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A new species of *Ameloblastella* Kritsky, Mendoza-Franco & Scholz, 2000 (Monogenoidea: Dactylogyridae) from South American freshwater catfishes (Siluriformes: Pimelodidae)

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Abstract *Ameloblastella martinae* n. sp. is described from the gills of the pimelodid catfishes (Siluriformes: Pimelodidae) *Sorubim lima* (Bloch & Schneider) (type-host) and *Hemisorubim platyrhynchos* (Valenciennes) in the Peruvian Amazonia, and on *Pseudoplatystoma corruscans* (Spix & Agassiz) and *P. recticulatum* Eigenmann & Eigenmann in Argentina. The new species is distinguished from other congeners mainly by the morphology of the male copulatory organ (MCO), which has a form of a corkscrew with tight rings, whereas in other species of *Ameloblastella* Kritsky, Mendoza-Franco & Scholz, 2000, the MCO is formed by a delicate and coiled tube forming loose rings. Sclerotised structures (haptoral elements and MCO) of specimens of *A. martinae* n. sp. were used to compare two parasite populations (from Peru and Argentina) using Euclidean distances. Despite the geographical isolation and different host-associations, both populations belong to the same species. The phylogenetic position of *A. martinae* n. sp. was analysed using partial sequences of the 28S rDNA gene along with 46 species of dactylogyrid parasites of siluriforms (Siluriformes) under Maximum Likelihood (ML) and Bayesian Inference (BI) criteria. Phylogenetic reconstructions showed that *Ameloblastella* represented by five species, including its type-species *A. chavarriai* (Price, 1936) from the heptapterid *Rhamdia guatemalensis* and *A. martinae*

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n. sp., was recovered as a well-supported monophyletic group (in both analyses, ML and BI). An additional species, *Ameloblastella* sp., was found on *P. corruscans* and *P. reticulatum* in Argentina. The morphology of the MCO and haptoral elements suggests that *Ameloblastella* sp. may represent a new species. However, the few specimens found and the lack of genetic sequences of this species precluded its formal description.

Introduction

In recent years, Neotropical catfishes of the Pimelodidae have attracted attention of parasitologists due to several reasons: (i) pimelodids harbour the most diverse monogenoidean fauna of all Neotropical siluriforms, with 51 species included in 10 genera (Acosta et al., 2019; Mendoza-Palmero et al., 2019); (ii) the Pimelodidae represents the second most diverse group of siluriforms in the Neotropics (114 valid species) after the Loricariidae; (iii) most pimelodid species are distributed along South American Rivers, including Orinoco, Amazonas, Paraná, São Francisco, and Parnaíba (Froese & Pauly, 2018; Lundberg et al., 2011; Fricke et al., 2019; van der Sleen & Albert, 2018); and (iv) large pimelodids particularly those of the genera *Hemisorubim* Bleeker, *Pseudoplatystoma* Bleeker, and *Sorubim* Spix & Agassiz are considered economically important, being commercialised in fish markets for local consumption; some species are used for recreational fishing and others as ornamental fish (Loubens & Panfili, 2000; Littmann, 2007; Buitrago-Suarez & Burr, 2007).

Several dactylogyrids have been found on species of *Hemisorubim* Bleeker, *Pseudoplatystoma* Bleeker and *Sorubim* Cuvier throughout their distributional range in South America: *Nanayella amplofalcis* Acosta, Mendoza-Palmero, Silva & Scholz, 2019, *N. processusclavis* Acosta, Mendoza-Palmero, Silva & Scholz, 2019 and *Vancleaveus platyrhynchi* Kritsky, Thatcher & Boeger, 1986 on *H. platyrhynchos* (Valenciennes) in Brazil; *Ameloblastella unapioides* Mendoza-Franco, Mendoza-Palmero & Scholz, 2016, *N. aculeatrium* Acosta, Mendoza-Palmero, Silva & Scholz, 2019, *N. fluctuatrium* Acosta, Mendoza-Palmero, Silva & Scholz, 2019 and *N. megorchis* (Mizelle & Kritsky, 1969) Acosta, Mendoza-Palmero, Silva & Scholz, 2019 on *S. lima* (Bloch & Schneider) in Peru, Brazil and Argentina; *Pavanelliela pavanelli* Kritsky & Boeger, 1998, *Vancleaveus fungulus* Kritsky, Thatcher & Boeger, 1986 and *Amphocleithrum paraguayensis* Price & González-Romero, 1969 have been recorded on several species of *Pseudoplatystoma* Bleeker in Brazil, Argentina and Paraguay (see Acosta et al., 2019 for details).

Previously, Mendoza-Palmero et al. (2012) listed about 60 undescribed dactylogyrids parasitising catfishes from the Peruvian Amazonia, of which 15 were preliminarily identified as members of *Ameloblastella* Kritsky, Mendoza-Franco & Scholz, 2000. The main objectives of the present study are to characterise morphologically and molecularly dactylogyrid parasites found on the gills of the pimelodids *Sorubim lima* (Bloch & Schneider) and *Hemisorubim platyrhynchos* (Valenciennes) from the Peruvian Amazonia (previously listed in Mendoza-Palmero et al., 2012), and to compare the morphometry of sclerotised structures, based on Euclidean distances, from two different parasite populations, one infecting *S. lima* in Peru and the other parasitising *P. corruscans* (Spix & Agassiz) and *P. reticulatum* Eigenmann & Eigenmann in Argentina.

