability of the phylogeny was verified by a likelihood mapping analysis, which was run in Tree-Puzzle 5.2, following the approach of [37]. The genetic distances were calculated in PAUP*, 4.0b1 [38] using the standard p parameter for the SSU rDNA gene.

2.4. Data analysis

A principal component analysis (PCA) was carried out on the variable's length and width of the myxospores (SL and SW), as well as length and width of the polar capsules (PL and PW). Furthermore, the Pearson correlation approach was used to assess the relationship between the variables, both of which were performed using the Past Statistics software [39].

3. Results

3.1. Morphological description and taxonomic summary

The analysis of the 33 host specimens revealed the presence of several disporic plasmodia irregular morphology, observed free and attached to the gallbladder of all the individuals (Fig. 1A), that is, a prevalence of 100 %, varying only in the intensity of infection. Free mature myxospores, with extruded polar tubule that presented morphological characteristics typical of the genus *Ellipsomyxa* (Fig. 1B).

Mature myxospores that were slightly elongated and ellipsoid, measuring 13.1 ± 1.0 (11.9–14.4) µm in length and 8.0 ± 0.8 (7.2–9.4) µm in width, with a slight valvular projection in the apical region and curved suture line. Slightly pyriform polar capsules of equal size, 4.9 ± 0.3 (4.4–5.4) µm in length and 3.2 ± 0.6 (2.6–3.9) µm in width, with subterminal openings, in opposite extremities of the myxospores, space between polar capsules 3.4 ± 0.5 (3.1–3.7) µm in apical view, with 6–7 polar tubule coils was arranged perpendicularly to the longitudinal axis of each polar capsule (Fig. 1C and D) (Table 1).

The histological analysis with the ZN staining revealed myxospores with highlighted polar capsules floating freely in the bile or adhering to the epithelium of the organ (Fig. 1E and F). No histopathological alterations, lesions, or inflammatory responses, in the epithelial layer were observed or anywhere in the tissue.

Genus: *Ellipsomyxa* Køie, 2003.

Species: *Ellipsomyxa matosi* n. sp. (Fig. 2).

Host species: *A. ucayalensis* Castelnau, 1855.

Infection site: gallbladder.

Type locality: Brazil, state of Pará, municipality of Belém, Jutuba Island (01°15'0" S, 48°30'0" W).

Type specimens: A glass slide with a histological section, stained with ZN, containing a syntype of the new myxozoan species was deposited in the Museum of Zoology of the National Institute of Amazonian Research (INPA) in Manaus, Amazonas, Brazil – Number: 000106.

