Journal of Helminthology

www.cambridge.org/jhl

Research Paper

Cite this article: Santos Neto JF and Domingues MV (2023). Integrative taxonomy of *Urocleidoides* spp. (Monogenoidea: Dactylogyridae) parasites of characiform and gymnotiform fishes from the coastal drainages of the Eastern Amazon, Brazil. *Journal of Helminthology*, **97**, e64, 1–19
https://doi.org/10.1017/S0022149X2300041X

Received: 13 April 2023
Revised: 22 June 2023
Accepted: 22 June 2023

Keywords:
parasites; Erythrinidae; Hypopomidae; COI mtDNA; 28S rDNA

Corresponding author:
M.V. Domingues;
Email: mvdomingues@ufpa.br

Integrative taxonomy of *Urocleidoides* spp. (Monogenoidea: Dactylogyridae) parasites of characiform and gymnotiform fishes from the coastal drainages of the Eastern Amazon, Brazil

J.F. Santos Neto[1,2] and M.V. Domingues[1,2]

[1]Laboratório de Sistemática e Coevolução, Universidade Federal do Pará, Campus Universitário de Bragança, Instituto de Estudos Costeiros, Travessa Leandro Ribeiro, s/n, Aldeia, 68600–000, Bragança, Pará, Brazil and [2]Programa de Pós-Graduação em Biologia Ambiental, Universidade Federal do Pará.

Abstract

Eight species (four new) of *Urocleidoides* are reported from Characiformes and Gymnotiformes fishes of the coastal drainages of the Eastern Amazon. *Urocleidoides vanini* n. sp. is characterized by having a male copulatory organ (MCO) with three and a half counterclockwise rings, absence of vaginal sclerite, and a V-shaped ventral bar. *Urocleidoides atilaiamarinoi* n. sp. has MCO with two and a half counterclockwise rings, dumbbell-shaped accessory piece, similar anchors, open V-shaped ventral bar, and open U-shaped dorsal bar. *Urocleidoides macrosoma* n. sp. exhibits an elongate and robust body, MCO comprising one counterclockwise ring, similar anchors with wavy point, and dumbbell-shaped ventral and dorsal bars. *Urocleidoides nataliapasternakae* n. sp. has MCO comprising two and a half counterclockwise rings, vaginal canal convoluted, point of the dorsal anchor with ornamentation as sclerotized shredded filaments, elongate dumbbell-shaped ventral bar, and U-shaped dorsal bar. *Urocleidoides naris* and *Urocleidoides brasiliensis* from *H. malabaricus* (Characiformes) and the *incertae sedis* species, *Urocleidoides gymnotus* and *Urocleidoides carapus,* from *Sternopygus macrurus* (Gymnotiformes) are reported, and their molecular sequences are presented in this study. Phylogenetic analyses based on molecular data (28S rDNA and COI mtDNA) reveal that species of *Urocleidoides* lacking vaginal sclerite are closely related to species that possess vaginal sclerite, suggesting that the absence of vaginal sclerite in *Urocleidoides* may be the result of a secondary loss. The relationships between species of *Urocleidoides* and other Neotropical dactylogyrids are also addressed.

Introduction

Among the Neotropical dactylogyrids, members of *Urocleidoides* Mizelle & Price, 1964 stand out for their wide distribution in host groups, with species parasitizing the gills and nasal cavities of fishes of the orders Characiformes, Gymnotiformes, Cyprinodontiformes, and Siluriformes (Oliveira *et al.* 2020; Zago *et al.* 2020; Freitas *et al.* 2021; Oliveira *et al.* 2021). The genus *Urocleidoides* was proposed by Mizelle & Price (1964) to accommodate *U. reticulatus* Mizelle & Price, 1964, collected from the gills of *Poecilia reticulata* Peters (Cyprinodontiformes, Poeciliidae) of the Capital Aquarium, Sacramento, California, USA. The genus was characterized by the presence of a sinistral vagina and copulatory complex comprising an accessory piece and a non-articulated male copulatory organ (MCO). Subsequently, Mizelle *et al.* (1968) and Mizelle & Kritsky (1969) reviewed the diagnosis of *Urocleidoides* and proposed new species from hosts of the orders Atheriniformes, Characiformes, Cypriniformes, Perciformes, and Siluriformes. However, Kritsky & Thatcher (1983) viewed the diversity of morphological structures of internal organ systems and absence of shared characteristics among previously known species of *Urocleidoides* as strongly suggesting the non-monophyly of the genus. Kritsky *et al.* (1986) amended the diagnosis of the genus to only include monogenoids with the following main characteristics: presence of hook-shaped vaginal sclerite, coiled MCO with counterclockwise rings, and hook pairs 1 and 5 usually reduced.

