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Morphological and molecular characterization of *Ameloblastella pirarara* sp. n. (Monogenoidea: Dactylogyridae) parasitizing the large Amazonian catfish *Phractocephalus hemioliopterus*

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ABSTRACT

In this study, integrative taxonomy is applied to describe a new dactylogyrid species, *Ameloblastella pirarara* sp. n. from the gills of *Phractocephalus hemioliopterus*, a commercially and ecologically important Amazonian catfish. *Ameloblastella pirarara* sp. n. can be distinguished from its congeners mainly by the morphology of the male copulatory organ (MCO), accessory piece, and anchors. The new species most resembles Ameloblastella unapi, from the Peruvian Amazon, but differs from it by the number of MCO rings, morphology of the vaginal canal and sclerotized structures of the haptor. Phylogenetic analyses based on sequences of the partial 28S rDNA (D1-D2 domains) gene placed the new species in a well-supported subclade of *Ameloblastella* spp. parasites of Neotropical siluriform fish, as a sister taxon to *Ameloblastella unapioides*. Thus, the new species described herein expands our knowledge of the diversity of monogenoid parasites from Amazonian freshwater fish.

1. Introduction

Monogenoids are ectoparasitic platyhelminths widely diversified with approximately 5000 known species [1,2]. They have direct life-cycles, are parasites mainly of freshwater and marine fish [2–4], and generally present high host-specificity [5]. Some species are associated with severe diseases in aquaculture and wild fish populations, causing substantial economic losses, such as *Dactylogyrus extensus* and *Dactylogyrus* vastador in cultures of cyprinid fish and *Linguadactyloides brinkmanni* from *Colossoma macropomum* [3,6]. Recently, an expressive number of monogenean species have been described infecting Amazonian fishes [3,7], some of them reported to be pathogenic, like *Gussevia tucunarense* and *Notozothecium bethae* from *Chaetobranchus semifasciatus* and *Myleus schomburgkii,* respectively [8–10].

The large Amazonian catfish, *Phractocephalus hemioliopterus* Bloch and Schneider, 1801 (Siluriformes: Pimelodidae) popularly known as "pirarara" or "red tail catfish" is widely distributed in the Amazon and Orinoco River basins and is one of the most important species for sport and commercial fisheries with potential yield estimated to be almost 900 tons per year [11,12]. This species is a medium-distance migrator and it plays a key ecological role as top predator [12,13], reaching up to 1.35 m in length and 44.2 kg of total weight [14]. Despite the importance of *P. hemioliopterus* in the Amazon region, its parasitic fauna is still little known, particularly concerning monogenean parasites.

In this study, a new species of *Ameloblastella* Kritsky, Mendoza-Franco and Scholz, 2000 infecting the gills of *P. hemioliopterus* is described, supported by morphological and molecular data (partial 28S rDNA gene).

2. Material and methods

2.1. Ethical approval

The euthanasia method was approved by the Ethics Committee on

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Animal Research of the State University of Campinas (CEUA No. 3179–1) in accordance with Brazilian law for scientific use of animals (Federal Law No. 11794, dated 8 October 2008). The sampling and access to genetic heritage was authorized by the Brazilian Ministry of the Environment (authorization SISBIO # 42427-3 and SISGEN # AD28DC2).

2.2. Fish specimens

In October 2014, a total of seven wild specimens of *P. hemioliopterus* (ranging from 56 to 59.1 cm in total length and 27.05–32.95 g in weight) were collected from the Igarapé Jari (2°20′24″ S, 54°53′59″ W), in the Tapajós River, State of Pará, Brazil. The fish were transported live to the field laboratory, where they were euthanized by pit transaction and had the gills examined for parasites using a light microscope. The fishes were identified according to Queiroz et al. [15] and its current taxonomic status (valid species name or synonym) were reviewed according to Fricke et al. [16]. Prevalence, mean intensity and mean abundance of infestation was calculated according to Bush et al. [17].