Materials and methods

Specimen collection and processing

Specimens of *Sorubim lima* and *Hemisorubim platyrhynchos* were captured by local fishermen in the surroundings of Iquitos (03°45′51″S, 73°14′50″W), Peru in 2004, 2009 and 2011. Field codes (PI = Peru, Iquitos) of each fish examined are provided in the species taxonomic summary. Specimens of *P. corruscans* and *P. reticulatum* were collected in November 2017 by gill nets and fishing rod from the stream Canelones (31°54′5″S, 60°49′12″W), a tributary of the River Coronda, Santa Fe Province, Argentina. Dactylogyrids were removed from the gills and fixed either with hot water (*c.*80°C) and stored in vials with 96% ethanol for molecular characterization or with hot (*c.*80°C) 4% buffered formaldehyde solution for morphological evaluation.

Dactylogyrids collected from the gills of Peruvian catfishes were fixed in GAP (a mixture of glycerine and ammonium picrate) in order to study their sclerotised structures (Malmberg, 1957). After the morphological evaluation, these specimens were remounted in Canada balsam following the procedure of Ergens (1969). Sclerotised structures of specimens collected in Argentina were studied from wet mounts using 10% sodium dodecyl sulphate (SDS) (Wong et al., 2006; Rossin et al., 2017); and after morphological evaluation, these were also remounted in Canada balsam. Images of haptoral structures and male copulatory organ (MCO) were captured at magnifications of 40× and 100× using Leica Application Suite (LAS) software and a Leica DFC 295 digital camera mounted on a Leica DM 2500 compound microscope, using a 0.55× interfacing lens. Drawings were made either with the aid of an optical microscope (Olympus BX51, Tokyo, Japan) equipped with a drawing tube or from captured images by a Leica DFC 295 digital camera and processed by Serif Draw Plus (Serif) software and Photoshop.

Other specimens were stained with Gomori's trichrome and mounted in Canada balsam to study their internal and external anatomy (Mendoza-Palmero & Sholz, 2011; Mendoza-Palmero et al., 2012). Measurements, all in micrometres, represent straight-line distances between extreme points of the structures measured and are expressed as the range followed by the mean and the number of measurements (n) in parentheses. Numbering and distribution of hook pairs followed Mizelle (1936) (see also Mizelle & Price, 1963). Direction of the MCO (i.e. counterclockwise *vs* clockwise) was determined using the procedure suggested by Kritsky et al. (1985). Type- and voucher specimens were deposited in the Helminthological Collection of the Institute of Parasitology, Biology Centre of the Czech Academy of Sciences, České Budějovice, Czech Republic (acronym IPCAS), in the Helminthological Collection of the División Zoología Invertebrados of the Museo de La Plata, La Plata, Argentina (acronym MLP-He), and in the Colección Nacional de Helmintos (acronym CNHE), Universidad Nacional Autónoma de Mexico, Ciudad de México, Mexico. Host names follow Froese & Pauly (2019).

For comparative purposes, the following type- and voucher specimens were studied: *Ameloblastella chavarriai* (Price, 1938) Kritsky, Mendoza-Franco & Scholz, 2000 (vouchers IPCAS M-354); *A. edentensis* Mendoza-Franco, Mendoza-Palmero & Scholz, 2016 (holotype and paratypes IPCAS M-622); *A. formatrium* Mendoza-Franco, Mendoza-Palmero & Scholz, 2016 (holotype and paratypes IPCAS M-624); *A. peruensis* Mendoza-Franco, Mendoza-Palmero & Scholz, 2016 (holotype and paratypes IPCAS M-623); *A. unapi* Mendoza-Franco & Scholz, 2009 (vouchers IPCAS M-482); and *A. unapioides* (holotype and paratypes IPCAS M-625). Due to low amount of fish examined of each species, and mixed parasite infection (e.g. up to six dactylogyrid species in *S. lima*), no infection parameters are provided.

Morphometric analyses

To study morphological similarities between specimens recovered from catfishes from Peru and Argentina, ten morphometric variables of sclerotised structures of 15 specimens (11 from Peru and four from Argentina) were analysed. In order to minimise the effect of large over small structures (e.g. ventral bars *vs* hooks), we used the deviation of the mean for each measurement as a standardised value.

To visualise the distances among specimens in the multivariate morphospace, we used a non-metric multidimensional scaling (nMDS) based on the Euclidean distance resemblance matrix. To test for significant differences, a one-way non-parametric permutation-based multivariate analysis of variance (PERMANOVA) was carried out, based on a permutation of residuals under a reduced model (Anderson et al., 2008). Since PERMANOVA is sensitive to differences in multivariate dispersions, the PERMDISP routine was carried out (Anderson et al., 2008). PERMANOVA and PERMDISP analyses were conducted with the software PERMANOVA+ for PRIMER (Anderson et al., 2008).

