

Research Article

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A new genus and four new species of dactylogyrids (Monogenea), gill parasites of pimelodid catfishes (Siluriformes: Pimelodidae) in South America and the reassignment of *Urocleidoides megorchis* Mizelle et Kritsky, 1969

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Abstract: *Nanayella* gen. n. is proposed to accommodate four new species of dactylogyrid monogeneans found on the gills of two species of pimelodid catfishes (Siluriformes) from the Amazon River basin in Peru and the Upper Paraná River basin in Brazil. *Nanayella* gen. n. is mainly characterised by the presence of modified hook pairs 5 and 6, which have a slender shank with slightly enlarged base, inconspicuous thumb, and straight point. *Nanayella aculeatrium* gen. n. et sp. n. (type species) from *Sorubim lima* (Bloch et Schneider) (type host) differs from its congeners mainly by possessing seven sclerotised spines on one side of circular ornamentation of the vaginal atrium. *Nanayella fluctuatrium* gen. n. et sp. n. is characterised by the presence of sclerotised undulations surrounding the circular ornamentation of the vaginal atrium. *Nanayella amplofalcis* gen. n. et sp. n. is typified by possessing hook pairs 1 and 2 with a robust, wide shank and a round, weakly sclerotised subunit at the base. *Nanayella processusclavis* gen. n. et sp. n. differs from congeners by the presence of a conspicuous posterior medial process on the dorsal bar. *Urocleidoides megorchis* Mizelle et Kritsky, 1969 described from the gills of *S. lima* in Brazil is transferred to *Nanayella* gen. n. as *Nanayella megorchis* comb. n. based on morphological and molecular evidence. Analyses of partial sequences of the 28S rRNA gene revealed all five species of the new genus to form a monophyletic clade within a bigger clade comprised of dactylogyrids of South American pimelodids.

Keywords: Ancyrocephalinae, morphology, integrative taxonomy, 28S rRNA, Sorubiminae, Neotropical region

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The Pimelodidae (Siluriformes) represents a diverse and abundant monophyletic group of freshwater fishes, with 31 recognised genera including 112 valid species, distributed exclusively in South America, showing the highest species diversity in the Amazon, Paraná and Orinoco River basins (Lundberg and Littmann 2003, Lundberg et al. 2011, Eschemeyer et al. 2017). Pimelodids harbour the richest diversity of dactylogyrid monogeneans compared to that of other siluriforms in South America, with 44 species belonging to eight genera (Table 1). The porthole shovelnose catfish *Hemisorubim platyrhynchos* (Valenciennes) and the duckbill catfish *Sorubim lima* (Bloch et Schneider) share their distribution in the Amazon, Orinoco and Paraná River basins, but *H. platyrhynchos* is also present in the Maroni River (Suriname) and *S. lima* in the Parnaíba River, northern Brazil (Froese and Pauly 2018). These two fish species

belong to the subfamily Sorubiminae (see Lundberg et al. 2011).

Even though the dactylogyrid fauna of pimelodids is rich and diverse (see Cohen et al. 2013, Aguiar et al. 2017), only *Urocleidoides megorchis* Mizelle et Kritsky, 1969 and *Ameloblastella unapioides* Mendoza-Franco, Mendoza-Palmero et Scholz, 2016 have been described from *S. lima* (see Mizelle and Kritsky 1969, Mendoza-Franco et al. 2016), and *Vancleaveus platyrhynchi* Kritsky, Thatcher et Boeger, 1986 from *H. platyrhynchos* (see Kritsky et al. 1986, Mendoza-Palmero et al. 2012).

Based on morphological and molecular evidence, this study proposes a new genus to accommodate four new species of dactylogyrids found on the gills of *S. lima* and *H. platyrhynchos*. In addition, *U. megorchis* from *S. lima*, which was considered as *incertae sedis* by Kritsky et al. (1986), is transferred to the new genus.

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Table 1. List of dactylogyrids described for pimelodid catfishes from South America.

Species	Host	Country	Reference
<i>Ameloblastella edentensis</i> Mendoza-Franco, Mendoza-Palmero et Scholz, 2016	<i>Hypophthalmus edentatus</i> Spix et Agassiz	Peru	Mendoza-Franco et al. (2016)
<i>Ameloblastella formatrium</i> Mendoza-Franco, Mendoza-Palmero et Scholz, 2016	Pimelodidae gen. sp.	Peru	Mendoza-Franco et al. (2016)
<i>Ameloblastella mamaevi</i> (Kritsky et Thatcher, 1976)	<i>Zungaro zungaro</i> (Humboldt)	Colombia	Kritsky et al. (2000)
<i>Ameloblastella paranaensis</i> (França, Isaac, Pavanelli et Takemoto, 2003)	<i>Iheringichthys labrosus</i> (Lütken)	Brazil	Mendoza-Franco and Scholz (2009)
<i>Ameloblastella peruensis</i> Mendoza-Franco, Mendoza-Palmero et Scholz, 2016	<i>Hypophthalmus</i> sp.	Peru	Mendoza-Franco et al. (2016)
<i>Ameloblastella platensis</i> (Suriano et Incorvaia, 1995)	<i>Pimelodus maculatus</i> Lacepède	Argentina	Kritsky et al. (2000)
<i>Ameloblastella satoi</i> Monteiro, Kritsky et Brasil-Sato, 2010	<i>Pimelodus maculatus</i>	Brazil	Monteiro et al. (2010)
<i>Ameloblastella unapioides</i> Mendoza-Franco, Mendoza-Palmero et Scholz, 2016	<i>Sorubim lima</i> (Bloch et Schneider)	Peru	Mendoza-Franco et al. (2016)
<i>Amphocleithrum paraguayensis</i> Price et Romero, 1969	<i>Pseudoplatystoma</i> sp.	Paraguay	Price and Romero (1969)
<i>Cosmetocleithrum longivaginatatum</i> Suriano et Incorvaia, 1995	<i>Pimelodus albicans</i> (Valenciennes)	Argentina	Suriano and Incorvaia (1995)
<i>Demidospermus annulus</i> Marcotegui et Martorelli, 2011	<i>Parapimelodus valenciennis</i> (Lütken)	Argentina	Marcotegui and Martorelli (2011)
<i>Demidospermus araguaiaensis</i> Cepeda et Luque, 2010	<i>Brachyplatystoma filamentosum</i> (Lichtenstein)	Brazil	Cepeda and Luque (2010)
<i>Demidospermus armostus</i> Kritsky et Gutiérrez, 1998	<i>Pimelodus clarias</i> (Linnaeus)	Argentina	Kritsky and Gutiérrez (1998)
<i>Demidospermus bidiverticulatum</i> (Suriano et Incorvaia, 1995)	<i>Pimelodus clarias</i> and <i>Pimelodus albicans</i>	Argentina	Kritsky and Gutiérrez (1998)
<i>Demidospermus brachyplatystomae</i> Cepeda et Luque, 2010	<i>Brachyplatystoma filamentosum</i>	Brazil	Cepeda and Luque (2010)
<i>Demidospermus brevicirrus</i> Mendoza-Palmero, Scholz, Mendoza-Franco et Kuchta, 2012	<i>Pimelodus</i> sp.	Peru	Mendoza-Palmero et al. (2012)
<i>Demidospermus ceccarelli</i> Cepeda et Luque, 2010	<i>Brachyplatystoma filamentosum</i>	Brazil	Cepeda and Luque (2010)
<i>Demidospermus corcinus</i> Kritsky et Gutiérrez, 1998	<i>Iheringichthys westermanni</i> (Lütken)	Argentina	Kritsky and Gutiérrez (1998)
<i>Demidospermus curvovaginatatus</i> Mendoza-Palmero et Scholz, 2011	<i>Pimelodus</i> sp.	Peru	Mendoza-Palmero and Scholz (2011)
<i>Demidospermus ichthyocercus</i> Monteiro, Kritsky et Brasil-Sato, 2010	<i>Pimelodus maculatus</i>	Brazil	Monteiro et al. (2010)
<i>Demidospermus idulus</i> Kritsky et Gutiérrez, 1998	<i>Pimelodus albicans</i>	Argentina	Kritsky and Gutiérrez (1998)
<i>Demidospermus lebedevi</i> (Kritsky et Thatcher, 1976)	<i>Pimelodus grosskopfii</i> Steindachner	Colombia	Mendoza-Palmero and Scholz (2011)
<i>Demidospermus leptosynophallus</i> Kritsky et Gutiérrez, 1998	<i>Iheringichthys westermanni</i>	Argentina	Kritsky and Gutiérrez (1998)
<i>Demidospermus lucky</i> (Kritsky, Thatcher et Boeger, 1987)	<i>Pinirampus pirinampu</i> (Spix et Agassiz)	Brazil	Kritsky and Gutiérrez (1998)
<i>Demidospermus macropteri</i> Mendoza-Franco et Scholz, 2009	<i>Calophysus macropterus</i> (Lichtenstein)	Peru	Mendoza-Franco and Scholz (2009)
<i>Demidospermus majusculus</i> Kritsky et Gutiérrez, 1998	<i>Pimelodus albicans</i>	Argentina	Kritsky and Gutiérrez (1998)
<i>Demidospermus mortenthaleri</i> Mendoza-Palmero, Scholz, Mendoza-Franco et Kuchta, 2012	<i>Brachyplatystoma juruense</i> (Boulenger)	Peru	Mendoza-Palmero et al. (2012)
<i>Demidospermus paravalenciennesi</i> Gutiérrez et Suriano, 1992	<i>Pimelodus clarias</i>	Argentina	Gutiérrez and Suriano (1992)
<i>Demidospermus peruvianus</i> Mendoza-Palmero et Scholz, 2011	<i>Pimelodus ornatus</i> Kner	Peru	Mendoza-Palmero and Scholz (2011)
<i>Demidospermus pinirampi</i> (Kritsky, Thatcher et Boeger, 1987)	<i>Pinirampus pirinampu</i>	Brazil	Kritsky and Gutiérrez (1998)
<i>Demidospermus striatus</i> Mendoza-Palmero et Scholz, 2011	<i>Pimelodus</i> sp.	Peru	Mendoza-Palmero and Scholz (2011)
<i>Demidospermus uncusvalidus</i> Gutiérrez et Suriano, 1992	<i>Pimelodus clarias</i>	Argentina	Gutiérrez and Suriano (1992)
<i>Demidospermus valenciennesi</i> Gutiérrez et Suriano, 1992	<i>Parapimelodus valenciennis</i>	Argentina	Gutiérrez and Suriano (1992)
<i>Pavanelliella jarri</i> Aguiar, Maia, Silva, Ceccarelli, Domingues et Adriano, 2017	<i>Brachyplatystoma rousseauxii</i> (Castelnau)	Brazil	Aguiar et al. (2017)
<i>Pavanelliella laertei</i> Aguiar, Ceccarelli et Luque, 2011	<i>Pimelodus heraldoi</i> Azpelicueta	Brazil	Aguiar et al. (2011)
<i>Pavanelliella pavanellii</i> Kritsky et Boeger, 1998	<i>Pseudoplatystoma corruscans</i> (Spix et Agassiz)	Brazil	Kritsky and Boeger (1998)
<i>Pavanelliella takemotoi</i> Aguiar, Ceccarelli et Luque, 2011	<i>Pimelodus maculatus</i>	Brazil	Aguiar et al. (2011)
<i>Unibarra paranoplatensis</i> Suriano et Incorvaia, 1995	<i>Paulicea luetkeni</i> Steindachner	Argentina	Suriano and Incorvaia (1995)
<i>Urocleidoides amazonensis</i> Mizelle et Kritsky, 1969	<i>Phratocephalus hemiliopterus</i> (Block et Schneider)	Brazil	Mizelle and Kritsky (1969)
<i>Urocleidoides catus</i> Mizelle et Kritsky, 1969	<i>Phratocephalus hemiliopterus</i>	Brazil	Mizelle and Kritsky (1969)
<i>Urocleidoides megorchis</i> Mizelle et Kritsky, 1969	<i>Sorubim lima</i>	Argentina	Mizelle and Kritsky (1969)
<i>Vancleavus cicinnus</i> Kritsky, Thatcher et Boeger, 1986	<i>Phratocephalus hemiliopterus</i>	Brazil	Kritsky et al. (1986)
<i>Vancleavus fungulus</i> Kritsky, Thatcher et Boeger, 1986	<i>Pseudoplatystoma tigrinum</i> (Valenciennes)	Brazil	Kritsky et al. (1986)
<i>Vancleavus platyrhynchi</i> Kritsky, Thatcher et Boeger, 1986	<i>Hemisorubim platyrhynchos</i> (Valenciennes)	Brazil	Kritsky et al. (1986)