2.3. Morphological characterization

Some monogenean specimens were stained with Gomori's trichrome and mounted in Damar gum to investigate the internal and soft structures, while others were mounted in Gray & Wess's medium to study the sclerotized structures [18]. Photographs were taken using a differential interference contrast (DIC) and a computer equipped with Axivision 4.1 image capture software coupled to an Axioplan 2 Zeiss Microscope (Carl Zeiss AG, Oberkochen, Germany). Measurements were taken in micrometers, following Mizelle and Klucka [19] and Kritsky et al. [20] and are expressed as mean (μm) followed by range, and number of specimens measured (N) in parentheses. The monogenean illustrations were carried out with the aid of a drawing tube attached on a Motic BA310 E LED microscope. Type specimens were deposited in the platyhelminths collection of the Museum of Zoology of State University of Campinas, State University of Campinas, State of Sao Paulo, Brazil (ZUECPLA) and in the Helminthological Collection of the Museum of Zoology of the University of São Paulo (MZUSP). All details of the new taxa were submitted to ZooBank.

2.4. Molecular characterization and sequencing

The genomic DNA was extracted using DNeasy® Blood & Tissue Kit (Qiagen Inc., California, USA), in accordance with Aguiar et al. [21]. The DNA concentration was measured using a NanoDrop 2000 spectrophotometer (Thermo Scientific, Wilmington, USA.). Polymerase chain reactions (PCRs) were conducted in a final volume reaction of 25 μL, which comprised 3 μL of DNA, 0.2 Mmol for each primer, 10.5 μL of Dream Taq 2 × Green PCR Master Mix (Thermo Scientific, Massachusetts, USA), and nuclease-free water. Partial 28S rDNA (D1-D2 domains) sequence was amplified using the primer pairs 1200F, CAGGTCTGTGATGCCC [22] and D2, TGGTCCGTGTTTCAAGAC [23]. PCRs amplification were done by initial denaturation at 94 °C for 5 min, followed by 35 cycles of 94 °C for 45s, 50 °C for 30s, 72 °C for 90s, and then a final elongation at 72 °C for 7 min. PCRs were performed in a ProFlex™ PCR System Thermal Cycler (Thermo Scientific Wilmington, USA). The PCRs products were subjected to electrophoresis in 1.5% agarose gel (Bio-America, Florida, USA) in a TAE buffer (Tris-Acetate EDTA: Tris 40 mM, acetic acid 20 mM, EDTA 1 mM), stained with Sybr Safe DNA gel stain (Invitrogen by Life Technologies, Carlsbad, USA), and then analyzed in a scanner K33-3333 (Kasvi, Paraná, Brazil). The size of the amplicons was estimated by comparison with the 1 Kb Plus DNA Ladder (Invitrogen by Life Technologies). PCR products were purified using USB® ExoSap-IT® (Thermo Fisher Scientific) in accordance with the manufacturer's instructions. Sequencing was performed at the Human Genome Research Center (HGRC), at the University of São Paulo, with a BigDye® Terminator v3.1 cycle sequencing kit (Applied Biosystems Inc., California, USA) in an ABI 3730 DNA sequencing analyzer (Applied Biosystems) and using the same PCR primers plus one additional (C1, ACCCGCTGAATTTAAGCAT) primer [23]. The resulting sequences were visualized, assembled, and edited using BioEdit 7.1.3.0 software [24]. A standard nucleotide BLAST search was carried out to verify the similarity of the sequence obtained in this study with other sequences available in GenBank [25]. The phylogenetic analysis was conducted with 49 closely related monogenoidean sequences (similarity >80% in nucleotide BLAST). The sequences were aligned with the algorithm ClustalW Version 2 [26] implemented in the SeaView Version 4 [27]. Phylogenetic analysis were performed using Maximum likelihood (ML) and Bayesian inference (BI). ML was done in the PhyML 3.0 with Smart Model Selection [28]. Bootstrap analysis with 1000 replicates was employed to assess the robustness of the branches in ML tree. BI was performed in MrBayes version 3.2 software package [29], set up to run two independent Markov Chain Monte Carlo (MCMC) trials over 10^6 generations, sampled each 100th and diagnosed every 1000th generation, with the first 25% of the samples discarded in the burn-in phase. To sample across the substitution models and combine a gamma-distributed rate variation across sites with a proportion of invariable sites, the lset nst = mixed rates = invgamma function was used [29]. The sequences of *Haliotrema dongshaense* Sun, Gibson, Yang, 2011 and *Haliotrema pratasense* Sun, Kritsky, Yang, 2007 were used as outgroups.