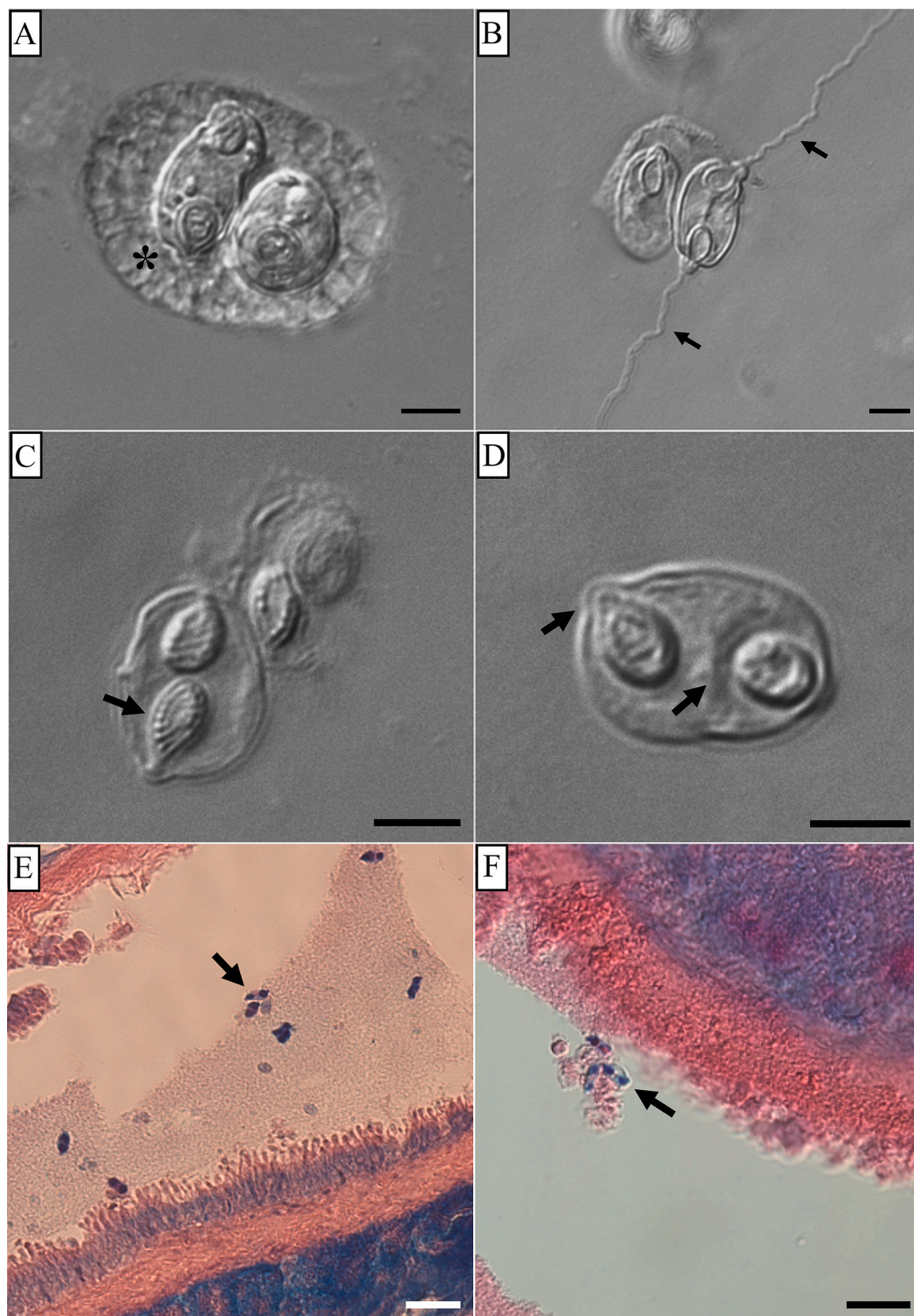


Fig. 1. Light photomicrographs (DIC) of *Ellipsomyxa matosi* n. sp. from the gall bladder of *A. ucayalensis*: (A) Plasmodium (*) containing two mature spores floating in the bile (Scale bar = 5 µm); (B) Spore undergoing the extrusion of the polar tubule (arrow) (Scale bar = 5 µm); (C) Spore showing the polar capsules in the opposite extremities, and the polar tubule, with 6–7 coils (arrow) (Scale bar = 5 µm); (D) Spore with valvular projection and curved suture line (arrow) (Scale bar = 5 µm). Histological section of the gall bladder of *A. ucayalensis*, prepared using the ZN staining technique (E) *Ellipsomyxa matosi* n. sp. spores floating in the bile (Scale bar = 20 µm); (F) Spores adhered to the wall of the gall bladder (Scale bar = 20 µm).

Table 1

Descriptive parameters of the spore and polar capsule (mean length and width, with standard deviation and amplitude) of *Ellipsomyxa matosi* n. sp. and comparisons with the same parameters recorded in other *Ellipsomyxa* species. N = number of coils of the polar tubule.

Species	Host	Spore shape	Spore (µm)		Spore (µm)		N	Country	References
			Long	Wide	Long	Wide			
<i>Ellipsomyxa matosi</i> n. sp.	<i>Ageneiosus ucayalensis</i>	ellipsoid	13.1 ± 1.0 (11.9–14.4)	8.0 ± 0.8 (7.2–9.4)	4.9 ± 0.3 (4.4–5.4)	3.2 ± 0.6 (2.6–3.9)	6–7	Brazil	Present study
<i>Ellipsomyxa santarenensis</i>	<i>Satanoperca jurupari</i>	ellipsoid	12.0 (10.7–13.7)	7.6 (5.6–8.2)	2.8 (2.0–3.6)	2.8 (2.1–3.7)	4–5	Brazil	[4]
<i>Ellipsomyxa tucujuensis</i>	<i>Satanoperca jurupari</i>	ellipsoid	10.11 ± 0.86	7.81 ± 1.14	3.1 ± 0.53	2.5 ± 0.32	5–6	Brazil	[17]
<i>Ellipsomyxa paraensis</i>	<i>Cichla monoculus</i>	ellipsoid	11.5 (10.5–12.4)	7.5 (6.6–8.6)	3.2 (2.1–3.9)	2.6 (2–3.3)	2–3	Brazil	[15]
<i>Ellipsomyxa plagioscioni</i>	<i>Plagioscion squamosissimus</i>	ovoid	11.1 (10.2–12.8)	6.6 (5.6–7.6)	3.8 (3.2–4.4)	2.8 (2.3–3.3)	5–6	Brazil	[15]