MATERIAL AND METHODS

Sampling and morphological evaluation

Three specimens of *Sorubim lima* (field codes PI 526a, 598, 862a; PI = Peru, Iquitos,) were captured in the Nanay River in the municipality of Iquitos, Loreto Region, Peru in October 2009, 2011 and 2018. A total of 19 *Hemisorubim platyrhynchos* and 26 *S. lima* were sampled using gill nets and multifilament cast nets in the Aguapeí River (21°03'36"S, 51°45'39"W), a tributary of the Paraná River, in the municipality of Castilho, São Paulo State, Brazil, from August 2013 to November 2014, and in January 2016. The hosts from Brazil were collected under the license number 577/2015 IBAMA (Brazilian Institute of Environment and Renewable Natural Resources).

After capture, some fishes from Brazil were frozen and later examined in the laboratory, whereas others were examined *in situ*, having the gills removed from the carcasses, fixed with hot water (cca. 60°C), shaken and preserved in vials with 95% ethanol. To study the morphology of sclerotised structures of the haptor and copulatory complexes, some specimens were mounted on slides with Hoyer's medium and the coverslip was sealed with nail polish. Alive worms were mounted in a mixture of glycerine and picric acid (GAP) and after their morphological evaluation, they were remounted in Canada balsam following the procedure of Ergens (1969). Some specimens were stained with Gomori's trichrome to study their internal organs (Kritsky et al. 1986).

Parasites were studied using an optical microscope (Olympus BX51) equipped with phase contrast optics and V3 Leica Application Suite computerised system for image analysis with differential interference contrast. Illustrations were made with the aid of a drawing tube mounted on a Leica DMLS microscope. Measurements were taken according to Mizelle and Klucka (1953) and Kritsky et al. (1985); they represent straight lines between extreme points and are expressed in micrometres as the range followed by mean and number of specimens measured in parentheses. Hook pairs are numbered according to Mizelle (1936).

Type specimens and vouchers are deposited in the Helminthological Collection of the Institute of Parasitology, Biology Centre of the Czech Academy of Sciences, České Budějovice, Czech Republic (IPCAS), Helminthological Collection of the Instituto Oswaldo Cruz, Rio de Janeiro, Brazil (CHIOC), and Helminthological Collection of the Instituto de Biociências, Universidade Estadual Paulista, Botucatu, Brazil (CHIBB).

For comparative purposes, the following specimens were studied: *Demidospermus araguaiaensis* Cepeda et Luque, 2010 (paratypes – CHIOC 37327); *Demidospermus brachyplatystomae* Cepeda et Luque, 2010 (paratypes – CHIOC 37321a–b); *Demidospermus ceccarellii* Cepeda et Luque, 2010 (paratypes – CHIOC 37324a–d); *Demidospermus curvovaginatulus* Mendoza-Palmero et Scholz, 2011 (holotype and paratypes – IPCAS M-513); *Demidospermus striatus* Mendoza-Palmero et Scholz, 2011 (holotype and paratypes – IPCAS M-514); and *Demidospermus mortenhali* Mendoza-Palmero, Scholz, Mendoza-Franco et Kuchta, 2012 (holotype and paratypes – IPCAS M-522).

Molecular characterisation

Partial sequences of the 28S rRNA gene of the type species of *Nanayella* gen. n. (Dactylogyridae gen. sp. 12 of Mendoza-Palmero et al. 2015; KP056228) and another three new species

of *Nanayella* (former Dactylogyridae gen. sp. 3 from *S. lima* and Dactylogyridae gen. sp. 1 and 2 from *H. platyrhynchos* of Acosta et al. 2018; MG001327, MG001325 and MG001328, respectively) were analysed. Partial sequences of the 28S rRNA gene of three isolates of *Uroleidoides megorchis* (1,443–1,473 bp long) from *S. lima* collected in the Peruvian Amazon and two isolates of *Aphanoblastella travassosi* (Price, 1938) (type species of the genus) from *Rhamdia guatemalensis* (Günther) (Heptapteridae) collected in Lake Catemaco, Veracruz, Mexico, were newly generated in the present study.