Prior to the present study, from the species of *Urocleidoides* previously considered *incertae sedis* by Kritsky *et al.* (1986), 14 have been synonymized or relocated into other genera as follows: *Palombitrema* Price & Bussing, 1968 (1 species); *Demidospermus* Suriano, 1983 (1 species); *Philocorydoras* Suriano, 1986 (2 species); *Sciadicleithrum* Kritsky, Thatcher & Boeger, 1989 (1 species); *Ameloblastella* Kritsky, Mendoza-Franco & Scholz, 2000 (2 species), *Aphanoblastella* Kritsky, Mendoza-Franco & Scholz, 2000 (2 species), *Diaphorocleidus* Jogunoori, Kritsky & Venkatanarasaiah, 2004 (3 species), *Characithecium* Mendoza-Franco, Reina & Torchin, 2009 (1 species); *Nanayella* Acosta *et al.*, 2019 (1 species) (Price & Bussing 1968; Kritsky *et al.* 1989;

Kritsky *et al.* 2000; Mendoza-Franco *et al.* 2003; Jogunoori *et al.* 2004; Mendoza-Franco *et al.* 2009; Mendoza-Palmero & Scholz 2011; Yamada *et al.* 2015; Acosta *et al.* 2019). However, even though the correct taxonomic status of several species has been established, nine are still considered *incertae sedis* – namely, *Urocleidoides stictus* Mizelle, Kritsky & Crane, 1968, *Urocleidoides strombicirrus* (Price & Bussing, 1967) Kritsky & Thatcher, 1974, and *Urocleidoides trinidadensis* Molnar, Hanek & Fernando, 1974 reported from the gills of Characiformes; *Urocleidoides gymnotus*, *Urocleidoides carapus*, *Urocleidoides virescens* Mizelle, Kritsky & Crane, 1968, and *Urocleidoides advenai* found in the gills of Gymnotiformes; and *Urocleidoides amazonensis* Mizelle & Kritsky, 1969 and *Urocleidoides catus* Mizelle & Kritsky, 1969 from the gills of Siluriformes.

The integration of morphological and molecular data has been used to improve the understanding of the taxonomic status of species of *Urocleidoides*, as well as to delimit the diagnosis of the genus. Gasques *et al.* (2016) investigated the COI sequences of *U. malabaricusi* Rosim, Mendoza-Franco & Luque, 2011 and *U. cuiabai* Rosim, Mendoza-Franco & Luque, 2011 and detected that the mean divergence rate among the specimens of *U. malabaricusi* indicates the existence of the cryptic species. Acosta *et al.* (2019) used combined morphological and molecular data from the partial 28S rDNA gene and relocated *Urocleidoides megorchis* Mizelle & Kritsky, 1969 reported in *Surubim lima* (Bloch & Schneider) (Siluriformes) to the genus *Nanayella* as *Nanayella megorchis* (Mizelle & Kritsky, 1969) Acosta *et al.*, 2019. Furthermore, Zago *et al.* (2020) proposed a study based on morphological and molecular data (*i.e.*, 28S rDNA and Cytochrome Oxidase I – COI) for species of *Urocleidoides* described from characiform and gymnotiform fishes. In their study, the COI mtDNA gene revealed a close relationship between *U. strombicirrus* (*incertae sedis*) and the other species of *Urocleidoides* (*sensu stricto*). These authors suggested that future investigation should focus on molecular characterization of *stricto sensu* and *incertae sedis* species to test the monophyly of *Urocleidoides.* The study of Oliveira et al. (2021), also based on 28S rDNA analysis, supported the close relationship among some species of *Urocleidoides* and *Cacatuocotyle papilionis* Zago *et al.*, 2018, suggesting that *Urocleidoides* may represent a non-monophyletic group.

The present study describes four new species of *Urocleidoides* reported from Erythrinidae (Characiformes) and Hypopomidae (Gymnotiformes) fishes from different hydrographic basins of the Northeastern Pará mesoregion (Eastern Amazon) based on morphological and molecular data (28S rDNA and COI mtDNA). In addition, it seeks to understand the phylogenetic relationships between some *incertae sedis* species (*i.e.*, *U. carapus* and *U. gymnotus*) with species of *Urocleidoides* (*sensu stricto*) and other Neotropical dactylogyrids.