<i>Ellipsomyxa arariensis</i>	<i>Pigocentrus nattereri</i>	ellipsoid	12.6 (12.0–13.4)	7.3 (6.7–8.0)	3.5 (3.4–4.0)	2.6 (2.5–3.2)	5–6	Brazil	[18]
<i>Ellipsomyxa amazonensis</i>	<i>Pimelodus ornatus</i>	ellipsoid	12.8 (12.3–13.6)	7.6 (6.7–8.7)	3.8 (3.8–4.0)	3.1 (2.5–3.4)	2–3	Brazil	[16]
<i>Ellipsomyxa gobioides</i>	<i>Brachyplatystoma rousseauxii</i>	ellipsoid	6.8 (6.5–7.0)	7.2 (6.9–7.5)	4.6 (4.3–4.8)	2.5 (2.1–2.7)	5–6	Brazil	[14]
<i>Ellipsomyxa manilensis</i>	<i>Gobioides broussonnetii</i>	ellipsoid	11.8 ± 1.1 (10.2–13.3)	15.2 ± 1.1 (13.8–17.1)	5.6 ± 0.6 (4.6–6.6)	4.5 ± 0.3 (4.2–5.0)	3–4	Australia	[9]
<i>Ellipsomyxa arothroni</i>	<i>Arothron hispidus</i>	ovoid	11.7 ± 0.9 (9.9–13.6)	15.4 ± 1.3 (12.3–17.7)	6.6 ± 0.6 (5.4–7.9)	4.5 ± 0.4 (3.9–5.4)	4	Australia	[9]
<i>Ellipsomyxa nigropunctatus</i>	<i>Arothron nigropunctatus</i>	ovoid	9.9 ± 1.5 (8.0–12.9)	13.8 ± 1.1 (11.9–16.3)	4.7 ± 0.6 (3.5–5.7)	3.6 ± 0.5 (2.8–4.6)	5	Australia	[9]
<i>Ellipsomyxa adlardi</i>	<i>Gobiosoma bosc</i>	ellipsoid	12.4 (11.3–14.4)	7.7 (7.1–8.8)	4.3 (3.9–4.9)	3.6 (3.3–4.1)	5–6	USA	[10]
<i>Ellipsomyxa syngnathi</i>	<i>Syngnathus typhle</i>	ellipsoid	6.8 (6.3–7.2)	8.1 (7.2–8.6)	3.6 (3.2–4.1)	2.9 (2.7–3.2)	5–6	Denmark	[11]
<i>Ellipsomyxa boleophthalmi</i>	<i>Boleophthalmus dussumieri</i>	ellipsoid	9.8 ± 0.5 (9.0–10.7)	7.2 ± 0.6 (6.0–7.8)	2.8 ± 0.3 (2.6–2.8)	–	3–4	India	[12]
<i>Ellipsomyxa gobii</i>	<i>Pomatoschistus microps</i>	ellipsoid	7.0 (6.6–7.5)	8.7 (8.0–9.0)	3.1 (3.0–3.2)	–	6–7	Denmark	[8]
<i>Ellipsomyxa mugili</i>	<i>Liza saliens</i> ; <i>Mugil cephalus</i> ; <i>Liza ramada</i>	ovoid	11.5 (10–13.5)	6.8 (5.5–8.0)	2.9 (2.7–4.0)	–	5	Spain	[13]
<i>Ellipsomyxa apogoni</i>	<i>Apogon doederlein</i>	ellipsoid	10.2 (8.8–11.1)	6.9 (6.0–9.1)	3.7 (2.9–4.8)	2.7 (2.1–3.4)	2–3	Australia	[9]
<i>Ellipsomyxa kalthoumi</i>	<i>Liza saliens</i>	ellipsoid	17.2 (13–21)	13.2 (10–15)	5.5 (5.0–6.0)	–	9	Tunisia	[40]
<i>Ellipsomyxa papantla</i>	<i>Dormitator maculatus</i>	ovoid	12.9 ± 0.8 (11.6–15.0)	9.1 ± 0.5 (7.6–9.9)	3.8 ± 0.5 (2.6–4.6)	3.3 ± 0.5 (2.2–4.2)	3–4	México	[7]