The specimens used for molecular characterisation were cut in half with fine needles. The anterior part of the body containing the male copulatory organ (MCO) and vagina was mounted in a mixture of glycerine and picric acid (GAP) for morphological identification, then remounted in Canada balsam following the procedure of Ergens (1969) and deposited as molecular vouchers (hologenophores, see Pleijel et al. 2008 for terminology). Sequencing followed the procedure outlined by Acosta et al. (2018).

Phylogenetic analyses

A total of 43 partial sequences of the 28S rRNA gene of dactylogyrid parasites from siluriforms previously published (Mendoza-Palmero et al. 2015, Acosta et al. 2017, 2018, Franceschini et al. 2018, Yamada et al. 2018) along with three species of the Diplectanidae (used as outgroup), were retrieved from GenBank (see Fig. 5) and aligned with the longest newly generated sequences of *U. megorchis* and *A. travassosi*. Forty-seven sequences (720–1,575 bp long) were aligned using default parameters of MAFFT implemented in Geneious version 11.1.4 (Kearse et al. 2012); the extremes were trimmed leaving an alignment of 800 bp long.

Phylogenetic analyses were run under Maximum Likelihood (ML) and Bayesian Inference (BI) criteria, applying the model of nucleotide evolution GTR + I + G, selected by JModelTest 2.1.1 (University of Vigo and University of A Coruña, Spain), Darriba et al. (2012). ModelTest analyses were carried out using RAxML (Guindon and Gascuel 2003). Model parameters and bootstrap support values (1,000 repetitions) were estimated using RAxML. Bayesian Inference trees were created using MrBayes (Ronquist et al. 2012), running two independent MCMC runs of four chains for 10 million generations and sampling tree topologies every 1,000 generations. Burn-in periods were set to the first 25,000 generations. Both ML and BI analyses were performed on the computational resource CIPRES (Miller et al. 2010). Genetic divergence was calculated using uncorrected p-distances model in MEGA (Kimura 1980, Tamura et al. 2013). Phylogenetic trees were edited in the software Molecular Evolution, Phylogenetics and Epidemiology – FigTree v1.4.4, Rambaut (2009).

RESULTS

Nanayella gen. n.

Zoobank number for genus:

urn:lsid:zoobank.org:act:4B7A4CBA-7F42-44D3-9518-58B4C72A84BD

Diagnosis. Dactylogyridae, Ancyrocephalinae. Body divided into cephalic region, trunk, peduncle and haptor. Tegument thin, surface smooth. Head organs and cephalic lobes present; cephalic glands unicellular, comprising 2 bi-

lateral groups posterolateral to pharynx. Eyespots absent, subspherical granules scattered in anterior region. Mouth subterminal, midventral; pharynx muscular, glandular; oesophagus present; intestinal caeca 2, confluent posterior to testis, lacking diverticula. Genital pore midventral, near level of intestinal bifurcation. Gonads in tandem, intercaecal; testis posterior to ovary; ovary folding on itself in ventral/dorsal direction, bent dorsoventrally. Vas deferens looping left intestinal caecum, forming thick-walled seminal vesicle. Copulatory complex comprising tubular J-shaped or coiled male copulatory organ (MCO), margin with fringes and lateral flap when ornamented; coil (when present) of MCO counterclockwise. Accessory piece composed of single unit with variable folds, articulated or not to base of MCO. Genital pore midventral, at level of intestinal bifurcation. Seminal receptacle at level of anterior margin of ovary; vaginal pore sinistrolateral, vagina sclerotised with funnel-shaped distal atrium; sclerotised ornamented atrium present or absent; sclerotised spines as part of ornamented atrium present or absent. Vitelline follicles scattered throughout trunk, except in regions of reproductive organs. Haptor armed with 2 pairs of anchors (dorsal and ventral), 14 hooks with ancyrocephaline distribution (see Mizelle 1936). Ventral and dorsal bars present. Anchors robust, moderately developed superficial roots and inconspicuous deep roots, anchor points extending beyond anchor base. Ventral and dorsal bars bowed or broadly U- and V-shaped. Hooks variable in shape and size, pairs 5 and 6 modified – slender shank proximally enlarged, straight points, inconspicuous thumb; other pairs – recurved point, erect thumb. Parasites of Neotropical catfishes (Pimelodidae).

Type species: *Nanayella aculeatrium* gen. n. et sp. n.

Additional species: *Nanayella fluctuatrium* gen. n. et sp. n., *Nanayella amplofalcis* gen. n. et sp. n., *Nanayella processus-clavis* gen. n. et sp. n., *Nanayella megorchis* comb. n.

Etymology: The new genus is named according to the locality (Nanay River, a tributary of the Amazon River in Iquitos, Peru), where its type species was found; this name is appended to the diminutive (*-ella*) and should be treated as feminine.

Remarks. *Nanayella* gen. n. differs from all other dactylogyrid genera mainly by the possession of modified hook pairs 5 and 6, which have a slender shank with slightly enlarged base, inconspicuous thumb, and straight point. The diagnosis of the new genus most closely resembles that of the Neotropical genus *Demidospermus*, the species of which parasitise auchenipterids, loricariids and mostly pimelodids (23 of 30 species of the genus; see Table 1 for parasite-host interactions). Species of both genera share gonads in tandem, MCO counterclockwise, vaginal aperture sinistral, with a distal variably sclerotised vestibule (or atrium), bars U- or V-shaped, and hooks variable in shape and size. However, both genera differ from each other by different shape of hook pairs 5 and 6, and the presence of ovary folding on itself in ventral/dorsal direction, which has never been reported in any species of *Demidospermus*.

Modified hook pairs 5 and 6 with slender shank slightly enlarged at base, inconspicuous thumb, and straight point

were also reported in species originally placed in the genus *Urocleidoides* Mizelle et Price, 1964, which is still pending revision, namely *Urocleidoides amazonensis* Mizelle et Kritsky, 1969, *Urocleidoides catus* Mizelle et Kritsky, 1969, and *Urocleidoides megorchis* (see Mizelle and Kritsky 1969). These three dactylogyrid species are parasites of South American pimelodids and were considered *incertae sedis* by Kritsky et al. (1986). Based on the presence of morphological characteristics typical of the new genus and molecular evidence, *U. megorchis* is transferred to the new genus as *Nanayella megorchis* (Mizelle et Kritsky, 1969) comb. n. (see Remarks to the individual species below).

The proposal of the new genus is also supported by the results of the phylogenetic analyses of the partial sequences of the 28S rRNA gene (Fig. 5). The sequences of the four species described herein together with sequences of *U. megorchis* collected in Peru in 2018 form a monophyletic clade supported by Bayesian Inference (BI) and Maximum Likelihood (ML) within a bigger clade including species of the polyphyletic *Demidospermus* from pimelodids (*Demidospermus mortenthaleri* Mendoza-Palmero, Scholz, Mendoza-Franco et Kuchta, 2012, *Demidospermus* sp. 11 and *Demidospermus* sp. 23) and Dactylogyridae gen. spp. from pimelodids of Mendoza-Palmero et al. (2015) (see Fig. 5).

***Nanayella aculeatrium* gen. n. et sp. n. – type species**

Fig. 1

Zoobank number for species:

urn:lsid:zoobank.org:act:BD98AD43-581A-4B7F-B78D-6375BDED3E2F

Description (based on ten specimens fixed in GAP and four stained with Gomori's trichrome). Body fusiform, 293–326 (307; n = 4) long, maximum width 44–59 (49; n = 4) at mid-length. Cephalic lobes poorly developed; 4 bilateral head organs. Few subspherical granules scattered from cephalic lobes to level of male copulatory organ. Pharynx spherical, 20–21 (20; n = 3) long, 17–18 (17; n = 3) wide; oesophagus short; intestinal caeca confluent posterior to testis. Peduncle short; haptor subhexagonal, 43–49 (45; n = 4) long, 52–67 (57; n = 4) wide.

Anchors similar in shape, robust shaft, point evenly curved, extending beyond anchor base, base broad, deep root inconspicuous, superficial root moderately developed, double anchor filament present; ventral anchor 30–33 (31; n = 10) long, base 17–20 (18; n = 10) wide; dorsal anchor 25–28 (27; n = 10), base 14–17 (15; n = 10) wide. Ventral bar bowed, with posteromedial reduced process directed anteriorly, ends directed posteriorly, 30–40 (35; n = 10) long; dorsal bar broadly V-shaped, expanded ends directed posteriorly, 29–34 (32; n = 10) long.