The pairwise comparison with the Maximum Composite Likelihood model [30], was executed in MEGA-X [31] to evaluate the genetic distance between the monogenoidean species clustering together with the new sequence obtained. This analysis was configurated with a rate variation among sites with a gamma distribution (shape parameter = 1) and removing all ambiguous positions for each sequence pair.

3. Results

Out of seven wild specimens of *P. hemioliopterus* examined, two (28.6%) had the gills infected by a new monogenean dactylogyrid species of the genus *Ameloblastella*, described herein.

3.1. Taxonomic summary

Class: Monogenoidea Bychowsky, 1937.
Subclass: Polyonchoinea Bychowsky, 1937.
Order: Dactylogyridea Bychowsky, 1937.
Family: Dactylogyridae Bychowsky, 1933.
Genus: *Ameloblastella* Kritsky, Mendoza-Franco and Scholz, 2000.
Species: *Ameloblastella pirarara* sp. n.
Type host: *Phractocephalus hemioliopterus* (Siluriformes: Pimelodidae).
Site of infection: Gills.
Type locality: Igarapé Jari, Tapajós River Basin, (2°20′24″ S, 54°53′59″ W), municipality of Santarém, State of Pará, Brazil.
Prevalence: 2/7(28.6%), mean intensity (4.5) and mean abundance of infection (1.3).
Type material: Holotype (ZUECPLA 140), 8 paratypes (ZUECPLA 141-144 and MZUSP 7959a-b, MZUSP 7960a-b). Partial 28S rDNA sequence was deposited in GenBank under accession number MW827113.
Etymology: The specific name is derived from the common name of the host, "pirarara," used by the people of the Amazon, Brazil.

3.2. Morphological characterization (Figs. 1 and 2)

674 μm (299–888 μm; n = 9), long, fusiform, tapering posteriorly, peduncle absent; greatest width of trunk 232 μm (155–300 μm; n = 9) at level of medium body. Tegument smooth. Cephalic margin tapered; cephalic lobe poorly developed or absent; nine bilateral pairs of rod-shaped head organs; cephalic glands unicellular, posterolateral to

pharynx. Eyes and accessory chromatic granules absent. Mouth subterminal, midventral; pharynx subspherical 75 μm (56–122 μm; n = 9) in diameter, muscular, glandular; esophagus not observed; two intestinal caeca, posteriorly confluent to gonads, lacking diverticula. Absence of haptoral peduncle; haptor subhexagonal, 66 μm (42–90 μm; n = 9) long and 121 μm (108–136 μm; n = 9) wide (Figs. 1A and 2A). Ventral bar 36 μm (31–46 μm; n = 9) long, distance between ends 35 μm (28–45 μm; n = 9), slightly curved rod with anteromedial projection, tapering ends (Figs. 1D and 2C). Dorsal bar 26 μm (23–29 μm; n = 9), long, distance between ends 23 μm (21–26 μm; n = 9), slightly straight rod, and presents slight expanded rounded ends (Figs. 1F and 2D). Anchors similar; each with well-developed superficial root, short deep root; evenly curved shaft and point; point acute, extending to level of tip of superficial root. Ventral anchor 25 μm (20–31 μm; n = 9) long, 16 μm (13–22 μm; n = 6) wide (Figs. 1E and 2C); dorsal anchor 26 μm (21–30 μm; n = 9) long, 14 μm (13–16 μm; n = 3) wide (Figs. 1G and 2D). Hooks similar in shape distally expanded, erected thumb and curved point; filamentous hook loop with about 2/3 of shank length; hooks pairs 1–2, 23 μm (19–26 μm; n = 9), pair 3–4, 25 μm (19–32 μm; n = 13), pairs 5–7, 27 μm (20–36 μm; n = 20) (Fig. 1H). Common genital pore opening midventral near level of cecal bifurcation; genital atrium muscular. Intercaecal gonads, overlapping. Testis dorsal to germarium, pyriform, 174 μm (141–249 μm; n = 5) long, 67 μm (43–86 μm; n = 5) wide; vas deferens looping left intestinal cecum; seminal vesicle sigmoid, representing a dilation in the vas deferens, lying to left of midline in anterior trunk. Single prostatic reservoir, posterior to copulatory complex. Copulatory complex comprising male copulatory organ (MCO) and accessory piece (Figs. 1B and 2B). MCO sclerotized, tubular, spiral, counterclockwise, with 11 rings, 832 μm (659–995 μm; n = 9) total length, 24 μm (19–29 μm; n = 9) proximal ring diameter, expanded base with thicken wall, distal aperture acute. Accessory piece articulated with MCO, 35 μm (22–49 μm; n = 9) total length, comprising a sheath enclosing the distal portion of MCO, with distal auricular projection and proximally partite in two parts, one of them, narrow from which arises the copulatory ligament. Germarium ovate 226 μm (124–309 μm; n = 9) long, 96 μm (59–118 μm; n = 9) wide. Uterus delicate. Eggs, Mehlis' glands, oviduct, ootype, seminal receptacle not observed. Vagina single, sclerotized, opening ventrally at the left body margin, at level of vitelline commissure; vaginal vestibule sinistral, cup shaped, with soft tissue at distal portion, sclerotized at proximal portion; vaginal canal sclerotized, sinuous, with five proximal loops, being the three first larger, and one smaller distal loop, after which the vaginal canal enters the vaginal atrium and constitutes an expansion pick – like (Fig. 1C). Seminal receptacle not observed. Vitellaria well developed, coextensive with intestinal ceca, absent in the region of the reproductive organs.