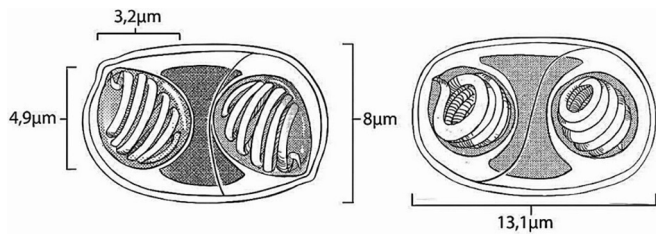


Fig. 2. Diagram of the spore of *Ellipsomyxa matosi* n. sp.

GenBank accession number: Partial sequence of 18S rDNA gene 1324 bp (PQ373927).

Etymology: The specific name is a homage to Dr. Edilson Matos, one of the pioneers in studying myxospores in the Brazilian Amazon Basin.

3.2. Morphometric analysis

In the PCA, component 1 accounted for 64.9 % of variance, whereas component 2 accounted for 34.4 %. *Ellipsomyxa matosi* n. sp. had a negative relationship with component 1 (Fig. 3), had been close to *E. amazonensis* and *E. papantla* due to its proximity to SL (Table 1). However, it can be shown that the main variable that influenced component 1 was SW, with the species *E. nigropunctatus*, *E. arothroni*, *E. manilensis*, and *E. kalthoumi* having the highest positive correlation, while PL and SL mainly influenced component 2, presenting respectively 32.2 % and 2.2 % of the variance. Overall, SW demonstrates a strong positive and significant relationship with both PW and PL, as has PL and

PW (Fig. 4).

3.3. Phylogenetic analysis

The partial SSU rDNA sequence of *Ellipsomyxa matosi* n. sp. presented 1324 base pairs, differing from the available aligned sequences of other *Ellipsomyxa* species, available in GenBank. BLAST searches revealed that the greatest genetic identity with *E. paraensis* 92.12 % (MH364399), followed by *E. amazonensis* 92.04 % (MF193889).

Analysis of the genetic distances between *Ellipsomyxa* species, revealed smaller distance with *E. santarenensis* (OR142132) 5.82 %, and greater divergence with *E. tucujuensis* (MN999871) 13.48 % (Table 2).

The phylogenetic analysis obtained high nodal support, grouping *E. matosi* n. sp. as an ancestor of the well-defined clade of *Ellipsomyxa* species described in the Amazon region, with hosts from freshwater. The molecular analysis presented here included 26 myxozoans and identified clades containing species of the genera *Myxidium*, *Tetracapsuloides*, *Buddenbrockia* and *Ellipsomyxa*. the outer group being formed by *Tetracapsuloides bryosalmonae* and *Buddenbrockia plumatellae* (Fig. 5).