Two types of hook pairs (Fig. 1F–I); pairs 5 and 6 similar, 21–23 (22; n = 6) long (Fig. 1F), slender shank slightly enlarged at base, straight shaft and point, inconspicuous thumb; round weakly sclerotised subunit at base present, filamentous hooklet (FH) loop about 3/4 of shank length; pairs 1–4 and 7 similar in shape, slender shank slightly enlarged at base, straight shaft and recurved point, erect thumb, FH loop about 3/4 of shank length; round weakly sclerotised subunit

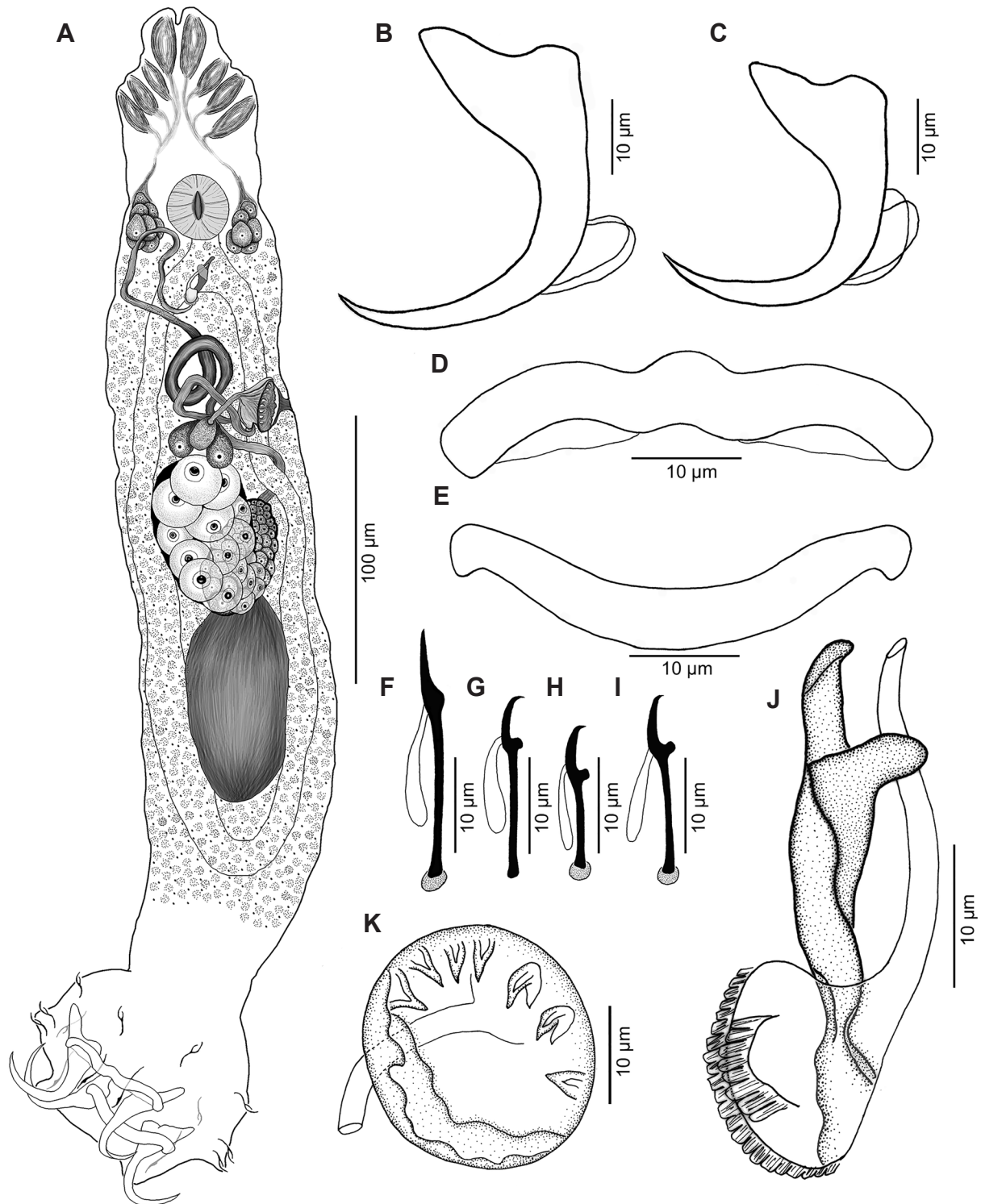


Fig. 1. *Nanayella aculeatrium* gen. n. et sp. n. from the gills of *Sorubim lima* (Bloch et Schneider), Peru. **A** – whole mount (ventral view; composition); **B** – ventral anchor; **C** – dorsal anchor; **D** – ventral bar; **E** – dorsal bar; **F** – hook pairs 5 and 6 with presence of round, weakly, sclerotised subunit at base; **G** – hook pairs 1 and 7; **H** – hook pair 2 with presence of round, weakly sclerotised subunit at base; **I** – hook pairs 3 and 4 with presence of round, weakly sclerotised subunit at base; **J** – male copulatory complex (ventral view); **K** – vagina composed of tube and sclerotised ornamented atrium.

at base present in pairs 2–4; pairs 1 and 7, 15–16 (16; n = 7) long; pair 2, 12 (n = 6) long; pairs 3 and 4, 13–14 (14; n = 6) long.

MCO 29–32 (30; n = 9) long, J-shaped tube, broad base with peripheral ornamentations (fringes) and lateral flap. Accessory piece, 20–31 (23; n = 9) long, articulated to

base of MCO, sheath-like, variable folds along its length, conspicuous flap extending laterally guiding distal part of MCO (Fig. 1J). Testis 45–66 (54; n = 4) long, 20–34 (25; n = 4) wide; vas deferens with convoluted trajectory to anterior part of body, passing level of MCO (Fig. 1A),