Molecular characterisation and phylogenetic analyses

Partial sequences of the 28S rRNA gene of three isolates of *Ameloblastella martinae* n. sp. from *S. lima* were generated in the present study. Procedures of DNA extraction, gene amplification and sequencing followed those of Acosta et al. (2019) and Mendoza-Palmero et al. (2019). Molecular vouchers were deposited in IPCAS (hologenophores of *A. martinae* n. sp. M-724) (see Pleijel et al., 2008 for terminology).

Newly generated sequences in the present study along with 46 previously published sequences of the 28S rDNA fragment (720–1,480 bp long) of a total of 43 species of dactylogyrids from siluriforms (see

Mendoza-Palmero et al., 2015, 2019; Acosta et al., 2017, 2018, 2019; Franceschini et al., 2018; Yamada et al., 2018) were subjected to phylogenetic analyses to assess the relationships of the new species within *Ameloblastella* spp. and other dactylogyrid parasites of catfishes. Sequences of three species of the Diplectanidae were used as the outgroup.

Sequences were aligned using default parameters of MAFFT implemented in Geneious v.11.1.4 (Kearse et al., 2012). The extremes of the alignment were trimmed, resulting in 1,238 nucleotide positions for analyses. Phylogenetic analyses were run under Maximum Likelihood (ML) and Bayesian Inference (BI) methods, applying the model of nucleotide evolution GTR+Γ+I, estimated using jModelTest 2.1.1 (Darriba et al., 2012). ML analyses were performed with RAxML v.8 (Guindon & Gascuel, 2003); model parameters and bootstrap support values (1,000 pseudoreplicates) were estimated with RAxML. BI trees were generated using MrBayes v.3.2 (Ronquist et al., 2012) running two independent MCMC runs of four chains for 10^7 generations and sampling tree topologies every 10^3 generations. 'Burn-in' was set to the first 25,000 generations. MrBayes and RAxML analyses were carried out on the computational platform CIPRES (Miller et al., 2010). Phylogenetic trees were edited using FigTree v.1.3.1 (Raumbaut, 2009).

Subclass Polyonchoinea Bychowsky, 1937
Order Dactylogyridea Bychowsky, 1937
Family Dactylogyridae Bychowsky, 1933
Genus *Ameloblastella* Kritsky, Mendoza-Franco & Scholz, 2000

Ameloblastella martinae n. sp.

Type-host: *Sorubim lima* (Bloch & Schneider) (Siluriformes: Pimelodidae) (PI 598, PI 647, PI 862).
Other hosts: *Hemisorubim platyrhynchos* (Valenciennes) (PI 432), *Pseudoplatystoma corruscans* (Spix & Agassiz) and *P. reticulatum* Eigenmann & Eigenmann (all Pimelodidae).
Type-locality: Iquitos, Peru (03°45′51″S, 73°14′50″W) (precise locality of fish hosts is not known).
Other localities: Iquitos, Peru (*H. platyrhynchos*; precise locality of fish host is not known); stream Canelones (31°54′5″S, 60°49′12″W), tributary of the River Coronda, Santa Fe Province, Argentina (*P. corruscans* and *P. reticulatum*).
Type-material: Holotype (IPCAS M-724) collected on *S. lima* (07/10/2011); 4 paratypes from *S. lima* (IPCAS M-724); 2 paratypes (CNHE 11260, CNHE 11261) and 1 voucher (CNHE 11262, respectively); and 4 vouchers collected from *P. curruscan* (2) and from *P. reticulatum* (2), respectively (MLP-He 7654).
Site in host: Gill lamellae.
Representative DNA sequences: 1,429, 1,439 and 1,459 bp long partial sequences of the 28S rRNA gene of *Ameloblastella martinae* n. sp. from *S. lima* (PI 862) (GenBank: MT174171-MT174173).
ZooBank registration: To comply with the regulations set out in Article 8.5 of the amended 2012 version of the *International Code of Zoological Nomenclature* (ICZN, 2012), details of the new species have been submitted to ZooBank. The Life Science Identifier (LSID) for *Ameloblastella martinae* n. sp. is urn:lsid:zoobank.org:act:FBA73B87-0821-47FA-ACE4-5236B62EBF13.
Etymology: The species is named after Mrs Martina Borovková in recognition of her excellent and precise work in more than 25 years of uninterrupted activities at the Laboratory of Helminthology, Institute of Parasitology, České Budějovice, Czech Republic.

Description

[Based on 11 specimens fixed in GAP and 10 stained with Gomori's trichrome and mounted in Canada balsam, all collected from *S. lima*; Fig. 1A–H.] Body elongate, 295–445 (388; n = 10) long, with greatest width at level of gonads, 70–100 (83; n = 10) wide. Cephalic lobes poorly developed, only bilateral lobes slightly conspicuous, each with 2 pairs of cephalic organs. Bilateral cephalic glands located posteriorly to pharynx. No chromatic granules in anterior region. Pharynx subspherical, 23–30 (26; n = 10) wide, oesophagus short (Fig. 1A).