4. Discussion

The general morphology of the myxospores of *Ellipsomyxa matosi* n. sp. is typical of that of the other species of the genus *Ellipsomyxa* described [8,9,10,11,12,13,36]. Mature Plasmodium disporic were also observed in *E. tucujuensis*, *E. arariensis*, *E. amazonensis*, *E. gobioides*, *E. kalthoumi*, *E. gobii*, *E. syngnathi* [8,11,14,16,17,18,40]. All *Ellipsomyxa* species described from the Brazilian Amazon region have ellipsoid spores [4,14,15,16,17,18].

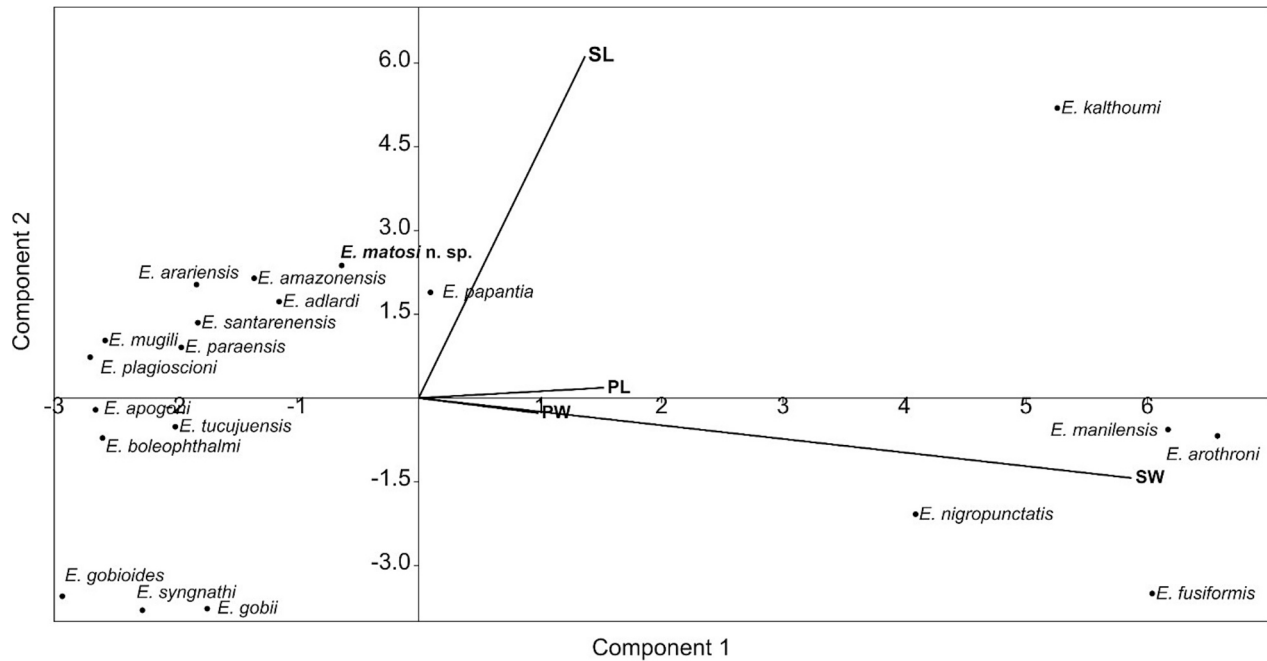


Fig. 3. PCA of *Ellipsomyxa* myxospores using the variables SL, SW, PL, and PW.

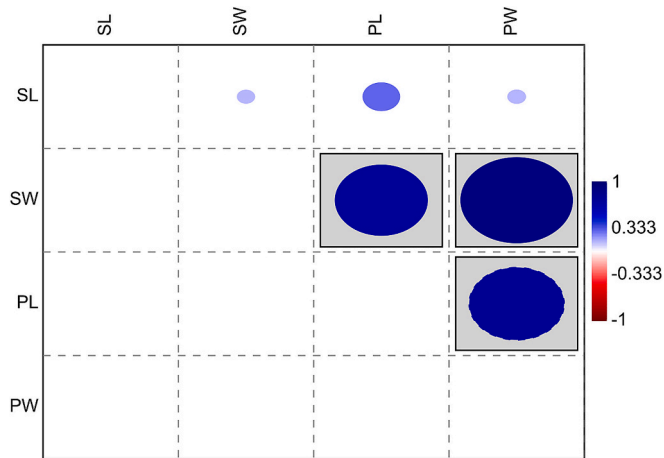


Fig. 4. Coefficient of relationship of the morphometric variables of myxospores, the boxes indicate positive correlations with significant value (p-value<0.05).

Table 2
Genetic distances (p distances) between pairs of *Ellipsomyxa* species from the Brazilian Amazon region.

Species	(1)	(2)	(3)	(4)	(5)	(6)	(7)
(1) <i>Ellipsomyxa matosi</i> n. sp.	–						
(2) <i>Ellipsomyxa santarenensis</i>	5.82	–					
(3) <i>Ellipsomyxa plagioscioni</i>	5.90	3.71	–				
(4) <i>Ellipsomyxa paraensis</i>	6.16	0.058	3.99	–			
(5) <i>Ellipsomyxa amazonensis</i>	6.16	0.070	3.87	0.11	–		
(6) <i>Ellipsomyxa arariensis</i>	6.84	2.11	5.37	2.01	2.13	–	
(7) <i>Ellipsomyxa tucujuensis</i>	13.48	8.50	11.27	7.90	8.02	10.17	–

The dimensions of the myxospores of *Ellipsomyxa matosi* n. sp. are similar to *E. amazonensis*, captured in the Tapajós rivers, municipality of Santarém, State of Pará, Brazil [16]. However, the polar capsule of the new species of this study is larger than that of the other *Ellipsomyxa* species described in the region, and its Polar tubule has a larger number of coils.