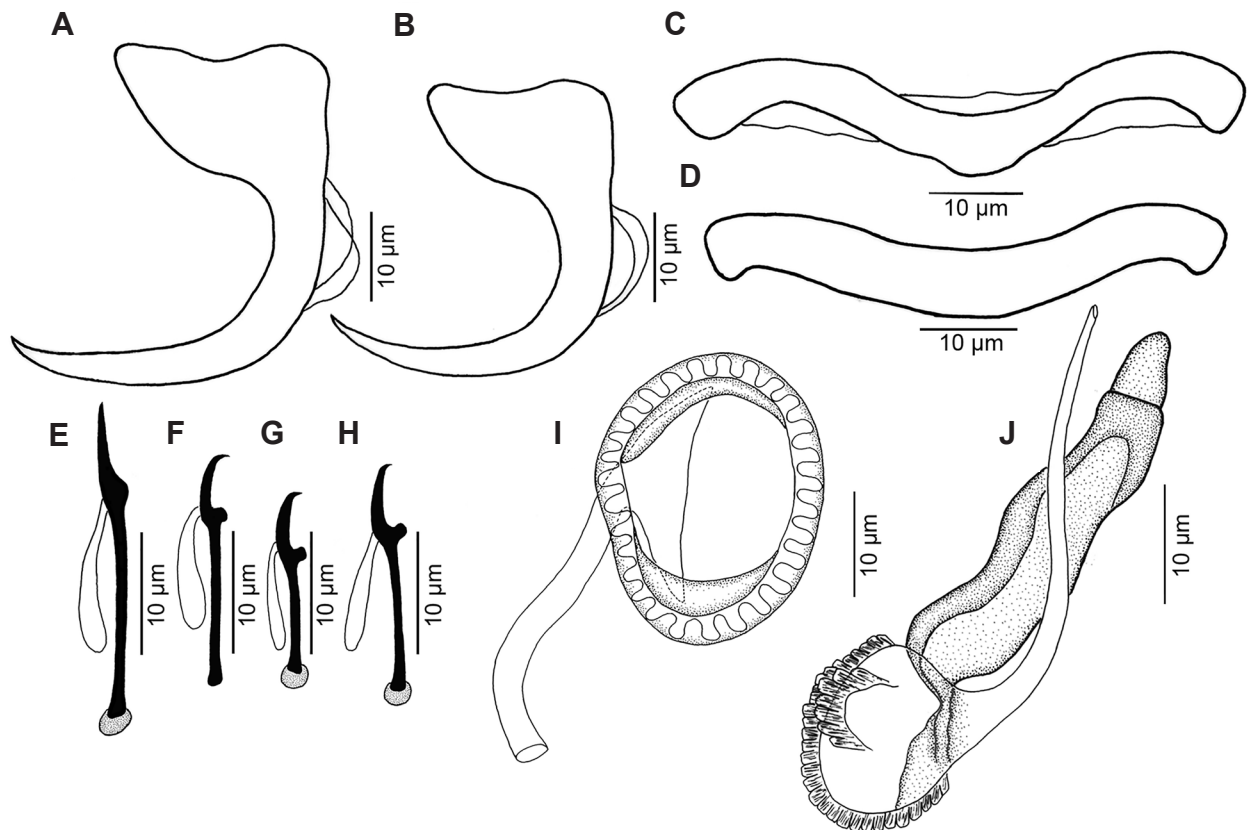


Fig. 2. Sclerotised structures of *Nanayella fluctuatrum* gen. n. et sp. n. from the gills of *Sorubim lima* (Bloch et Schneider), Brazil. **A** – ventral anchor; **B** – dorsal anchor; **C** – ventral bar; **D** – dorsal bar; **E** – hook pairs 5 and 6 with presence of round, weakly sclerotised subunit at base; **F** – hook pairs 1 and 7; **G** – hook pair 2 with presence of round, weakly sclerotised subunit at base; **H** – hook pairs 3 and 4 with presence of round, weakly sclerotised subunit at base; **I** – vagina composed of tube and sclerotised ornamented atrium; **J** – male copulatory complex (ventral view).

forming thick-walled seminal vesicle in its medial portion; prostatic reservoir not observed.

Ovary 32–38 (36; n = 4) long, 19–24 (21; n = 4) wide; oviduct, ootype, and uterus not observed. Vaginal aperture sinistrolateral, vagina sclerotised, funnel-shaped atrium armed with seven sclerotised robust spines distributed in one half, heavy sclerotised margin in other half (Fig. 1K), connected to short and delicate tube emptying seminal receptacle (Fig. 1A). Vitelline follicles scattered throughout trunk, except in regions of reproductive organs.

Type host: *Sorubim lima* (Bloch et Schneider) (host codes: PI 526a, 598, 862a).

Type locality: Iquitos – fish market in Belén, Peru (03°46'23"S, 73°18'52"W).

Site: Gills.

Type material: Holotype (specimen from fish PI 598 collected on 12 October 2009; IPCAS M-694); nine paratypes (IPCAS M-694); hologenophore (IPCAS M-694).

Representative DNA sequence: 925 bp long partial sequence of the 28S rRNA gene (GenBank accession number KP056228; designated as Dactylogyridae gen. sp. 12 by Mendoza-Palmero et al. 2015).

Etymology: The name is from Latin and is related to the presence of spines in the vaginal atrium (*aculeus* = spine + *atrium* = atrium).

Remarks. This new species is the type species of the newly erected genus and differs from species of other dactylogyrid genera by the characteristics mentioned in the diagnosis of the new genus (see above). *Nanayella aculeatrium* gen. n. et sp. n. differs from *Nanayella megorchis* comb. n. (both from *S. lima*) mainly by the shape of the MCO that is J-shaped in the first versus counterclockwise coiled (2–3 rings) in the latter. The vaginal atrium of *N. megorchis* contains many small and delicate sclerotised spines whereas that of *N. aculeatrium* has only seven sturdy spines of different shape (see Mizelle and Kritsky 1969 for description of *U. megorchis*).

Nanayella fluctuatrum gen. n. et sp. n.

Fig. 2

Zoobank number for species:

urn:lsid:zoobank.org:act:E0A58860-2F8E-4914-9C48-4B01D67822D9

Description (based on 20 specimens fixed in Hoyer's medium and nine stained with Gomori's trichrome). Body fusiform, 341–496 (418; n = 9) long, maximum width 90–131 (104; n = 9) at mid-length. Cephalic lobes poorly developed; four bilateral head organs. Subspherical accessory granules scattered in anterior region. Pharynx spherical 27–31 (29; n = 9) long, 25–34 (29; n = 9) wide; oesophagus short; intestinal caeca confluent posterior to testis. Pe-

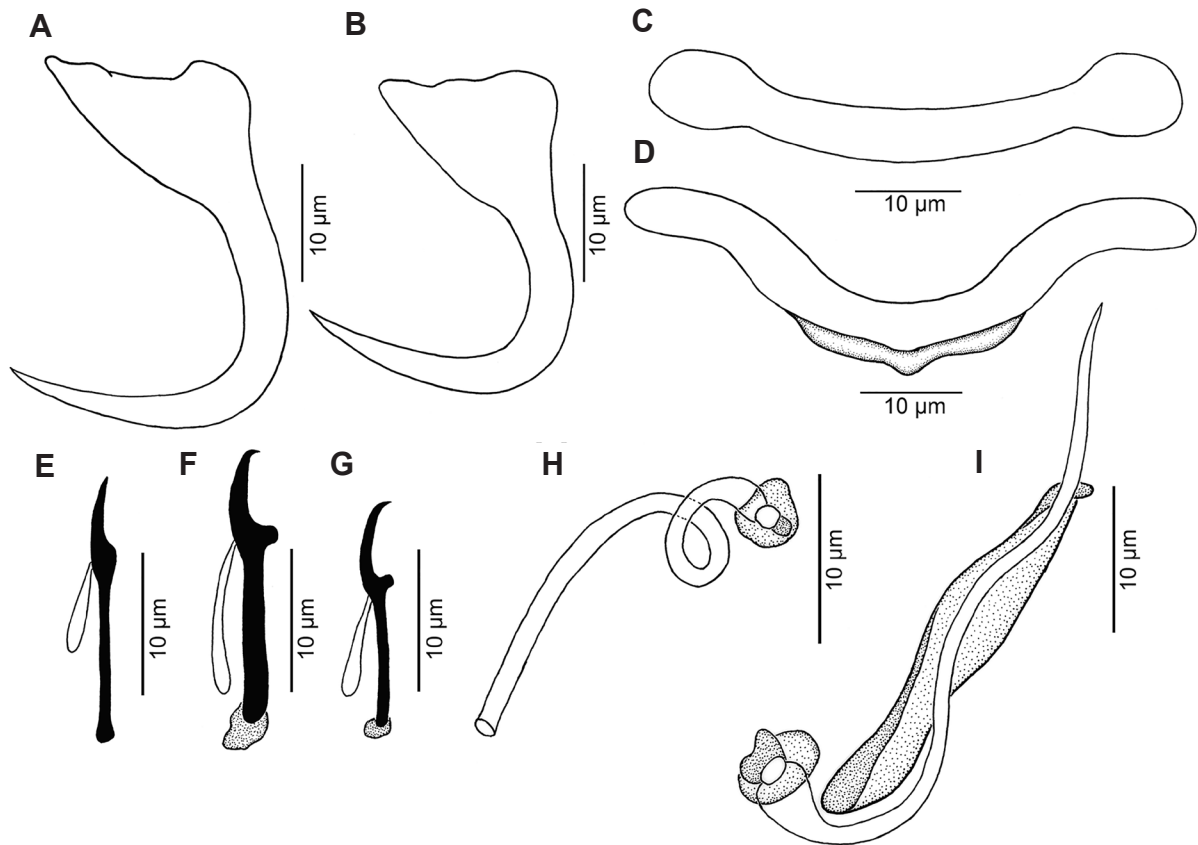


Fig. 3. Sclerotised structures of *Nanayella amplofalcis* gen. n. et sp. n. from the gills of *Hemisorubim platyrhynchos* (Valenciennes), Brazil. **A** – ventral anchor; **B** – dorsal anchor; **C** – ventral bar; **D** – dorsal bar; **E** – hook pairs 5 and 6; **F** – hook pairs 1 and 2 with presence of round, weakly sclerotised subunit at base; **G** – hook pairs 3, 4 and 7 with presence of round, weakly sclerotised subunit at base; **H** – vaginal tube; **I** – male copulatory complex (ventral view).

duncle short; haptor subhexagonal 36–48 (41; n = 6) long, 49–66 (56; n = 6) wide.

Anchors similar in shape, robust shaft, point evenly curved extending beyond anchor base, inconspicuous deep and superficial roots, double anchor filament present; ventral anchor 27–35 (31; n = 20) long, base 17–22 (20; n = 18) wide; dorsal anchor 25–31 (28; n = 20), base 13–18 (16; n = 19) wide. Ventral bar bowed, with delicate membranes in both anterior and posterior borders, ends directed posteriorly, inconspicuous medial process, 41–56 (48; n = 19) long; dorsal bar bowed, expanded ends directed posteriorly, 34–48 (43; n = 20) long.