Material and methods

Host collection

Hosts were collected with the use of trammel net and landing nets in four locations in the Northeastern Pará mesoregion: Igarapé Maratininga – Moju River, municipality of Tailândia (2°27'55.7"S, 48°53'27.6"W); Balneário Aracu – Guamá River, municipality of Ourém (1°34'1.02"S, 47°9'52.35"W); Vila Perseverança – Palheta River, municipality of São Domingos do Capim (1°51'41.8"S, 47°38'26.5"W); and Vila Segredo – Segredo River, municipality of Capanema (1°5'32.44"S, 47°5'37.02"W).

Parasitological procedures

The gill arches were removed and placed in labeled vials containing heated water (~65°C). Each vial was shaken vigorously, and the sediment and gills were then fixed in 5% formalin for morphological studies or 96% ethanol for molecular characterization. In the laboratory, the content of each vial was examined with a stereoscopic microscope (LEICA S6D, Leica Microsystems, Wetzlar, Germany); the helminths found were removed from the gills or sediments using dissection needles and sent for morphological/molecular analysis. Monogenoid specimens intended for studies of internal structures were stained with Gomori's Trichrome (Humason 1979; Boeger & Vianna 2006) and mounted in Dammar gum. For the study of sclerotized structures, the remaining specimens were mounted in Hoyer's or Grey & Wess medium (Humason 1979; Boeger & Vianna 2006). The measurements were obtained according to the procedures of Mizelle & Klucka (1953) and are presented in micrometers. The internal organs and other structures were measured in the dorsoventral view with an ocular micrometer. The length of curved or bent structures (*i.e.*, anchors, bars, accessory piece) reflects the straight-line distances between ends. The total length of the MCO was obtained using ImageJ 1.43m (Rasband 2016). Hooks were classified according to Mizelle and Price (1963). The averages of the measurements were calculated from the minimum and maximum length and the number of structures measured (n). Illustrations of the species and their structures were prepared using a drawing tube on a microscope with differential interference contrast and phase-contrast optics (LEICA DM 2500, Leica Microsystems, Wetzlar, Germany). Definitions of prevalence and mean intensity were calculated according to Bush *et al.* (1997). Type specimens, vouchers, and hologenophores presented in this study were deposited in the Helminthological Collection of the Instituto Oswaldo Cruz (CHIOC, Portuguese acronym), Rio de Janeiro, Rio de Janeiro State, Brazil. Acting in accordance with the regulations in article 8.5 of the amended 2012 version of the International Code of Zoological Nomenclature, details of the new taxa have been submitted to ZooBank.

DNA extraction, amplification, and sequencing

Each parasite specimen submitted to molecular analysis was divided with small dissection needles using a stereoscopic microscope for morphological identification. When the species was identified using haptoral structures, the anterior region of the body was placed in a 1.5 ml microtube with 96% ethanol for DNA extraction. However, when the morphology of the MCO was used for identification, the posterior region of the body was used for DNA extraction. The anterior or posterior regions of the parasite body were mounted in Hoyer medium between the slide and cover slip to identify the species. Genomic DNA was extracted with the DNeasy® Blood and Tissue kit (QIAGEN, Hilden, Germany), according to the manufacturer's protocol, with a final volume of 30 µl. DNA concentration was verified using a NanoDrop 2000 spectrophotometer (Thermo Fisher Scientific, Massachusetts, USA).

The partial region of the 28S rDNA gene was amplified by PCR in two steps. In the first step, DNA was amplified with primer pairs 1200F (Littlewood & Olson 2001) and D2 (Wu *et al.* 2006). In the second step, nested PCR was performed using C1 (Wu *et al.* 2006) and D2 primers, amplifying a fragment of ~800 bp. The amplification program was configured for an initial denaturation step of 94°C for 5 minutes, followed by 35 cycles of 94°C for 45 seconds, 50°C for 30 seconds, 72°C for 90 seconds, and a final extension of 72°C for 7 minutes. Nested PCR was conducted with 1 μl of the PCR product, diluted 1:1 in ultrapure water, with the same amplification program described above. Sequencing was performed using C1 and D2 primers. The partial sequence of gene COI mtDNA was amplified using the primers COI_Mono_5 and COI_Mono_3 and/or COI_Mono_int3 (Plaisance *et al.* 2008). The amplification program was configured for an initial denaturation step of 94°C for 3 minutes, followed by 40 amplification cycles at 94°C for 30 seconds, 44°C for 30 seconds, 72°C for 4 minutes, and a final extension of 72°C for 7 minutes (Plaisance *et al.* 2008). COI_Mono_int3 was used for sequencing.