Most of the species described as *Ellipsomyxa* are parasites of marine fish, such as *E. gordey* (PP296411), *E. nigropunctatis* (KF179050) *E. arothroni* (KF179049) [9,41]. In the Amazon basin, only the species *E. paraensis* parasitizing *C. monoculus* [15], *E. tucujuensis* [17], and *E. santarinensis* [4] infecting the fish *S. jurupari* were considered species restricted to freshwater environments due to the distribution of their hosts. The new species was captured in a freshwater environment, but its host, *A. ucayalensis*, carries out migrations as observed in many other species of the Auchenipteridae family [20], therefore, we cannot state that *Ellipsomyxa matosi* n. sp. is an exclusive freshwater species.

Although the species *Ellipsomyxa matosi* n. sp. did not present pathological changes in its host, [42] observed changes in the epithelial layers of the gallbladder of the infected marine catfish, *Arius arius*, with swelling and vacuolization, in addition to changes in the color of the bile of infected individuals. Changes in bile color were also recorded in *E. gobioides* [14] and *E. kalthomi* [40], and were probably related to mucus reduction, due to the presence of parasites and necrotic cells. Modification of mucus production likely affects the activity of host digestive enzymes [42].

Ellipsomyxa species formed subclades, one composed species from freshwater hosts from the Amazon basin, only *E. plagioscioni* was not included in the clade of species from the Amazon, due to its host *P. squamosissimus*, grouping in a marine lineage [15], the present origin with migratory behavior, showing that freshwater species do not form a monophyletic group [4,10,12,15,17]. [43] demonstrated that the evolution of phylogenetic relationships between myxozoans identified in marine and freshwater environments is influenced by the characteristics of their definitive host, whether they are marine or freshwater species.

The morphological characteristics of the specimens and the molecular phylogeny confirmed the existence of a new species, *Ellipsomyxa matosi* n. sp. The discovery of this new species represents an important advance in the scientific understanding of the morphology, evolution, and distribution of microparasites in the Amazon region.