Peduncle inconspicuous. Two pairs of longitudinal ligaments running dorsally from anterior region of body and proximally attached to haptoral elements (anchors and hooks) (Fig. 1A). Haptor trapezoidal, 43–79 (51; n = 9) long, 105–140 (120; n = 9) wide (Fig. 1A). Ventral anchor with well-developed superficial root, short deep root, evenly curved shaft and point; point elongate, 28–34 (30; n = 11) long, slightly exceeding base width, base width 14–19 (17; n = 11)

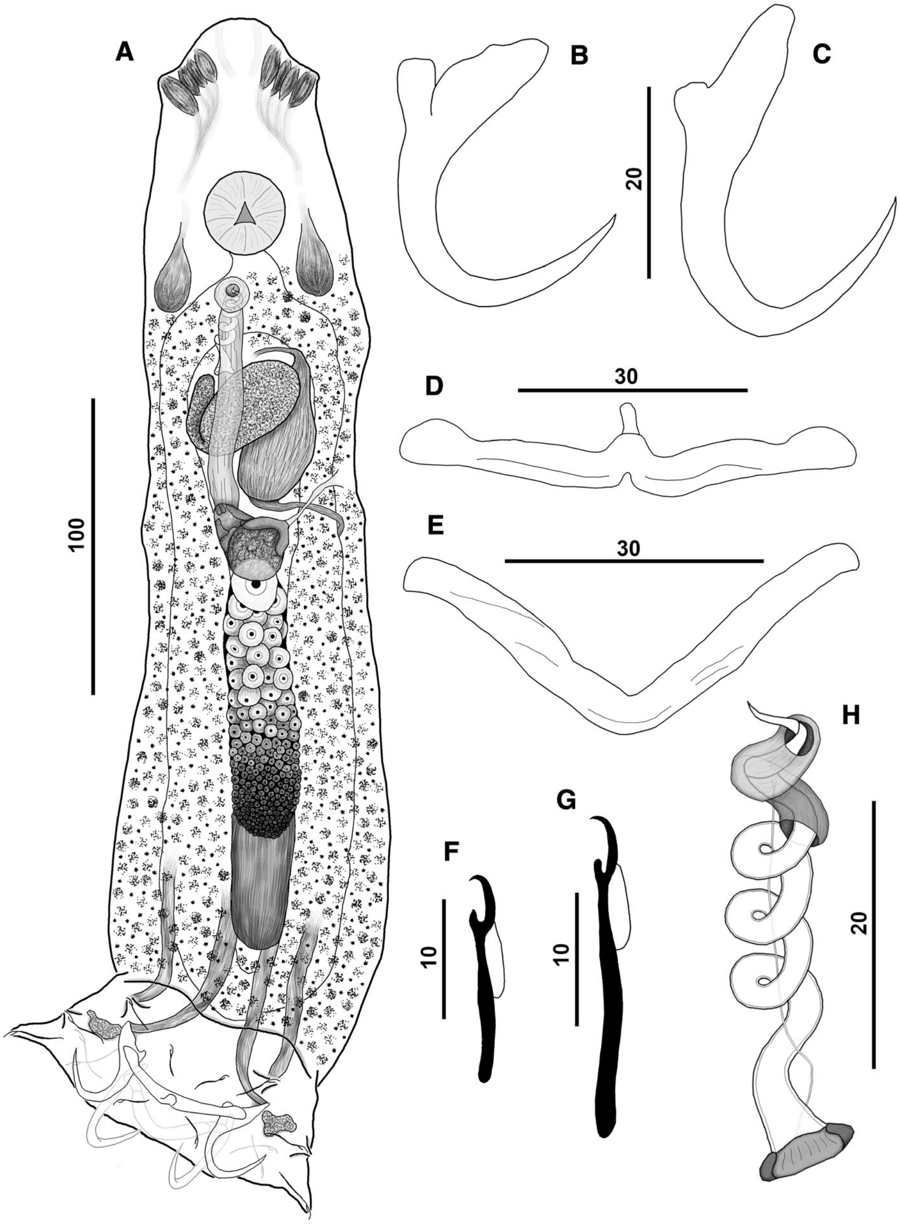

Fig. 1 *Ameloblastella martinae* n. sp. ex *Sorubim lima*. A, Whole specimen, ventral view (composite); B, Ventral anchor; C, Dorsal anchor; D, Ventral bar; E, Dorsal bar; F, Hook pairs 1 and 5; G, Hook pairs 2–4, 6 and 7; H, Copulatory complex (ventral). *Scale-bars*: A, 100 µm; B, C, H, 20 µm; D, E, 30 µm; F, G, 10 µm