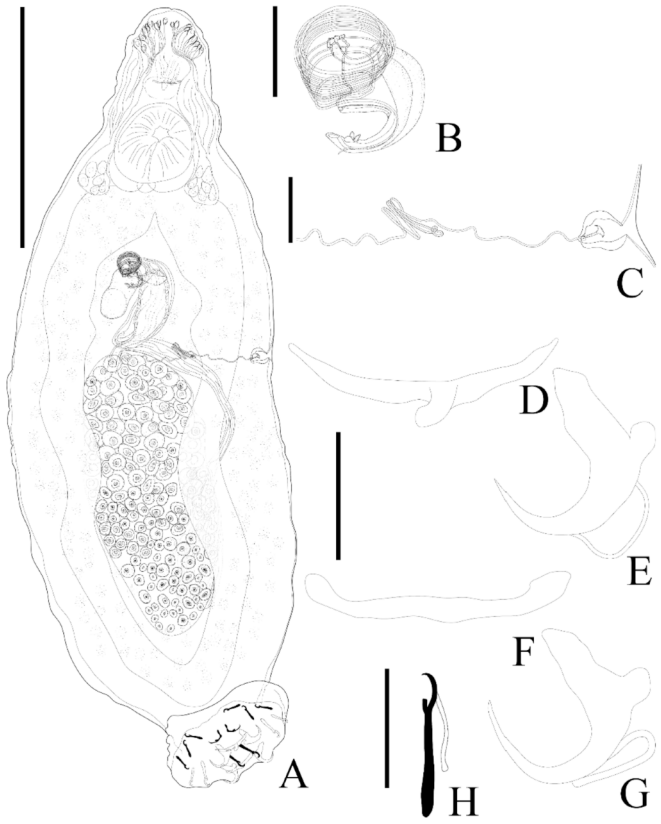

Fig. 1. Schematic illustrations of *Ameloblastella pirarara* sp. n. A: Whole composite drawn. Scale bar: 200 μm. B: Copulatory complex. Scale bar: 20 μm. C: Vagina. Scale bar: 25 μm. D: Ventral bar. E: Ventral anchor. F: Dorsal bar. G: Dorsal anchor. H: Hook. Scale bars: 15 μm.

3.3. Molecular characterization and phylogeny

A partial 28S rDNA sequence of 820 bp was obtained from *A. pirarara* sp. n. and the guanine-cytosine-GC content was of 50.53%. The BLAST analyses showed that it did not match any other monogenoidean sequence available in GenBank, and the highest similarity (83%, Table 1) was to *Ameloblastella unapioides* Mendoza-Franco, Mendoza-Palmero and Scholz, 2016, parasite of the gills of *Sorubim lima* Bloch and Schneider, 1801, another Amazonian pimelodid. ML and BI phylogenetic inferences recovered *A. pirarara* sp. n. in a well-supported subclade of *Ameloblastella* parasites of siluriform fish. In this subclade, *A. pirarara* sp. n. arose as sister species of *A. unapioides*, and both were closely related to *Ameloblastella chavarriai* Price, 1968 (Fig. 3).