PCRs were performed in a Matercycler® Nexus (Eppendorf, Hamburg, Germany) with a final volume of 25 μl using DreamTaq Green PCR Master Mix (2×) (Thermo Scientific Wilmington, USA), following the manufacturer's recommendations. The reactions were performed with 0.5 mM of each primer and 3 μl of extracted DNA. PCR products were run on 2% agarose gel stained with GelRed (Biotium Inc., Hayward, California, USA), and DNA quality was assessed in an ultraviolet transilluminator. The amplified products were purified with QIAquick PCR Purification Kit (QIAGEN, Hilden, Germany). Sequencing was performed with Big Dye® Terminator Cycle Sequencing Kit v.3.1 (Applied Biosystems, California, USA) in an ABI 3500 XL automatic sequencer (Applied Biosystems, California, USA) at the Instituto de Estudos Costeiros (IECOS), Universidade Federal do Pará (UFPA), Pará, Brazil.

Phylogenetic analyses

Sequences of the partial 28S rDNA gene were obtained from eight species of *Urocleidoides*, along with six sequences from the partial COI mtDNA gene. The sequences obtained were submitted to BLAST analysis (http://blast.ncbi.nlm.nih.gov) to verify similarities with other monogenoid sequences. The partial 28S rDNA sequences obtained in the present study were aligned with 30 species of Dactylogyridae, and three species of Diplectanidae were used as an outgroup (*Murraytrema pricei* Bychowsky & Nagibina, 1977, *Pseudorhabdosynochus lantauensis* (Beverley-Burton & Suriano, 1981) Kritsky & Beverley-Burton, 1986, and *Pseudorhabdosynochus epinepheli* (Yamaguti, 1938) Kritsky & Beverley-Burton, 1986) retrieved from GenBank (Table 1). The sequences obtained for the partial COI mtDNA gene were aligned with 21 sequences from *Urocleidoides*, with one sequence from Acanthocotylidae (*Acanthocotyle gurgesiella* Ñacari, Sepulveda, Escribano & Oliva, 2017) used as an outgroup (Table 1).

The sequences were aligned with the Clustal W algorithm (Thompson *et al.* 1994) implemented in Geneious version 7.1.3 (Kearse *et al.*, 2012). Genetic divergence was determined using the p-distance model matrix in MEGA X (Kumar *et al.* 2018). The JModelTest 2.1.1 software (Posada 2008) was used to select the most appropriate evolutionary model for the Maximum Likelihood (ML) and Bayesian Inference (BI) analyses based on the Akaike information criterion (AIC). The evolutionary model selected was GTR + I + G for the partial 28S rDNA and TPM3uf + I + G for the partial COI mtDNA. The search for the ML tree was performed with bootstrap confidence determined by performing 1,000 replicates using PhyML 3.0 implemented via the web server on the ATGC - Montpellier Bioinformatics Platform (http://www.atgc montpellier.fr/phyml/) (Guindon *et al.* 2010). BI analysis was performed using MrBayes v.3.2 (Ronquist & Huelsenbeck 2003). The TPM3uf + I + G evolutionary model indicated by JModelTest is not implemented in MrBayes, so it was replaced with the closest over-parameterized model available (GTR + I + G). BI analysis was implemented with posterior probability estimated from 1 million generations with two independent runs of four Markov Chain Monte Carlo (MCMC) with algorithms sufficient to keep the average standard deviation below 0.001. Trees were sampled every 1,000th generation, with diagnostics every 1,000th generation and a burn-in period covering the first 25,000 generations. Tracer v. 1.6 (Rambaut *et al.* 2014) was used to verify convergence and confirm the effective sample size (ESS) to provide reasonable estimates of the variance in model parameters (*i.e.*, ESS values > 200). Only nodes with a posterior probability above 90% and bootstrap above 60% were considered. Phylogenetic trees were generated in FigTree v.1.4.3 (Rambaut 2012) and edited using CorelDraw 2019©.

Results

Our present study provides information on the evolutionary relationships between species of *Urocleidoides* using phylogenetic analyses based on molecular data (28S rDNA and COI mtDNA). In addition, four new species are reported and described from Characiformes (Erytrinidae) and Gymnotiformes (Hypopomidae) hosts from the Eastern Amazon, expanding the genus to 52 valid species (Table 2).

Molecular data and phylogenetic inferences

Partial sequences of the 28S rDNA gene were obtained for four new species of *Urocleidoides* (*U. atilaiamarinoi* n. sp. – 767 bp long, *U. vanini* n. sp. – 773 bp long, *U. macrosoma* n. sp. – 731 bp long, and *U. nataliapasternakae* n. sp. 766 bp long), as well as for four previously described species (*U. carapus* [hologenophore, CHIOC No. 40202] – 750 bp long, *U. gymnotus* [hologenophore, CHIOC No. 40203] – 741 bp long, *Urocleidoides naris* Rosim, Mendoza-Franco & Luque, 2011 [hologenophore, CHIOC No. 40205] – 762 bp long, and *Urocleidoides brasiliensis* Rosim, Mendoza-Franco & Luque, 2011 [hologenophore, CHIOC No. 40201] – 731 bp long).