Two types of hooks (Fig. 2E–H); pairs 5 and 6 similar, 21–23 (22; n = 6) long, slender shank slightly enlarged at base, straight shaft and point, inconspicuous thumb, round weakly sclerotised subunit at base present, FH loop about 3/4 of shank length; pairs 1–4 and 7 similar in shape, slender shank slightly enlarged at base, straight shaft and recurved point, erect thumb, FH loop about 3/4 of shank length; round weakly sclerotised subunit at base present in pairs 2–4; pairs 1 and 7, 15–16 (16; n = 7) long; pair 2, 12 (n = 6) long; pairs 3 and 4, 13–14 (14; n = 6) long.

MCO 32–46 (40; n = 18) long, sigmoid tube, tapering in distal end, broad rounded base with ornamentations (fringes), lateral flap at base. Accessory piece 26–36 (32; n = 19) long, articulated to base of MCO, straight to sigmoid, sheath-like guiding distal part of MCO (Fig. 3J). Testis

69–101 (83; n = 5) long, 41–77 (55; n = 5) wide; vas deferens sinuous, forming in its medial portion a thick-walled seminal vesicle; prostatic reservoir not observed.

Ovary 44–66 (59; n = 5) long, 27–41 (33; n = 5) wide; oviduct, ootype and uterus not observed. Vaginal aperture sinistrolateral, vagina sclerotised, funnel-shaped atrium with sclerotised undulated ornamentations along its margin (Fig. 2I), connected with short and delicate tube emptying seminal receptacle. Vitelline follicles scattered throughout trunk, except around reproductive organs.

Type host: *Sorubim lima* (Bloch et Schneider) (host codes Aguapeí – *S. lima*: 1–6 Ago/13; 1–8 Jan/14; 1–3 Jun/14; 1–6 Nov/14; 1–3 Jan/16).

Type locality: Aguapeí River (Upper Paraná River basin), municipality of Castilho, São Paulo State, Brazil (21°3'36"S, 51°45'39").

Site: Gills.

Type material: Holotype (specimen from fish No. 3 collected on 22 January 2016; IPCAS M-695); four paratypes (IPCAS M-695); six paratypes (CHIOC 40001-4, 40005a-b); five paratypes (CHIBB 378–382L); paragenophore (IPCAS M-695).

Representative DNA sequence: 1,560 bp long partial sequence of the 28S rRNA gene (MG001327; designated as *Dactylogyridae* gen. sp. 3 by Acosta et al. 2018).

Etymology: The name is from Latin and is related to the presence of sclerotised undulations in the vaginal atrium (*fluctus* = wave + *atrium* = atrium).

Remarks. *Nanayella fluctuatricum* gen. n. et sp. n. differs from *N. megorchis* and *N. aculeatricum* mainly by the shape of the vagina that does not possess sclerotised spines but rather sclerotised undulations along its margin (see Figs. 1K, 2I in the present paper and figs. 56–64 in Mizelle and Kritsky 1969). *Nanayella fluctuatricum* differs from *N. megorchis* also by the presence of a sigmoid MCO versus counterclockwise coiled (2–3 rings) in the latter species. The new species also differs from *N. aculeatricum* by having larger ventral and dorsal bars, the medial region of the ventral bar is directed posteriorly, MCO longer, and absence of a lateral flap of the accessory piece (see Figs. 1J, 2J).

Nanayella amplofalcis gen. n. et sp. n.

Fig. 3

Zoobank number for species:

urn:lsid:zoobank.org:act:45D023B3-7CF5-4F4B-A75F-FC70E5D00B9E

Description (based on 24 specimens fixed in Hoyer's medium and six stained with Gomori's trichrome). Body fusiform, 230–322 (270; n = 6) long, maximum width 38–62 (49; n = 6) at mid-length. Cephalic lobes poorly developed; four bilateral head organs. Subspherical granules scattered in cephalic region. Pharynx spherical, 14–19 (16; n = 4) long, 13–19 (15; n = 4) wide; oesophagus short; intestinal caeca confluent posterior to testis. Peduncle long; haptor subhexagonal, 39–50 (44; n = 5) long, 50–52 (51; n = 5) wide.

Anchors similar in shape and size, point evenly curved extending beyond anchor base, broad base, lateral filaments absent, poorly differentiated roots. Ventral anchor 25–28 (27; n = 24), base 12–15 (14; n = 24) wide; dorsal anchor 23–26 (24; n = 24) long, base 12–14 (13; n = 24) wide. Ventral bar 34–48 (43; n = 20) long, slightly bowed with expanded ends; dorsal bar 45–53 (49; n = 21) long, open V-shaped, rounded ends directed laterally, inconspicuous posterior medial process represented by a strongly sclerotised patch (Fig. 3D).

Hooks of 3 types (Fig. 3E–G); pairs 5 and 6 equal 16–17 (17; n = 13) long, shank slender, slightly enlarged at base, straight shaft and point, inconspicuous thumb, FH loop about 1/2 of shank length; pairs 1 and 2 equal 16–17 (17; n = 14) long, straight shaft and recurved point, erect thumb, robust wide shank, round weakly sclerotised subunit at base absent, FH loop about 3/4 of shank length; pairs 3, 4 and 7 equal 13–14 (13; n = 14) long, recurved shaft and point, erect thumb, slender and short shank, FH loop about 3/4 of shank length.

MCO 30–36 (32; n = 24) long, slightly sinuous tube, tapering distally, semicircular base ornamented with irregular flap. Accessory piece 20–25 (22; n = 19) long, not articulated with base of MCO, sheath-like, slightly sinuous shaped. Testis 27–35 (33; n = 3) long, 10–13 (12; n = 3) wide; vas deferens forming thick-walled seminal vesicle in its medial portion; prostatic reservoir not observed.

Ovary 17–19 (18; n = 3) long, 10–13 (12; n = 3) wide; oviduct, ootype and uterus not observed. Vaginal aperture sinistrolateral, vagina sclerotised leading to delicate coiled vaginal tube. Vitelline follicles dense, coextensive with intestinal caeca.

Type host: *Hemisorubim platyrhynchus* (Valenciennes) (host codes Aguapeí – *H. platyrhynchus* 1–3 Ago/13; 1–8 Jan/14; 1–8 Jun/14).

Type locality: Aguapeí River (Paraná River basin), municipality of Castilho, São Paulo State, Brazil (21°3'36"S, 51°45'39").

Site: Gills.

Type material: Holotype (specimen from host No. 3 collected on 26 January 2014; IPCAS M-696); 2 paratypes (IPCAS M-696); 6 paratypes (CHIOC 39097a-b, 39098-99; 39100a-b); 6 paratypes (CHIBB 383–388L); paragenophore (IPCAS M-696).

Representative DNA sequence: 1,550 bp long partial sequence of the 28S rRNA gene (MG001325; designated as *Dactylogyridae* gen. sp. 1 by Acosta et al. 2018).

Etymology: The name is from Latin and is related to the characteristic hook pairs 1 and 2 that possess a wide and robust shank compared to other congeners (amplo = wide + falcis = hook).

Remarks. The new species presents unique shape of hook pairs 1 and 2 with a robust, wide shank (Fig. 3F). *Nanayella amplofalcis* gen. n. et sp. n. can be distinguished from *N. megorchis*, *N. aculeatricum* and *N. fluctuatricum* mainly by the shape of the accessory piece which is not articulated to the base of the MCO whereas it is articulated in the other species of *Nanayella* from *S. lima*.

Nanayella processusclavis gen. n. et sp. n.

Fig. 4

Zoobank number for species:

urn:lsid:zoobank.org:act:43861BAD-3EF8-429B-9F97-F78C534A9819

Description (based on ten specimens fixed in Hoyer's medium and one stained with Gomori's trichrome). Body fusiform 243 long, maximum width 43 at mid-length. Cephalic lobes poorly developed; four bilateral head organs. Accessory granules scattered from cephalic lobes to level of male copulatory organ. Pharynx spherical, 17 long, 15 wide; oesophagus short; intestinal caeca confluent posterior to testis. Peduncle long; haptor subhexagonal, 33 long, 43 wide.

Anchors similar in shape, evenly curved point extending beyond anchor base, broad superficial root, poorly differentiated deep root, double lateral filament; ventral anchor 29–32 (30; n = 10) long, base 15–18 (16; n = 10) wide; dorsal anchor 23–26 (25; n = 10), base 12–14 (13; n = 10) wide. Ventral bar 39–46 (43; n = 9) long, slightly bowed with enlarged ends directed laterally; dorsal bar open V-shaped, 30–37 (33; n = 8) long, short medial process, small sclerotised patch on medial process tip (Fig. 5D).