(Fig. 1B). Dorsal anchor with elongated superficial root, short and reduced deep root, robust shaft slightly curved, elongated point, not exceeding base width, 31–40 (37; n = 11) long, base width 14–20 (17; n = 11) (Fig. 1C). Ventral bar 49–65 (57; n = 11) long, rod-shaped, with short antero-medial process and expanded ends (Fig. 1D). Dorsal bar 47–64 (56; n = 11) long, open V-shaped, with not expanded ends (Fig. 1E). Hooks slightly different in size, similar in shape, each with inflated shank, upright thumb, straight shaft, short and curved point; hook pairs 1 and 5 similar, 15–21 (18; n = 19) long, filamentous hooklet (FH) loop about half of shank length (Fig. 1F); hook pairs 2–4, 6 and 7 similar, 22–27 (25; n = 19) long, filamentous hooklet (FH) loop about one-third of shank length (Fig. 1G).

Male copulatory organ 32–42 (37; n = 11) long, represented by a corkscrew-like tube of about 4.5 counterclockwise tight rings, distally acute, proximal ring diameter 7–10 (8; n = 11); base of MCO articulated to accessory piece (Fig. 1H). Accessory piece 9–15 (12; n = 8) long, represented by small and delicate sheath, variable in shape, guiding distal part of MCO; articulation piece appears as delicate tube extending from base of MCO, passing through rings up to base of accessory piece (Fig. 1H).

Gonads in tandem, slightly overlapping, germarium 69–130 (96; n = 10) long, 24–43 (29; n = 10) wide, pre-testicular, elongated, occupying about 1/4 of body length (Fig. 1A). Testis 100–140 (116; n = 4) long, 19–40 (29; n = 7) wide, elongated, partially covered by germarium (Fig. 1A). Vas deferens looping left intestinal caecum; seminal vesicle pyriform as dilatation of vas deferens lying sinistral of midline; prostatic reservoir single, located on midline, ventral to seminal vesicle, distally folded (Fig. 1A). Oviduct arising from seminal receptacle, forming the uterus running anteriorly emptying to genital pore, located slightly dextral of midline at level of intestinal bifurcation (Fig. 1A). Vaginal aperture sinistral, not sclerotised; vaginal tube empties to a semi-spherical seminal receptacle lying right anterior of germarium (Fig. 1A). Vitelline follicles scattered throughout trunk except in regions of reproductive organs.

Remarks

The dactylogyrids found on the pimelodids *S. lima*, *H. platyrhynchos*, *P. corruscans*, and *P. reticulatum* were assigned to *Ameloblastella* based on the presence of a ventral bar with an antero-medial process, accessory piece articulated to the base of the MCO, counter-clockwise coiled MCO, hooks with inflated shanks, vaginal aperture sinistral, gonads overlapped, and the absence of eye-spots (see Kritsky et al. 2000). *Ameloblastella martinae* n. sp. can be distinguished from other congeners mainly by the morphology of the MCO, which has a form of a corkscrew with 4.5 tight rings (see Fig. 1H), whereas in most species of *Ameloblastella*, the MCO is represented by a delicate tube with variable number of loose rings, ranging between 2–5.5, except in *A. unapi*, which possesses 13–14 rings.

Only three specimens of *A. martinae* n. sp. were found on *H. platyrhynchos* from Peru. Therefore, measurements of these specimens were not included in the species description. However, the morphometric data for the haptoral elements and copulatory complex of these specimens fall within the ranges in the description of *A. martinae* n. sp., and they are considered as conspecific.

Results of the MDS did not show a clear separation between specimens of *A. martinae* n. sp. from Peru and Argentina (Fig. 2), with a low stress level (0.08). PERMANOVA results showed no differences among multivariate data of morphometric measurements of specimens of *A. martinae* n. sp. found in fish hosts from Peru and Argentina (Table 1) (PseudoF$_{(1,13)}$ = 0.75, P (perm) = 0.58), although significant dispersion was found on data set (PERMDISP: PseudoF$_{(1,13)}$ = 11.77, *P* (perm) = 0.01).

Ameloblastella sp.

Hosts: *Pseudoplatystoma corruscans* (Spix & Agassiz) and *P. reticulatum* Eigenmann & Eigenmann (Siluriformes: Pimelodidae).