4. Discussion

Despite the growing description of monogenoids infecting Amazonian fish, the diversity of these platyhelminths in this neotropical realm remains largely unknown [3,7]. In this context, our study describes a new dactylogyrid species of *Ameloblastella*, *A. pirarara* sp. n., infecting gills of Amazonian siluriform *P. hemioliopterus*. *Ameloblastella* encompasses 12 recognized species (Table 2), all reported infecting neotropical siluriform fishes [32]. However, this is the first report of an *Ameloblastella* species infecting *P. hemioliopterus*, once, anterior studies described *Urocleidoides catus* Mizelle and Kritsky, 1969, *Urocleidoides amazonensis* Mizelle and Kritsky, 1969, and *Vancleaveus cicinnus* Kritsky, Thatcher and Boeger, 1986 infecting this host [33,34]. Thus, our results contribute to freshwater dactylogyrid taxonomy and to the knowledge of monogenoidean diversity from the Amazon basin.

The morphological comparisons of *A. pirarara* sp. n. with all congeners previously described [3,32,35–39], showed the new species resembles *Ameloblastella unapi* Mendoza-Franco and Scholz, 2009, a parasite of gills of *Calophysus macropterus* [36]. Both species share a coiled vaginal canal and have a coiled MCO with more than ten counterclockwise rings. However, the new species has five proximal loops and one smaller distal loop in the vaginal canal, while *A. unapi* has around five distally loops. Furthermore, the distal loop in the vaginal canal of *A. pirarara* sp. n. is smaller than the pick-like expansion at the end of its vaginal canal compared with *A. unapi*. These species also differ in the number of rings of MCO, while the new species has 11 rings, *A. unapi* has 13-14. Finally, *A. pirarara* sp. n. has anchors with a slightly curved and short shaft, with a long point while *A. unapi* has the ventral and dorsal anchors with slightly straight and long shaft with short point forming an angle of about 90°. Unfortunately, the unavailability of molecular data of 28S rDNA sequence of *A. unapi* made impossible the genetic comparison with the species described herein. However, noticed differences observed in important morphology characters support the taxonomic separation between these two *Ameloblastella* species.

In the phylogenetic inference, *A. pirarara* sp. n. was placed in a well-supported subclade composed exclusively of *Ameloblastella* spp., as a sister species of *A. unapioides* (Fig. 3). Nonetheless, such relationship can