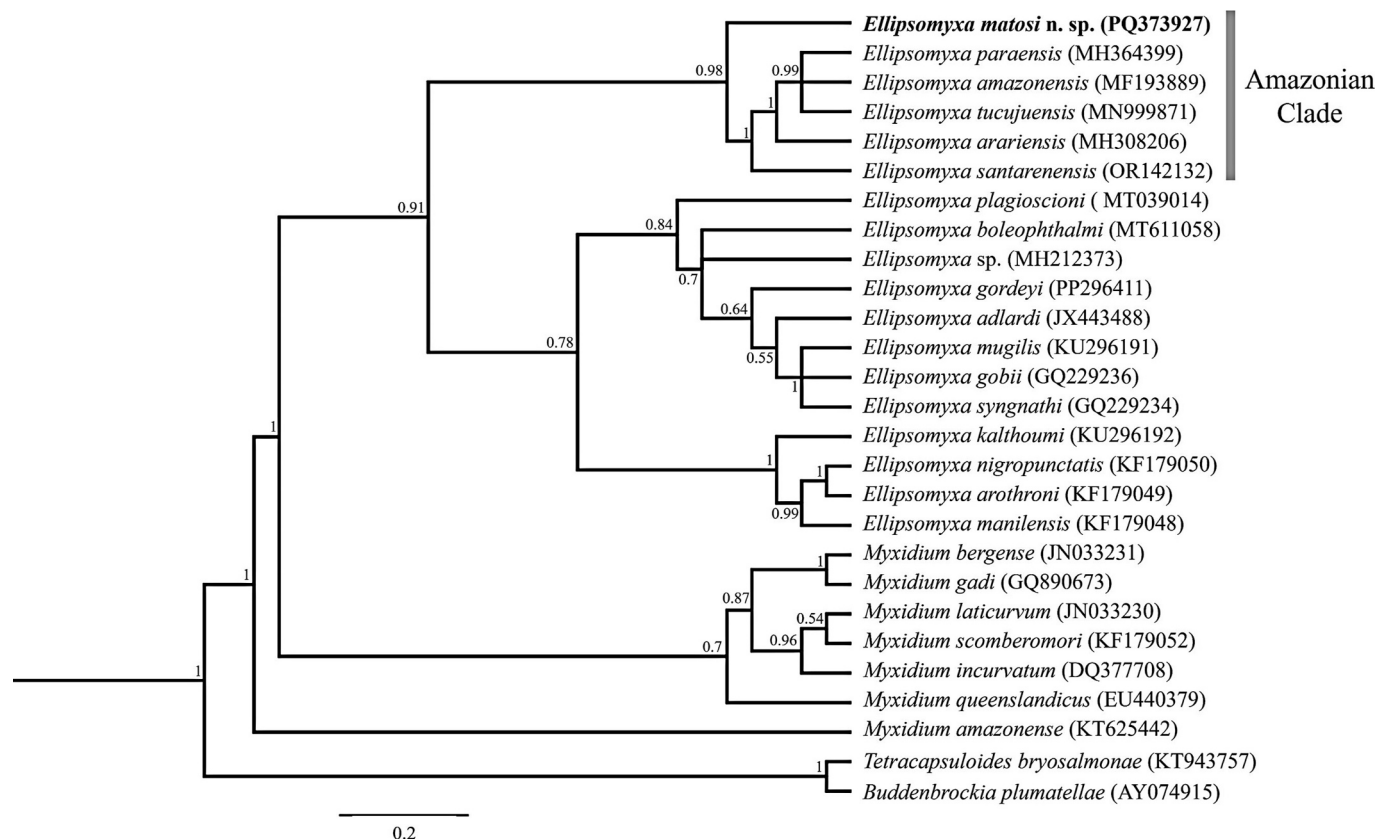


Fig. 5. Phylogenetic analysis of the partial sequence of *Ellipsomyxa matosi* n. sp. and other myxozoans. Numbers indicate Bayesian posterior probabilities. The new species is highlighted in bold and the clade of *Ellipsomyxa* species from the Brazilian Amazon region is highlighted.

CRediT authorship contribution statement

Camila Maria Barbosa Pereira: Writing – review & editing, Writing – original draft, Methodology, Investigation, Conceptualization. **Jhonata Eduard Farias de Oliveira:** Writing – review & editing, Methodology, Conceptualization. **Marcia de Nazaré Sacco dos Santos:** Methodology, Investigation. **Lana Priscila Barbosa Pereira:** Writing – review & editing, Investigation. **Igor Guerreiro Hamoy:** Methodology. **Marcelo Francisco da Silva:** Writing – review & editing, Writing – original draft, Methodology. **José Ledamir Sindeaux-Neto:** Writing – review & editing, Methodology, Conceptualization. **Michele Velasco Oliveira da Silva:** Writing – review & editing, Writing – original draft, Methodology, Investigation, Conceptualization.

Declaration of competing interest

The authors declare that there are no conflicts of interest.

Acknowledgments

We want to thank Dr. Edilson Matos, in memory, for his years of contribution to the research of fish microparasites in the Brazilian Amazon region.

References

- [1] M.L. Kent, K.B. Andree, J.L. Bartholomew, M. Elmatbouli, S.S. Desser, R.H. Devlin, S.W. Feist, R.P. Hedrick, R.W. Hoffmann, J. Khattra, S.L. Hallett, R.J.G. Lester, M. Longshaw, O. Palenzeula, M.E. Siddall, C. Xiao, Recent advances in our knowledge of the Myxozoa, *J. Eukaryot. Microbiol.* 48 (2001) 395–413.
- [2] I. Fiala, P. Bartošová-Sojčková, C.M. Whipps, Classification and Phylogenetics of Myxozoa, in: B. Okamura, A. Gruhl, J. Bartholomew (Eds.), *Myxozoan Evolution, Ecology and Development*, Springer, Cham, 2015, pp. 85–110, https://doi.org/10.1007/978-3-319-14753-6_5.
- [3] B. Okamura, A. Hartigan, J. Naldoni, Extensive uncharted biodiversity: the parasite dimension, *Integr. Comp. Biol.* 58 (2018) 1132–1145, <https://doi.org/10.1093/icb/icy039>.
- [4] R.T.A. Figueredo, M.I. Müller, P.F. Long, E.A. Adriano, Myxozoan Ceratomyxids Infecting the Gallbladder of Amazonian Ornamental Cichlid Fish: Description of *Ellipsomyxa santarenensis* n. sp. And Report of *Ceratomyxa amazonensis* in a New Host, *Diversity* 15 (2023) 830, <https://doi.org/10.3390/d15070830>.
- [5] J. Lom, I. Dyková, Myxozoan genera: definition and notes on taxonomy, life-cycle terminology and pathogenic species, *Folia Parasitol.* 53 (2006) 1–36.
- [6] M. Lisnerová, A. Lisner, D.M.P. Cantatore, B.C. Schaeffner, H. Pecková, T. Tým, I. Fiala, P. Bartošová-Sojčková, A.S. Holzer, Correlated evolution of fish host length and parasite spore size: a tale from myxosporeans inhabiting elasmobranchs, *Int. J. Parasitol.* 52 (2022) 97–110, <https://doi.org/10.1016/j.ijpara.2021.05.008>.
- [7] G. Alama-Bermejo, J.S. Hernández-Orts, M. García-Varela, A. Ocegüera-Figueroa, H. Pecková, I. Fiala, Diversity of myxozoans (Cnidaria) infecting Neotropical fishes in southern Mexico, *Sci. Rep.* 26 (2023), <https://doi.org/10.1038/s41598-023-38482-2>.
- [8] M. Koie, *Ellipsomyxa gobia* gen. et sp. n., (Myxozoa: Ceratomyxidae) in the common goby *Pomatoschistus microps* (Teleostei: Gobiidae) from Denmark, *Folia Parasitol.* 50 (2003) 269–271, <https://doi.org/10.14411/fp.2004.002>.
- [9] H. Heiniger, R.D. Adlard, Relatedness of novel species of *Myxidium* Bütschli, 1882, *Zschokkella* Auerbach, 1910 and *Ellipsomyxa* Koie, 2003 (Myxosporea: Bivalvulida) from the gall bladders of marine fishes (Teleostei) from Australian waters, *Syst. Parasitol.* 87 (2014) 47–72, <https://doi.org/10.1007/s11230-013-9454-3>.
- [10] C.M. Whipps, W.F. Font, Interaction of two myxozoan parasites from naked goby *Gobiosoma bosc*, in Lake Pontchartrain, Louisiana, *J. Parasitol. Res.* 99 (3) (2013) 441–448, <https://doi.org/10.1645/12-49.1>.
- [11] M. Koie, E. Karlsbakk, *Ellipsomyxa syngnathi* sp. n. (Myxozoa, Myxosporea) in the pipefish *Syngnathus typhle* and *S. rostellatus* (Teleostei, Syngnathidae) from Denmark, *Parasitol. Res.* 105 (2009) 1611–1616, <https://doi.org/10.1007/s00436-009-1598-3>.
- [12] M.G. Pratapa, N.K. Sanil, K.V. Rajendran, A novel myxozoan parasite, *Ellipsomyxa boleophthalmi* sp. nov. (Myxozoa: Ceratomyxidae) in the brackishwater fish, *Boleophthalmus dussumieri* Valenciennes, 1837 (Perciformes: Gobiidae) from India, *Parasitol. Res.* 4 (2021) 1269–1279, <https://doi.org/10.1007/s00436-021-07084-0>.
- [13] A. Sitj'a-Bobadilla, P. Alvarez-Pellitero, *Zschokkella mugilis* n. sp. (Myxosporea: Bivalvulida) from mullets (Teleostei: Mugilidae) of Mediterranean waters: light and electron microscopic description, *J. Eukaryot. Microbiol.* 40 (1993) 755–764, <https://doi.org/10.1111/j.1550-7408.1993.tb04471.x>.
- [14] C. Azevedo, M. Videira, G. Casal, P. Matos, E. Oliveira, S. Al-Quraishy, E. Matos, Fine structure of the plasmodia and myxospore of *Ellipsomyxa gobioides* n. sp.