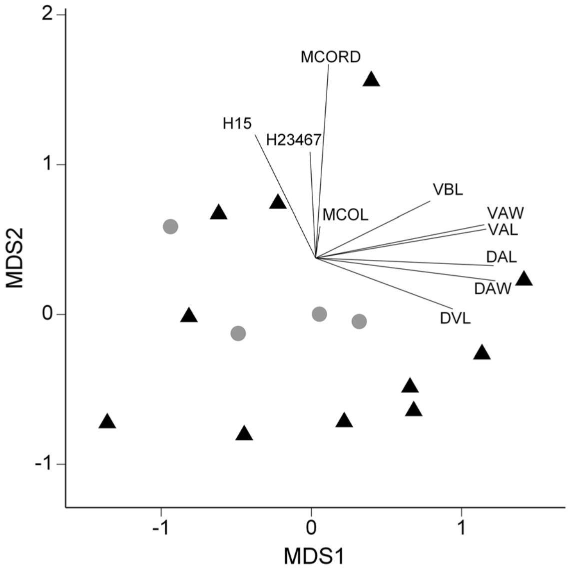

Fig. 2 Non-metric multidimensional scaling plot (nMDS) (Euclidean distances) of specimens of *Ameloblastella martinae* n. sp. from Peru (black triangles) and Argentina (grey circles). Vectors represent Pearson's correlations of each variable with the nMDS axes. *Abbreviations*: VAL, ventral anchor length; VAW, ventral anchor base width; DAL, dorsal anchor length; DAW, dorsal anchor base width; VBL, ventral bar length; DVL, dorsal bar length; MCOL, male copulatory organ length; MCORD, male copulatory organ 1st ring diameter; H15, mean of marginal hook 1 and 5; H23467, mean of marginal hook 2–4, 6 and 7

Locality: Stream Canelones (31°54’5″S, 60°49’12″W), tributary of the River Coronda, Santa Fe Province, Argentina.
Vouchers material: Five specimens deposited (MLP-He 7655).
Site in host: Gill lamellae.

Remarks

Based on the morphology of the copulatory complex and haptoral elements (Fig. 3), the specimens found on *P. corruscans* and *P. reticulatum* clearly represent a member of *Ameloblastella*. However, only few specimens were collected thus precluding their adequate morphological description and molecular characterisation. The morphology of the sclerotised structures in *Ameloblastella* sp. most closely resembles that of *A. martinae* n. sp. (see Figs. 1, 3). However, we observed differences between *Ameloblastella* sp. and *A. martinae* n. sp. mainly in the morphology of the MCO: looser rings at the distal section of the copulatory tube (*vs* tighter rings through its entire length) and comparatively larger accessory piece located in the medial portion of the MCO (*vs* smaller and distally located). Anchor-bar complexes in *Ameloblastella* sp. and *A. martinae* n. sp. are very similar in size and shape; therefore, to rule out the possibility that specimens designated here as *Ameloblastella* sp. represent only morphological variation of those of *A. martinae* n. sp., additional specimens of *Ameloblastella* sp. are needed to evaluate their morphology and their respective phylogenetic position within *Ameloblastella* based on molecular data.

Phylogenetic position of the new species

Results from both analyses (ML and BI) yielded similar topology (Fig. 4), where dactylogyrid parasites of catfishes formed two clades (A and B), each well supported. In the phylogenetic analyses, species of *Ameloblastella*, including *A. unapoiodes* Mendoza-Franco, Mendoza-Palmero & Scholz, 2016, *A. chavarriai* (type-species), *A. edentensis*, *Ameloblastella* sp. 23 of Mendoza-Palmero et al. (2015), and *A. martinae* n. sp., formed a well-supported group within clade A. *Ameloblastella martinae* n. sp. is closely related to the clade formed by *A. edentensis* and *Ameloblastella* sp. 23, and this clade is also well supported, therefore, the monophyly of *Ameloblastella* is herein confirmed (see Fig. 4). Species of *Ameloblastella* appeared as closely related to *Vancleaveus janauacanesis* Kritsky, Thatcher & Boeger, 1986 and *Unibarra paranoplatensis* Suriano & Incorvaia, 1995 (see Fig. 4). These results are in accordance to recent phylogenetic studies, where phylogenetic relationship between dactylogyrid parasites of Neotropical catfishes were analysed using partial sequences of the 28S gene (Acosta et al., 2019; Mendoza-Palmero et al., 2019).

Table 1 Morphometric variables of specimens of *Ameloblastellia martinae* n. sp. from Peru and Argentina used for the non-metric multidimensional scaling plot analysis

Variable	Peru (n = 11)	Argentina (n = 4)
VAL	28–34 (30)	28–29 (29)
VAW	14–19 (17)	14–17 (16)
DAL	31–40 (37)	35–36 (36)
DAW	14–20 (17)	14–19 (17)
VBL	49–65 (57)	52–55 (54)
DVL	47–64 (56)	50–54 (52)
MCOL	32–42 (37)	33–36 (35)
MCORD	7–10 (8)	8–9 (8)
H15	16–20 (18)	17–19 (19)
H23467	23–26 (24)	23–24 (24)

Note: Range is followed by the mean in parentheses

Abbreviations: VAL, ventral anchor length; VAW, ventral anchor base width; DAL, dorsal anchor length; DAW, dorsal anchor base width; VBL, ventral bar length; DVL, dorsal bar length; MCOL, male copulatory organ length; MCORD, male copulatory organ 1st ring diameter; H15, mean of marginal hooks 1 and 5; H23467, mean of marginal hooks 2–4, 6 and 7

Discussion

In this study, *A. martinae* n. sp. is described based on specimens found on the gills of *S. lima* (type-host), infecting also *H. platyrhynchos*, both host species collected in the Peruvian Amazonia, and morphologically compared with those specimens collected from *P. corruscans* and *P. reticulatum* in Argentina. Although molecular data for specimens of *A. martinae* n. sp. from *P. corruscans* and *P. reticulatum* were not available, statistical analysis (MDS and PERMANOVA) of sclerotised structures based on Euclidean distances revealed no significant differences between