Two types of hooks (Fig. 4E–G); pairs 5 and 6 equal 23 (22–23; n = 12) long, slender shank slightly enlarged at base, straight shaft and point, inconspicuous thumb, round weakly sclerotised subunit at base present, FH loop about 1/2 of shank length; pairs 1–4 and 7 similar in shape; slender shank, slightly enlarged at base, recurved point, erect thumb, FH loop about 3/4 of shank length, pairs 1–4, 16 (n = 9) long, pair 7, 18 (n = 10) long.

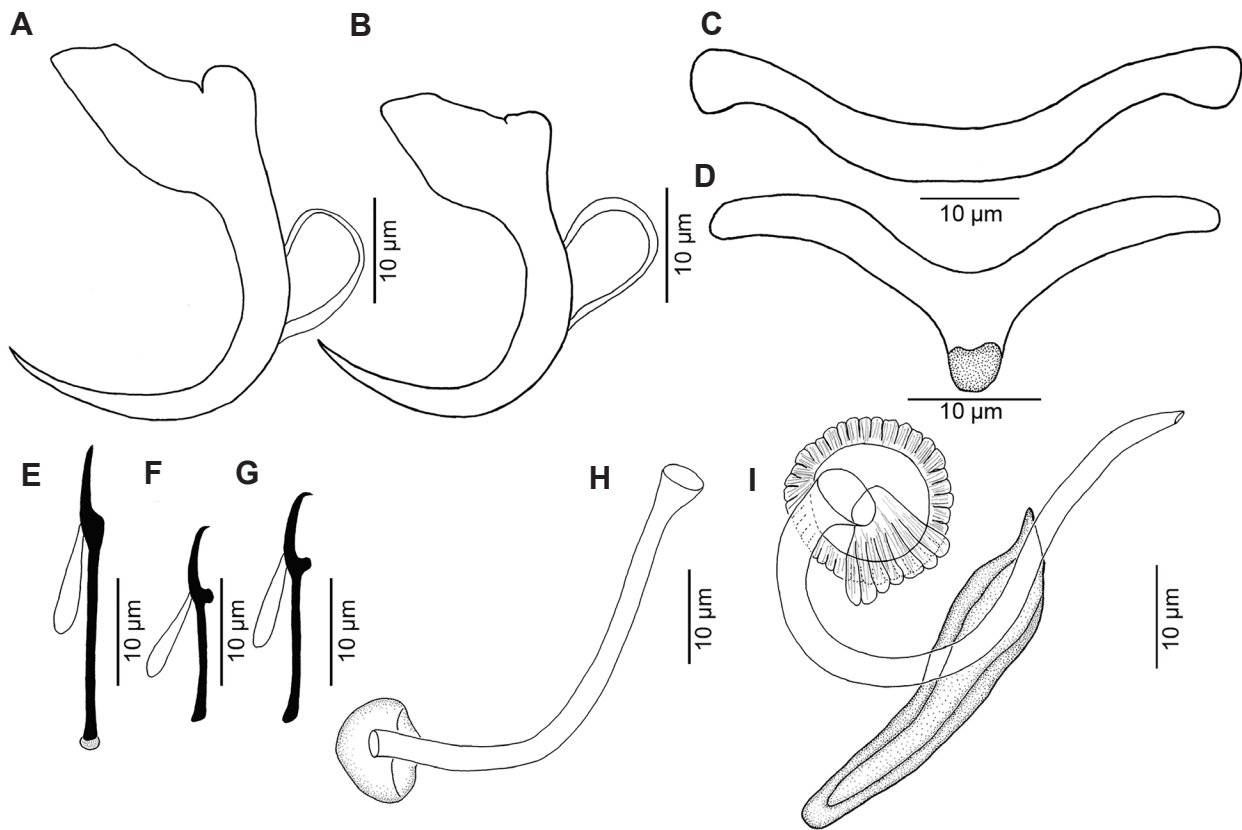


Fig. 4. Sclerotised structures of *Nanayella processusclavis* gen. n. et sp. n. from the gills of *Hemisorubim platyrhynchus* (Valenciennes), Brazil. **A** – ventral anchor; **B** – dorsal anchor; **C** – ventral bar; **D** – dorsal bar; **E** – hook pairs 5 and 6 with presence of round, weakly sclerotised subunit at base; **F** – hook pairs 1–4; **G** – hook pair 7; **H** – vagina tube with detail of sclerotised ornamentation present at inner end; **I** – male copulatory complex (ventral view).

Male copulatory organ 35–42 (40; n = 9) long, comprising J-shaped delicate tube, circular broad base with peripheral ornamentations (fringes) and trapezoidal lateral flap. Accessory piece 28–34 (30; n = 9) long, sheath-like not articulated to base of MCO, guiding distal part of MCO (Fig. 4I). Testis 64 long, 19 wide; vas deferens forming thick-walled seminal vesicle in its medial portion, prostatic reservoir not observed.

Ovary 44 long, 15 wide; oviduct, ootype and uterus not observed. Vaginal aperture sinistrolateral, sclerotised ornamentation surrounding inner end of vaginal tube (Fig. 4H). Vitelline follicles dense, scattered throughout trunk, except in regions of reproductive organs.

Type and only known host: *Hemisorubim platyrhynchus* (Valenciennes) (host codes Aguapeí – *H. platyrhynchus* 1–3 Ago/13; 1–8 Jan/14; 1–8 Jun/14).

Type locality: Aguapeí River (Paraná River basin), municipality of Castilho, São Paulo State, Brazil (21°3'36"S, 51°45'39"W).

Site: Gills.

Type material: Holotype (specimen from host No. 3 collected on 26 January 2014; IPCAS M-697); five paratypes (CHIOC 40006, 40007a-d); five paratypes (CHIBB 389–393L); paragenophore (IPCAS M-697).

Representative DNA sequence: 1,550 bp long partial sequence of the 28S rRNA gene (MG001328; designated as Dactylogyridae gen. sp. 2 by Acosta et al. 2018).

Etymology: The name is from Latin and is related to the shape of the medial process of the dorsal bar (*processus* = process + *clavis* = bar).

Remarks. The new species differs from the remaining species of the new genus mainly by the presence of a medial process on the dorsal bar (Fig. 4D), and the presence of sclerotised ornamentation surrounding the inner end of the vaginal tube (Fig. 4H). *Nanayella processusclavis* gen. n. et sp. n. does not present any articulation of the MCO with the accessory piece as in *N. amplofalci*, but can be distinguished from the latter by the shape of the MCO, which is J-shaped versus a slightly sinuous tube in *N. amplofalci*.

Nanayella megorchis (Mizelle et Kritsky, 1969) comb. n.

Synonym: *Urocleidoides megorchis* Mizelle et Kritsky, 1969

Type host: *Sorubim lima* (Bloch et Schneider).

Type locality: La Plata Drainage, Brazil.

New locality: Iquitos, Peru.

Additional material: five vouchers (IPCAS M-698), hologenophore (IPCAS M-698); all collected from *S. lima* (PI 1058).

Representative DNA sequences: 1,443–1,473 bp long partial sequences of the 28S rRNA gene of three isolates (GenBank accession numbers: MK367405–07).