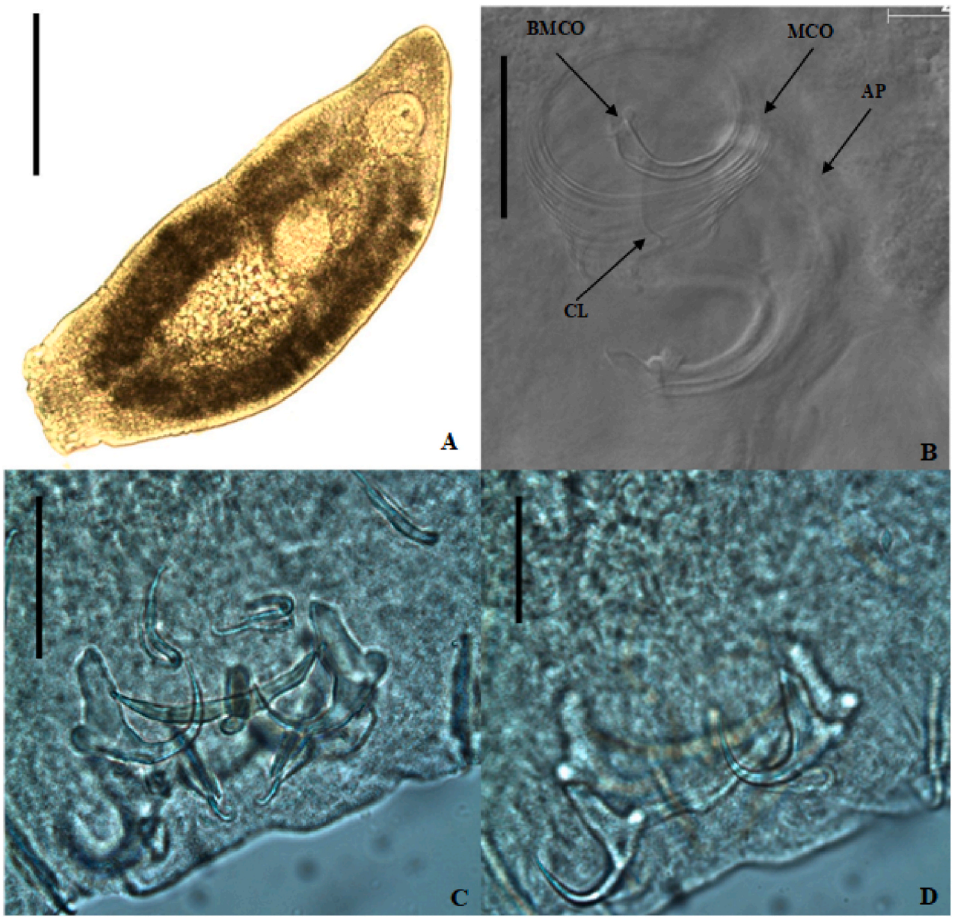

Fig. 2. Photomicrographs of *Ameloblastella pirarara* sp. n. parasite from the gills of *Phractocephalus hemioliopterus*. A: Whole worm. Scale bar: 200 μm. B: Copulatory complex, male copulatory organ (MCO), base of MCO (BMCO), copulatory ligament (CL) accessory piece (PA). Scale bar: 20 μm. C: Ventral bar and anchor. D Dorsal bar and anchor. Scale bars: 25 μm.

Table 1
Estimates of evolutionary divergence among sequences of the partial 28S rDNA of six species of *Ameloblastella*. Above the diagonal there are the percentages of similarity based on the number of base substitutions per site among sequences. Standard error estimates are shown below the diagonal and were obtained by a bootstrap procedure (1000 replicates) in a final dataset with 766 base pairs.

	1	2	3	4	5	6
1 *Ameloblastella pirarara* sp. n.		72	73	73	83	71
2 *Ameloblastella martinae* MT174172	0.03		88	87	74	71
3 *Ameloblastella* sp. 23 KP056233	0.03	0.02		94	75	71
4 *Ameloblastella edentensis* KP056255	0.03	0.02	0.01		73	69
5 *Ameloblastella unapioides* KP056254	0.02	0.03	0.03	0.03		77
6 *Ameloblastella chavarriai* KP056251	0.03	0.03	0.03	0.03	0.03	

be an artefact, result of the absence of a 28S rDNA sequence of *A. unapi*. However, pairwise analysis between *A. pirarara* sp. n. and *A. unapioides* evidenced 83% of genetic similarity in their 28S rDNA. Furthermore, remarkable morphometrical differences can be observed between these two *Ameloblastella* species: *A. unapioides* has four rings in the MCO versus 11 in *A. pirarara* sp. n.; the accessory piece is rod-shaped in *A. unapioides*, and sheath like with a distal auricular projection and proximally bilobate in *A. pirarara* sp. n.; hooks with two different sizes in *A. unapioides* while *A. pirarara* sp. n. presents three different sizes; and anchors with long point and long shaft forming an angle of about 90° bend near junction in *A. unapioides* while *A. pirarara* sp. n. present anchors different in shape with slightly curved and short shaft with long point. Moreover, A. pirarara sp. n. present sclerotized vaginal canal with loops while the vaginal canal was not observed in the description of *A. unapioides*.

Our phylogenetic inferences corroborate the studies of Mendoza-Palmero et al. [40], Acosta et al. [41] and Mendoza-Palmero et al. [32], which demonstrate a general tendency of dactylogyrids parasites of catfishes to cluster according to host phylogenetic, as family and/or order of the host, even when these fishes are from different geographical areas. The phylogenetic analysis of this study showed that the dactylogyrids from siluriforms formed two main lineages (Fig. 3). One of them (clade A) is exclusively represented by freshwater and marine parasites of siluriforms fish from Neotropical, Oriental and Afrotropical Region, suggesting that they are historically associated with this host order (Fig. 3). The other lineage (clade B), which contains the *Ameloblastella* spp., is formed by freshwater parasites of percomorphs, siluriforms and characiforms fish from Oriental, Palearctic and Neotropical Region (Fig. 3), suggesting some degree of host-switch throughout the diversification process of this group. However, it is important to highlight that there are few molecular sequences data available from dactylogyrids of neotropical catfishes, particularly members of *Ameloblastella*. Thus, a comprehensive data set including molecular data and phylogenetic analysis of the many yet-to-be-discovered dactylogyrid species from these underrepresented hosts should help to elucidate the patterns in host-parasite associations. Furthermore, these data will clarify the evolutionary context of *A. pirarara* sp. n. as well of the Neotropical dactylogyrids as a whole.