- (Myxozoa) found in the gallbladder of *Gobioides broussonnetii* (Teleostei: Gobiidae) from the lower Amazon River, J. Eukaryot. Microbiol. 60 (2013) 490–496, <https://doi.org/10.1111/jeu.12056>.
- [15] S.A. Zatti, A.A.M. Maia, E.A. Adriano, Growing diversity supports radiation of an *Ellipsomyxa* lineage into the Amazon freshwater: description of two novel species parasitizing fish from Tapajós and Amazon rivers, Acta Trop. 211 (2020) 105616, <https://doi.org/10.1016/j.actatropica.2020.105616>.
- [16] S.A. Zatti, S.D. Atkinson, A.A.M. Maia, L.L. Corrêa, J.L. Bartholomew, E. A. Adriano, Novel *Myxobolus* and *Ellipsomyxa* species (Cnidaria: Myxozoa) parasitizing *Brachyplatystoma rousseauxii* (Siluriformes: Pimelodidae) in the Amazon basin, Brazil, Parasitol. Int. 67 (2018) 612–621, <https://doi.org/10.1016/j.parint.2018.06.005>.
- [17] R.L.D.S. Ferreira, D.T. Da Silva, A.A. De Carvalho, L.S. Bittencourt, I. Hamoy, E. Matos, M. Videira, *Ellipsomyxa tucuijensis* n. sp. (Myxozoa: Ceratomyxidae), a parasite of *Satanoperca jurupari* (Osteichthyes: Cichlidae) from the Brazilian Amazon, Parasitol. Int. 83 (2021) 102332, <https://doi.org/10.1016/j.parint.2021.102332>.
- [18] D.T. Silva, P.S. Matos, A.M. Lima, A.P. Furtado, I. Hamoy, E.R. Matos, *Ellipsomyxa arariensis* n. sp. (Myxozoa: Ceratomyxidae), a new myxozoan parasite of *Pygocentrus nattereri* Kner, 1858 (Teleostei: Characidae) and *Pimelodus ornatus* Kner, 1858 (Teleostei: Pimelodidae) from Marajó Island, in the Brazilian Amazon region, Parasitol. Res. 117 (2018) 3537–3545, <https://doi.org/10.1007/s00436-018-6051-z>.
- [19] G.M. Santos, E.J.G. Ferreira, J.A.S. Zuanon, Peixes comerciais de Manaus, IBAMA, Manaus, 2006.
- [20] F.R. Ribeiro, L.H. Rapp Py-Daniel, S.J. Walsh, Taxonomic revision of the south American catfish genus *Ageneiosus* (Siluriformes: Auchenipteridae) with the description of four new species, J. Fish Biol. 90 (2017) 1388–1478, <https://doi.org/10.1111/jfb.13246>.
- [21] V.S. Batista, V.J. Isaac, N.N. Fabrê, J.C.A. Gonzalez, O.T. Almeida, S. Rivero, J.N. O. Júnior, M.L. Ruffino, C.O. Silva, U. Saint-Paul, Peixes e pesca no Solimões Amazonas: uma avaliação integrada, Ibama/PróVárzea, Brasília, 2012.
- [22] L.G. Luna, Manual of Histologic Staining Methods of the Armed Forces Institute of Pathology, third ed., MacGraw-Hill Book Company, New York, 1968.
- [23] J. Lom, J.R. Arthur, A guideline for the preparation of species descriptions in Myxosporea, J. Fish Dis. 12 (1989) 151–156, <https://doi.org/10.1111/j.1365-2761.1989.tb00287.x>.
- [24] D.M. Hillis, M.T. Dixon, Ribosomal DNA: molecular evolution and phylogenetic inference, Q. Rev. Biol. 66 (1991) 411–451, <https://doi.org/10.1086/417338>.
- [25] C.M. Whipps, R.D. Adlard, M.S. Bryant, R.G.J. Lester, V. Findlav, M.L. Kent, First report of three *Kudoa* species from eastern Australia: *Kudoa thyrsites* from mahi mahi (*Coryphaena hippurus*), *Kudoa anamiensis* and *Kudoa minithyrsites* n. sp. from sweeper (*Pempheris ypsilychnus*), J. Eukaryot. Microbiol. 50 (2003) 215–219, <https://doi.org/10.1111/j.1550-7408.2003.tb00120.x>.
- [26] K. Molnar, E. Eszterbauer, C. Szekely, A. Dan, B. Harrach, Morphological and molecular biological studies on intramuscular *Myxobolus* spp. of cyprinid fish, J. Fish Dis. 25 (2002) 643–652, <https://doi.org/10.1046/j.1365-2761.2002.00409.x>.
- [27] T.A. Hall, BioEdit: a user-friendly biological sequence alignment editor and analysis program for windows 95/98/NT, Nucleic Acids Symp. 41 (1999) 95–98.
- [28] S. Guindon, O. Gascuel, A simple, fast, and accurate algorithm to estimate large phylogenies by maximum likelihood, Syst. Biol. 52 (2003) 696–704, <https://doi.org/10.1080/10635150390235520>.
- [29] D. Posada, jModelTest: phylogenetic model averaging, Mol. Biol. Evol. 25 (2008) 1253–1256, <https://doi.org/10.1093/molbev/msn083>.
- [30] A.J. Drummond, M.A. Suchard, D. Xie, A. Rambaut, Bayesian phylogenetics with BEAUti and the BEAST 1.7, Mol. Biol. Evol. 29 (2012) 1969–1973, <https://doi.org/10.1093/molbev/ms075>.
- [31] A.J. Drummond, S.Y.W. Ho, M.J. Phillips, A. Rambaut, Relaxed phylogenetics and dating with confidence, PLoS Biol. 4 (2006), <https://doi.org/10.1371/journal.pbio.0040088>.
- [32] A. Mooers, O. Gascuel, T. Stadler, H. Li, M. Steel, Branch lengths on birth-death trees and the expected loss of phylogenetic diversity, Syst. Biol. 61 (2012) 195–203, <https://doi.org/10.1093/sysbio/syr090>.
- [33] S. Brooks, A. Gelman, G.L. Jones, X. Meng, Handbook of Markov Chain Monte Carlo, CRC Press, New York, 2011, <https://doi.org/10.1201/b10905>.
- [34] A. Rambaut, A.J. Drummond, D. Xie, G. Baele, M.A. Suchard, Posterior summarisation in Bayesian phylogenetics using tracer 1.7, Syst. Biol. 67 (2018) 901–904, <https://doi.org/10.1093/sysbio/syy032>.
- [35] A.J. Drummond, A. Rambaut, BEAST: Bayesian evolutionary analysis by sampling trees, BioMed. Cent. Evol. Biol. 7 (2007) 214, <https://doi.org/10.1186/1471-2148-7-214>.
- [36] A. Rambaut, FigTree version 1.4.0. [software], 2012.
- [37] H.A. Schmidt, K. Strimmer, M. Vingron, A. Von Haeseler, TREE-PUZZLE: maximum likelihood phylogenetic analysis using quartets and parallel computing, Bioinformatics 18 (2002) 502–504, <https://doi.org/10.1093/bioinformatics/18.3.502>.
- [38] D.L. Swofford, PAUP* Phylogenetic analysis using parsimony (* and other methods). Version 4, Sinauer Associates, Sunderland, 2003.
- [39] O. Hammer, D.A.T. Harper, P.D. Ryan, PAST: paleontological statistics software package for education and data analysis, Palaeontol. Electron. 4 (2001) 1–9.
- [40] A. Thabet, S. Tlig-Zouari, S.Y. Al Omar, L. Mansour, Molecular and morphological characterisation of two species of the genus *Ellipsomyxa* Kœie, 2003 (Ceratomyxidae) from the gallbladder of *Liza saliens* (Risso) off Tunisian coasts of the Mediterranean, Syst. Parasitol. 93 (2016) 601–611, <https://doi.org/10.1007/s11230-016-9647-7>.
- [41] V.M. Yurakhno, V.T. Ha, C.M. Whipps, Phylogenetic analysis of *Ellipsomyxa* species (Myxosporea) and description of *Ellipsomyxa gordeyi* n. sp. from the gall bladder of mullets (Mugiliformes: Mugilidae) in Nha Trang Bay of the East Sea, Vietnam, Parasitol. Int. 102 (2024) 102918, <https://doi.org/10.1016/j.parint.2024.102918>.
- [42] A. Chandran, P.U. Zacharia, T.V. Sathianandan, N.K. Sanil, *Ellipsomyxa ariusi* sp. nov. (Myxosporea: Ceratomyxidae), a new myxosporean infecting the gallbladder of threadfin sea catfish *Arius arius* in India, Dis. Aquat. Organ. 142 (2020) 83–97, <https://doi.org/10.3354/dao03529>.
- [43] A.S. Holzer, P. Bartošová-Sojčková, A. Born-Torrijos, A. Lövy, A. Hartigan, I. Fiala, The joint evolution of the Myxozoa and their alternate hosts: a cnidarian recipe for success and vast biodiversity, Mol. Ecol. 27 (2018) 1651–1666, <https://doi.org/10.1111/mec.14558>.