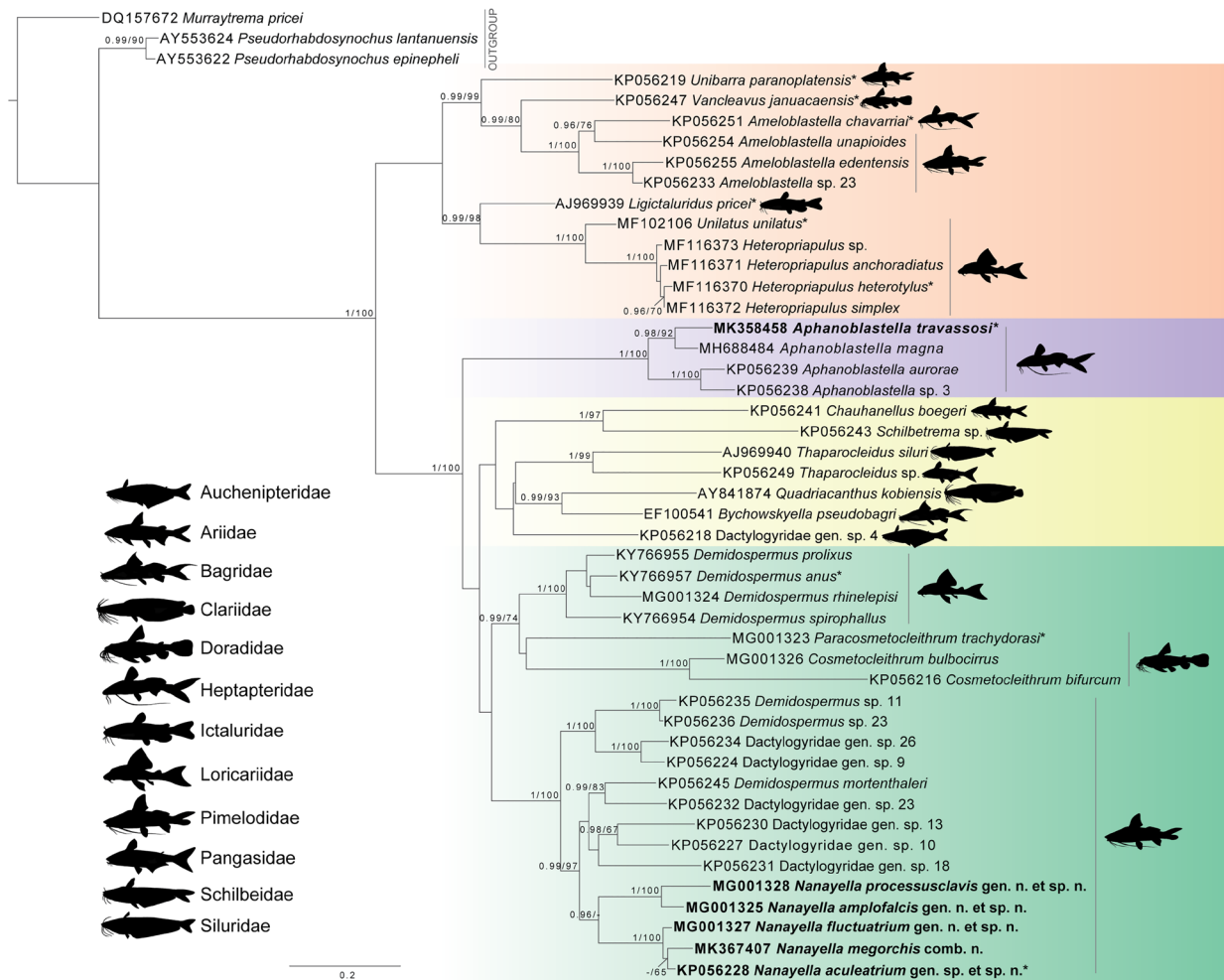


Fig. 5. Maximum likelihood phylogram based on partial sequences of the 28S rRNA gene. Species described in this study and those newly sequenced are in bold. Posterior probability followed by bootstrap support values are given above the branches (posterior probability < 0.90 and bootstrap < 60 not shown). Asterisk indicates type-species. Diplectanids were used as outgroup. Branch length scale bar indicates number of substitution per site.

Remarks. *Urocleidoides megorchis* was described from the gills of *S. lima* in Brazil by Mizelle and Kritsky (1969). Kritsky et al. (1986) considered this species as *incertae sedis* together with *U. amazonensis* and *U. catus* found in another pimelodid, redbtail catfish, *Phractocephalus hemioiopterus* (Bloch et Schneider), in the Amazon River Basin, Brazil (see Mizelle and Kritsky 1969). Kritsky et al. (2000) suggested that a new genus should be proposed to accommodate these three species. They all possess modified hook pairs 5 and 6 (slender shank, degenerate thumb, and straight point), in which they resemble species of *Nanayella*.

Based on the original description and evaluation of new material collected recently in *S. lima* from Peru, *U. megorchis* is transferred to *Nanayella* because it has modified hook pairs 5 and 6, sclerotised spines in the vaginal atrium, accessory piece composed of a single unit articulated to the base of the MCO, and morphology of ventral and dorsal bars similar to those of species of *Nanayella* from *S. lima* (see above). Newly generated molecular data support placement of this species in *Nanayella* as a new combination.

In contrast, *U. amazonensis* and *U. catus*, which somewhat resemble species of *Nanayella* in their morphology

(see Mizelle and Kritsky 1969), are provisionally retained in *Urocleidoides*. New material of these species and molecular data can provide evidence whether they also belong to *Nanayella*.

Phylogenetic analyses

ML and BI analyses yielded similar tree topology (Fig. 5). Species of *Nanayella* formed a monophyletic clade sister to the clades composed of *D. mortenthaleri* with *Dactylogyridae* gen. sp. 23, and *Dactylogyridae* gen. sp. 13 with *Dactylogyridae* gen. sp. 10, and *Dactylogyridae* gen. sp. 18. Results of ML and BI analyses suggested that interspecific relationships between *Nanayella* spp. follow a clear pattern of host-parasite associations, i.e., *N. aculeatrium*, *N. fluctuatrium*, and *N. megorchis* from *S. lima* form a clade sister to the other composed from two species of *H. platyrhynchos*, i.e. *N. amplofalci* and *N. processusclavis* (Fig. 5).

Genetic divergence in the partial sequences of the 28S rRNA gene ranged from 3 to 21% among the species of *Nanayella* (i.e. interspecific divergence), from 19 to 25% among species of *Nanayella* and those of the polyphyletic *Demidospermus* from pimelodids and from 25 to 29%

among species of *Demidospermus* from loricariids including its type species *Demidospermu anus* (Suriano, 1983), and from 17 to 25% among species of the new genus and unidentified species of Dactylogyridae (Dactylogyridae gen. sp. 9, 10, 13, 18, 23 and 26 of Mendoza-Palmero et al. 2015) from pimelodids (see Supplementary Table 1).

Aphanoblastella travassosi (type species of the genus – GenBank accession number MK358457–58) clustered with a strong support together with *Aphanoblastella magna* Yamada, Acosta, Yamada, Scholz et da Silva, 2018, *Aphanoblastella aurorae* Mendoza-Palmero, Scholz, Mendoza-Franco et Kuchta, 2012 and *Aphanoblastella* Kritsky, Mendoza-Franco et Scholz, 2000 sp. 3. Thus, the monophyly of *Aphanoblastella* (parasites specific to heptapterid catfishes) is herein supported.

DISCUSSION

Nanayella gen. n. is proposed to accommodate dactylogyrids of South American pimelodids based on the presence of a unique combination of morphological characteristics and also on molecular evidence (sequences of all four new species). Recent studies on the monogenean fauna of Neotropical siluriforms show that the current knowledge of the diversity of these fish parasites is still underestimated and many species are to be described and genera proposed (Mendoza-Palmero et al. 2012, 2015).

Even though the species of the new genus share morphological characteristics with some species of the polyphyletic *Demidospermus*, their unique combination together with a distinct position of the four new species in the phylogenetic tree of Neotropical monogeneans from catfishes (Fig. 5) support erection of *Nanayella*. It cannot be excluded that the morphologically similar species *Urocleidoides amazonensis* and *Urocleidoides catus* from South American pimelodids may also belong to the new genus. However, there are still no molecular data available on these taxa and some species of similar morphology previously assigned to the polyphyletic *Demidospermus* (see Mendoza-Palmero et al. 2015).

Demidospermus is one of the most speciose and taxonomically problematic genera of dactylogyrids from Ne-

otropical siluriforms (families Auchenipteridae, Loricariidae and Pimelodidae), with 30 species described so far (Acosta et al. 2018, Franceschini et al. 2018). Even though most species (23) have been described from pimelodids, it seems that the genus is in fact specific to loricariids and taxa from other catfish families belong to other genera, not yet formally proposed (Mendoza-Palmero et al. 2015, Acosta et al. 2018, Franceschini et al. 2018).

The present study increases the number of records of gill dactylogyrids from *Sorubim lima* and *Hemisorubim platyrhynchos*, which are relatively poorly studied fish hosts. The only species known prior to this study were *Nanayella megorchis* (previously in *Urocleidoides*) and *Ameloblastella unapioides* described from *S. lima*, and *Vancleaveus platyrhynchi* from *H. platyrhynchos*. The reassignment of *Urocleidoides megorchis* to *Nanayella* thus clarifies taxonomic position of one of numerous taxa considered *incertae sedis* (see Kritsky et al. 1986).

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