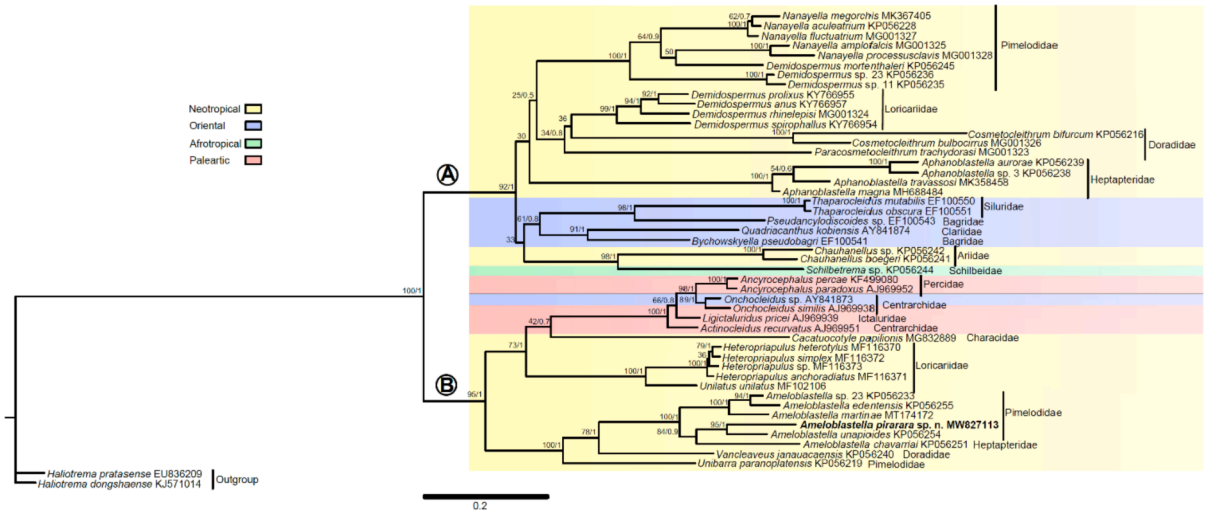

Fig. 3. Maximum Likelihood Phylogenetic tree based on sequences of the 28S rDNA gene (domains D1-D2) of selected dactylogyrids. Nodes are supported by 1000 replicates of bootstrapping from Maximum Likelihood and by posterior probability from Bayesian Inference. Names in front of vertical bars refer to host family. Letters within circles represent the two main lineages of dactylogyrids parasites of catfishes.

Table 2
List of *Ameloblastella* species parasites of siluriforms fishes.

Species	Host	Country	Reference
Ameloblastella edentensis	*Hypophthalmus edentatus*	Peru	[38]
Ameloblastella formatrium	Pimelodidae gen. sp.	Peru	[38]
Ameloblastella mamaevi	*Zungaro zungaro*	Colombia	[35]
Ameloblastella paranaensis	*Iheringichthys labrosus*	Brazil	[36]
Ameloblastella peruensis	*Hypophthalmus* sp.	Peru	[38]
Ameloblastella platensis	*Pimelodus maculatus*	Argentina	[35]
Ameloblastella satoi	*Pimelodus maculatus*	Brazil	[37]
Ameloblastella unapioides	*Sorubim lima*	Peru	[38]
Ameloblastella amazonica	*Pimelodus blochii*	Brazil	[39]
Ameloblastella chavarrai	*Rhamdia quelen*	Mexico	[35]
Ameloblastella unapi	*Calophysus macropterus*	Peru	[36]
Ameloblastella martinae	*Sorubim lima*	Peru	[32]

Author statement

Patrick D. Mathews: Formal analysis, Data curation,Writing–original draft. Marcus V. Domingues: Investigation, Supervision. Antonio M. Maia: Methodology. Marcia R. M. Silva: Methodology. Edson A. Adriano: Supervision, Writing–original draft, Funding acquisition. Julio C. Aguiar: Methodology, Investigation, Formal analysis, Data curation, Writing–original draft.

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.

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