After trimming the ends, the aligned 28S rDNA sequences had a length of 660 bp. ML and BI analyses based on the partial 28S rDNA gene recovered similar tree topologies but differed in the posterior probability (P) and bootstrap (B) values. The phylogenetic analyses revealed a tree with two major clades, Clades A and B (Figure 1). Clade A is well-supported and divided into two subclades (Clades A1 and A2), which group species of monogenoid parasites of Siluriformes. Clade A1 groups the species that have been reported as parasitizing pimelodids and doradids, whereas its sister group, Clade A2, comprises monogenoids from loricariids and heptapterids.

Clade B is divided into two subclades (Clades B1 and B2) (Figure 1). Clade B1 comprises *Urocleidoides* spp. (Characiformes and Gymnotiformes), *Cacatuocotyle papilionis* (Characiformes: Characidae), *Heteropriapulus* spp., *Trinigyrus anthus* Franceschini, Acosta *et al.*, 2020, *Unilatus unilatus* Mizelle & Kritsky, 1967 (Siluriformes: Loricariidae), and *Mymarothecium viatorum* Boeger, Piasecki, Sobecka, 2002 (Characiformes: Serrasalmidae). The clade formed by the species of *Urocleidoides* showed significant support for both analyses (BI, P = 1 and ML, B = 82). One group consists of the species that parasitize anostomids (*U. paradoxus* Kritsky, Thatcher & Boeger, 1986, *U. sinus* Zago *et al.*, 2020 and

https://doi.org/10.1017/S0022149X2300041X Published online by Cambridge University Press

Table 1. List of monogenoids included in the phylogenetic analyses with details of the parasite species, host species, host family, locality, and GenBank accession numbers

Parasite species	Host species	Host Family	Locality	Genbank ID 28S rDNA	Genbank ID COI mtDNA	Reference
Dactylogyridae						
Ameloblastella chavarrai	*Rhamdia quelen*	Heptapteridae	Catemaco Lake, Mexico	KP056251	–	Mendoza-Palmero *et al*. (2015)
Ameloblastella edentensis	*Hypophthalmus edentatus*	Pimelodidae	Nanay River, Iquitos, Peru	KP056255	–	Mendoza-Palmero *et al*. (2015)
Aphanoblastella aurorae	*Goeldiella eques*	Heptapteridae	Santa Clara, Iquitos, Peru	KP056239	–	Mendoza-Palmero *et al*. (2015)
Aphanoblastella magna	*Pimelodella avanhandavae*	Heptapteridae	Upper Paraná River basin, Brazil	MH688484	–	Mendoza-Palmero *et al*. (2015)
Aphanoblastella travassosi	*Rhamdia guatemalensis*	Heptapteridae	Lake Catemaco, Mexico	MK358458	–	Acosta *et al*. (2019)
Cacatuocotyle papilionis	*Astyanax lacustris* *Astyanax fasciatus*	Characidae	Sapucaí-Mirim River, Brazil	MG832889	–	Zago *et al*. (2018)
Cosmetocleithrum bulbocirrus	*Pterodoras granulosus*	Doradidae	Upper Paraná River basin, Brazil	MG001326	–	Acosta *et al*. (2018)
Cosmetocleithrum bifurcum	*Hassar orestis*	Doradidae	Aquarium Río Momón, Iquitos, Peru	KP056217	–	Mendoza-Palmero *et al*. (2015)
Demidospermus mortenthaleri	*Brachyplatystom juruense*	Pimelodidae	Santa Clara, Peru	KP056245	–	Mendoza-Palmero *et al*. (2015)
Demidospermis prolixu	*Loricaria prolixa*	Loricariidae	Upper Paraná River basin, Brazil	KY766955	–	Franceschini *et al*. (2017)
Demidospermus rhinelepisi	*Rhinelepis aspera*	Loricariidae	Upper Paraná River basin, Brazil	MG001324	–	Acosta *et al*. (2018)
Dactylogyridae gen. sp.13	*Hypophthalmus edentatus*	Pimelodidae	Nanay River, Iquitos, Peru	KP056229	–	Acosta *et al*. (2018)
Heteropriapulus anchoradiatus	*Pterygoplychthys ambrosettii*	Loricariidae	Upper Paraná River basin, Brazil	MF116371	–	Acosta *et al*. (2017)
Heteropriapulus heterotylus	*Pterygoplychthys ambrosettii*	Loricariidae	Upper Paraná River basin, Brazil	MF116370	–	Acosta *et al*. (2017)
Nanayella aculeatrium	*Sorubim lima*	Pimelodidae	Fish Market, Iquitos, Peru	KP056228	–	Acosta *et al*. (2019)
Nanayella fluctuatrium	*Sorubim lima*	Pimelodidae	Upper Paraná River basin, Brazil	MG001327	–	Acosta *et al*. (2019)
Mymarothecium viatorum	*Piriactus mesopotamicus*	Serrasalmidae	River Paraná, Brazil	MH843723	–	Moreira *et al*. (2019)
Trinigyrus anthus	*Hypostomus regain*	Loricariidae	Upper Paraná River basin, Brazil	MN947622	–	Franceschini *et al*. (2020)
Unibarra paranoplatensis	*Aguarunichthys torosus*	Pimelodidae	Santa Clara, Iquitos, Peru	KP056219	–	Mendoza-Palmero *et al*. (2015)
Unilatus unilatus	*Pterygoplychthys ambrosettii*	Loricariidae	Upper Paraná River basin, Brazil	MF102106	–	Acosta *et al*. (2017)
Urocleidoides malabaricusi	*Hoplias* aff. *malabaricus*	Erythrinidae	Upper River Paraná, Brazil	–	KT625587 KT625588 KT625589 KT625590	Gasques *et al*. (2016)
Urocleidoides strombicirrus	–	–	Panama	–	MF939748 MF939830 MF939838 MF939854 MF939876	Unpublished
Urocleidoides cultellus	–	–	Panama	–	MF939723 MF939848	Unpublished
Urocleidoides cuiabai	*Hoplias* aff. *malabaricus*	Erythrinidae	Upper River Paraná, Brazil	–	KT625591-95	Gasques *et al*. (2016)
Urocleidoides digitabulum	*Megaleporinus elongatus*	Anostomidae	Upper Paraná River basin, Brazil	MT556796	MT594400	Zago *et al*. (2020)