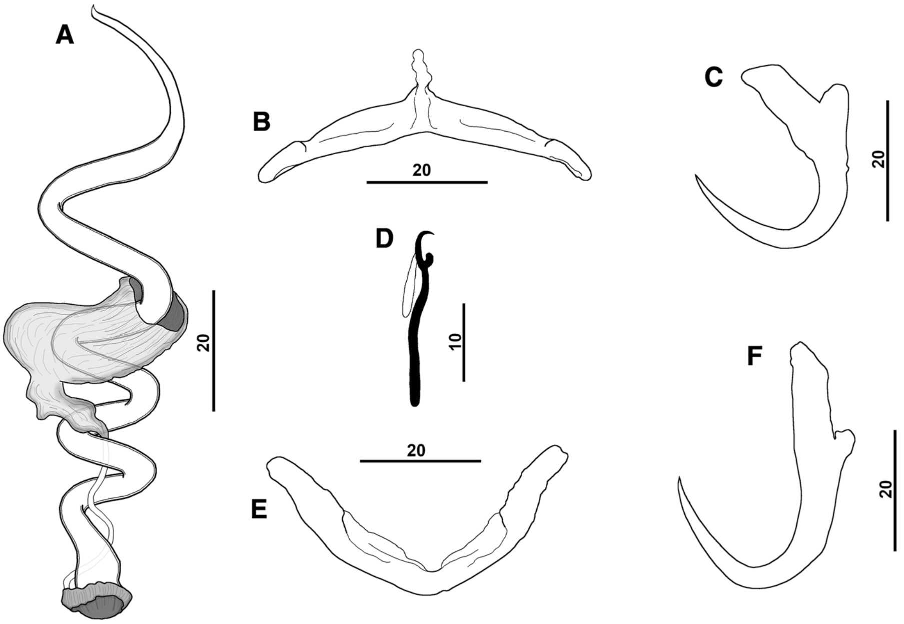

Fig. 3 *Ameloblastella* sp. ex *Pseudoplatystoma corruscans* of Argentina. A, Copulatory complex, ventral view; B, Ventral bar; C, Ventral anchor; D, Hook; E, Dorsal bar; F, Dorsal anchor. *Scale-bars:* A–C, E, F, 20 µm; D, 10 µm

two parasite populations of *A. martinae* n. sp. from Peru and Argentina. Therefore, we concluded that both parasite populations are conspecific despite their geographical isolation (Amazon River basin, northern Peru *vs* Coronda River basin, northeast Argentina) and different host-associations (*Sorubim* + *Hemisorubim vs Pseudoplatystoma* spp.).

Mendoza-Palmero et al. (2012) mentioned that only in the Peruvian Amazonia, a total of 15 undescribed species of *Ameloblastella* were recognised parasitising 17 host species. Of that total, four species have been recently described as new taxa: *Ameloblastella formatrium* on Pimelodidae gen. sp. (type-host) and *Duopalatinus* cf. *peruanus* Eigenmann & Allen; *A. edentensis* on *Hypophthalmus edentatus* Spix & Agassiz (type-host); *A. peruensis* on *Hypophthalmus* sp. (type-host); and *A. unapioides* from *Sorubim lima* (type-host) and *Pimelodus* sp. (see Mendoza-Franco et al., 2016).

To date, *Ameloblastella* comprises 12 species (including *A. martinae* n. sp.) infecting 15 species of the Heptapteridae and the Pimelodidae (França et al., 2003; Mendoza-Franco & Scholz, 2009; Mendoza-Franco et al., 2016; Monteiro et al., 2010; Negreiros et al., 2019). All species of *Ameloblastella* have been described from South America (Brazil, Peru, Colombia, Trinidad and Argentina), except for the type-species, *A. chavarriai*, which was originally described from Costa Rica, and subsequently reported in Nicaragua and southern Mexico (Mendoza-Franco et al., 2003; Mendoza-Garfias et al., 2017).

Species currently allocated in *Ameloblastella* are restricted parasites of the Pimelodidae and Heptapteridae; however, Mendoza-Palmero et al. (2012) reported species of *Ameloblastella* infecting catfishes of the Auchenipteridae (1 species), Callichthyidae (1 species) and Doradidae (3 species), although these species have not yet been morphologically and molecularly characterised.

The new species was found to infect pimelodid species of *Sorubim*, *Hemisorubim* and *Pseudoplatystoma* from Peru and Argentina. Considering that these catfishes live in sympatry (e.g. in the Paraná River basin), the presence of *A. martinae* n. sp. could be expected within the distributional range of its host species.