(*Continued*)

Table 1. (*Continued*)

Parasite species	Host species	Host Family	Locality	Genbank ID		Reference
				28S rDNA	COI mtDNA	
Urocleidoides paradoxus	*Leporinus friderici*	Anostomidae	Upper Paraná River basin, Brazil	MT556795	–	Zago *et al.* (2020)
Urocleidoides sinus	*Schizodon nasutus*	Anostomidae	Upper Paraná River basin, Brazil	MT556799	MT594474	Zago *et al.* (2020)
Urocleidoides tenuis	*Apareiodon piracicabae*	Parodontidae	Upper Paraná River basin, Brazil	MT556797 OK465455	MT594475	Zago *et al.* (2020), Oliveira *et al.* (2021)
Urocleidoides indianensis	*Parodon nasus*	Parodontidae	Upper Paraná River basin, Brazil	OK482868	–	Oliveira *et al.* (2021)
Urocleidoides parodoni	*Parodon nasus*	Parodontidae	Upper Paraná River basin, Brazil	OK482867	–	Oliveira *et al.* (2021)
Urocleidoides uncinus	*Gymnotus inaequilabiatus*	Gymnotidae	Upper Paraná River basin, Brazil	MT556798	MT594473	Zago *et al.* (2020)
Urocleidoides naris	***Hoplias malabaricus***	**Erythrinidae**	**Itabocal River, Irituia, Pará, Brazil**	**OR270163**	**OR285308**	**Present study**
Urocleidoides brasiliensis	***Hoplias malabaricus***	**Erythrinidae**	**Itabocal River, Irituia, Pará, Brazil**	**OR270165**	–	**Present study**
Urocleidoides carapus	***Gymnotus carapo***	**Gymnotidae**	**Guamá River, Ourém, Pará, Brazil**	**OR270166**	**OR270816**	**Present study**
Urocleidoides gymnotus	***Gymnotus carapo***	**Gymnotidae**	**Guamá River, Ourém, Pará, Brazil**	**OR270734**	**OR270814**	**Present study**
***Urocleidoides nataliapasternakae* n. sp.**	***Brachyhypopomus brevirostris***	**Hypopomidae**	**Guamá River, Ourém, Pará, Brazil**	**OR270733**	**OR270823**	**Present study**
***Urocleidoides vanini* n. sp.**	***Erythrinus erythrinus***	**Erythrinidae**	**São Domingos do Capim, Pará, Brazil**	**OR270736**	**OR285309**	**Present study**
***Urocleidoides macrosoma* n. sp.**	***Hoplias malabaricus***	**Erythrinidae**	**Quatipurú River, Taurí, Pará, Brazil**	**OR270735**	**OR270815**	**Present study**
***Urocleidoides atilaiamarinoi* n. sp.**	***Hoplerytrinus unitaeniatus***	**Erythrinidae**	**Guamá River, Ourém, Pará, Brazil**	**OR270164**	–	**Present study**
Vancleaveus janauacaensis	*Pterodoras granulosus*	Doradidae	Itaya River, Iquitos, Peru	KP056247	–	Mendoza-Palmero *et al.* (2015)
Boegeriella ophiocirrus (=*Walteriella ophiocirrus*)	*Platystomatichths sturio*	Pimelodidae	Iquitos, Peru	MK834515	–	Mendoza-Palmero *et al.* (2019)
Acanthocotyle						
*Acanthocotyle gurgesiella**	*Gurgesiella furvescens*	Rajidae	Waters off Valparaiso, Chile	–	KY379331	Ñacari *et al.* (2017)
Diplectanidae						
*Murraytrema pricei**	*Nibea albiflora*	Scianidae	Panyu, China	DQ157672	–	Wu *et al.* (2006)
*Pseudorhabdosynocus epinepheli**	*Epinephelus bruneus*	Serranidae	Huidong, China	AY553622	–	Wu *et al.* (2006)
*Pseudorhabdosynocu lantauensis**	*Epinephelus bruneus*	Serranidae	Huidong, China	AY553624	–	Wu *et al.* (2006)

The sequences obtained in the present study are in bold.*Outgroup used

Table 2. List of species *Urocleidoides*

Urocleidoides species	Type–host species	Order	Family	Reference
U. advenai Mendoza-Franco and Reina, 2008	*Brachyhypopomus occidentalis* (Regan 1914)	GYM	Hypopomidae	Mendoza-Franco & Reina (2008)
U. aimarai Moreira, Scholz & Luque, 2015	*Hoplias aimara* (Valenciennes)	CHA	Erythrinidae	Moreira *et al.* (2015)
U. amazonensis Mizelle and Kritsky, 1969	*Phractocephalus hemioliopterus* (Bloch & Schneider)	SIL	Pimelodidae	Mizelle and Kritsky (1969)
U. anops Kritsky & Thatcher, 1974	*Characidium caucanum* Eigenmann	CHA	Crenuchidae	Kritsky & Thatcher (1974)
U. atilaiamarinoi n. sp.	*Hoplerythrinus unitaeniatus* (Spix & Agassiz)	CHA	Erythrinidae	Present study
U. boulengerellae Freitas *et al.*, 2021	*Boulengerella cuvieri* (Spix & Agassiz)	CHA	Ctenoluciidae	Freitas *et al.* (2021)
U. bulbophallus Ferreira *et al.*, 2017	*Hoplias malabaricus* (Bloch)	CHA	Erythrinidae	Ferreira *et al.* (2017)
U. brasiliensis Rosim, Mendoza-Franco & Luque, 2011	*H. malabaricus*	CHA	Erythrinidae	Rosim *et al.* (2011)
U. carapus Mizelle, Kritsky & Crane, 1968	*Gymnotus carapo* Linnaeus	GYM	Gymnotidae	Mizelle *et al.* (1968)
Urocleidoides catus Mizelle & Kritsky, 1969	*P. hemioliopterus*	SIL	Pimelodidae	Mizelle and Kritsky (1969)
U. cuiabai Rosim, Mendoza-Franco & Luque, 2011	*H. malabaricus*	CHA	Erythrinidae	Rosim *et al.* (2011)
U. cultellus Mendoza-Franco & Reina, 2008	*Brachypopomus occidentalis* Regan	GYM	Hypopomidae	Mendoza-Franco & Reina (2008)
U. curimatae Molnar, Hanek & Fernando, 1974	*Curimata argentea* (Gill)	CHA	Curimatidae	Molnar *et al.* (1974)
U. digitabulum Zago *et al.* 2020	*Leporinus friderici* (Bloch)	CHA	Anostomidae	Zago *et al.* (2020)
U. eremitus Kritsky, Thatcher & Boeger, 1986	*H. malabaricus*	CHA	Erythrinidae	Kritsky *et al.* (1986)
U. falxus Zago *et al.* 2020	*Megaleporinus elongatus* (Valenciennes)	CHA	Anostomidae	Zago *et al.* (2020)
U. flegomai Mendoza-Franco, Aguirre-Macedo & Vidal-Martínez, 2007	*Piabucina panamensis* Gill	CHA	Lebiasinidae	Mendoza-Franco *et al.* (2007)
U. gymnotus Mizelle, Kritsky & Crane, 1968	*G. carapo*	GYM	Gymnotidae	Mizelle *et al.* (1968)
U. hypopomi Suriano, 1997	*Brachyhypopomus brevirostris* (Steindachner)	GYM	Hypopomidae	Suriano (1997)
U. indianensis Oliveira, da Silva, Vieira & Acosta, 2021	*Parodon nasus* Kner	CHA	Parodontidae	Oliveira *et al.* (2021)
U. jariensis Oliveira *et al.*, 2020	*Schizodon fasciatus* Spix & Agassiz	CHA	Anostomidae	Oliveira *et al.* (2020)
U. macrosoma n. sp.	*H. malabaricus*	CHA	Erythrinidae	Present study