In this study, ML and BI phylogenetic analyses of partial sequences of the 28S rDNA gene showed that dactylogyrid parasites of siluriform fishes form two well-supported clades (A and B). *Ameloblastella* (represented herein by five species; including the type-species *A. chavarriai* and *A. martinae* n. sp.) was

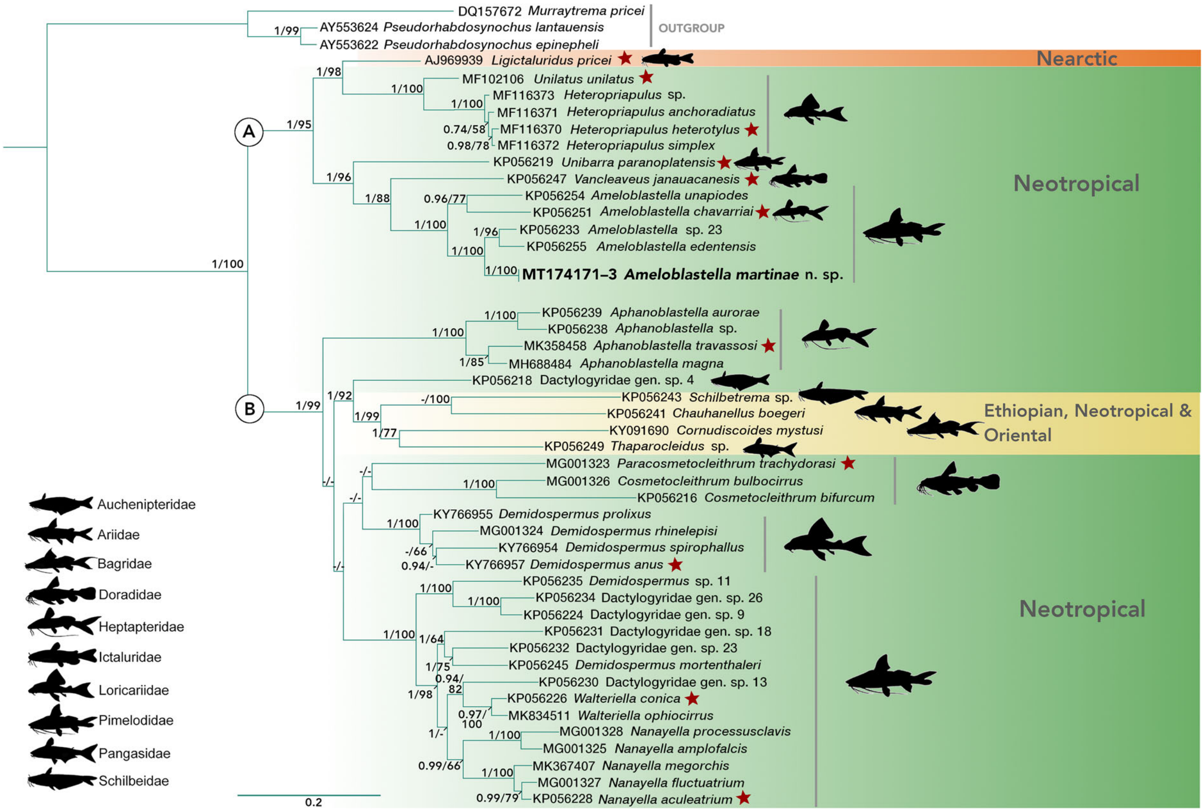

Fig. 4 Phylogenetic position of *Ameloblastella martinae* n. sp. within monogenoidean parasites of catfishes estimated by Maximum Likelihood (ML) criterion using partial sequences of the 28S rRNA gene. Species of the Diplectanidae were used as the outgroup. The newly generated sequences are indicated in bold. Type-species of selected genera are indicated by a red star. Posterior probabilities from Bayesian Inference (BI) analysis and bootstrap values (ML) are given above the nodes; posterior probabilities < 0.90 and bootstrap values < 60 are not shown

recovered as a monophyletic group with *A. martinae* n. sp. being closely related to a sister clade (within *Ameloblastella*) formed by *A. edentensis* and *Ameloblastella* sp. 23 of Mendoza-Palmero et al. (2015). Overall, the phylogenetic reconstructions showed that while relationships between species of clade A (Neotropical and Nearctic) appeared as well supported, those of species of clade B (Neotropical, Ethiopian and Oriental) remain unresolved.

Based on the current information on dactylogyrids parasitising Neotropical catfishes, it is evident that these parasites do not exhibit strict parasite-host associations at genus or species levels but rather at family level. For instance, species of *Unilatus* Mizelle & Kritsky, 1967, *Trinigyrus* Hanek, Molnar & Fernando, 1974, *Heteropriapulus* Kritsky, 2007 and *Demidospermus* Suriano, 1983 (*sensu stricto*) are exclusive parasites of loricariids (Loricariidae), whereas species of *Aphanoblastella* Kritsky, Mendoza-Franco & Scholz, 2000 are restricted to heptapterids (Heptapteridae). Further studies (combining morphological and phylogenetic approaches) focused on these parasite species, may reveal different phylogenetic patterns and host-parasite associations.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

Ethical approval All applicable institutional, national and international guidelines for the care and use of animals were followed.

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