U. malabaricusi Rosim, Mendoza-Franco & Luque, 2011	*H. malabaricus*	CHA	Erythrinidae	Rosim *et al.* (2011)
U. naris Rosim, Mendoza-Franco & Luque, 2011	*H. malabaricus*	CHA	Erythrinidae	Rosim *et al.* (2011)
U. nataliapasternakae n. sp.	*B. brevirostris*	GYM	Hypopomidae	Present study
U. neotropicalis Mendoza-Franco & Reina, 2008	*Saccodon dariensis* (Meek & Hildebrand)	CHA	Parodontidae	Mendoza-Franco & Reina (2008)
U. paradoxus Kritsky, Thatcher & Boeger, 1986	*Rhytiodus microlepis* Kner	CHA	Anostomidae	Kritsky *et al.* (1986)
U. paranae Ferreira *et al.*, 2017	*H. malabaricus*	CHA	Erythrinidae	Ferreira *et al.* (2017)
U. paratriangulus Freitas *et al.*, 2021	*Psectrogaster amazonica* Eigenmann & Eigenmann	CHA	Curimatidae	Freitas *et al.* (2021)
U. parodoni Oliveira *et al.*, 2021	*Parodon nasus*	CHA	Parodontidae	Oliveira *et al.* (2021)
U. piriatiu Mendoza-Franco & Reina, 2008	*Ctenolucius beani* (Fowler)	CHA	Ctenoluciidae	Mendoza-Franco & Reina (2008)
U. ramentacuminatus Oliveira *et al.*, 2020	*Laemolyta proxima* Garman	CHA	Anostomidae	Oliveira *et al.* (2020)
U. reticulatus Mizelle & Price, 1964	*Poecilia reticulata*	CYP	Poeciliidae	Mizelle & Price (1964)
U. sapucaiensis Zago *et al.*, 2020	*M. elongatus*	CHA	Anostomidae	Zago *et al.* (2020)
U. similuncus Mendoza-Franco *et al.*, 2015	*Poecilia gillii* (Kner)	CYP	Poeciliidae	Mendoza-Franco *et al.* (2007)
U. simonae Mendoza-Franco *et al.*, 2015	*Profundulus punctatus* (Günther)	CYP	Profundulidae	Mendoza-Franco *et al.* (2015)
U. sinus Zago *et al.*, 2020	*Schizodon nasutus* Kner	CHA	Anostomidae	Zago *et al.* (2020)

(*Continued*)

https://doi.org/10.1017/S0022149X2300041X Published online by Cambridge University Press

Table 2. (*Continued*)

Urocleidoides species	Type–host species	Order	Family	Reference
U. stictus Mizelle, Kritsky & Crane, 1968	*Hemigrammus stictus* (Durbin)	CHA	Characidae	Mizelle *et al.* (1968)
U. solarivaginatus Zago *et al.,* 2020	*L. friderici*	CHA	Anostomidae	Zago *et al.* (2020)
U. strombicirrus (Price & Bussing, 1967) Kritsky & Thatcher, 1974	*Astyanax aeneus* (Günther)	CHA	Characidae	Kritsky & Thatcher (1974)
U. surianoae Rossin & Timi, 2016	*Cyphocharax voga* (Hensel)	CHA	Curimatidae	Rossin & Timi (2016)
U. tenuis Zago *et al.,* 2020	*Apareiodon piracicabae* (Eigenmann)	CHA	Parodontidae	Zago *et al.* (2020)
U. tocantinenses Freitas *et al.*, 2021	*P. amazonica*	CHA	Curimatidae	Freitas *et al.* (2021)
U. triangulus Rossin & Timi, 2016	*C. voga*	CHA	Curimatidae	Rossin & Timi (2016)
U. trinidadensis Molnar, Hanek & Fernando, 1974	*Astyanax bimaculatus* (Linnaeus)	CHA	Characidae	Molnar *et al.* (1974)
U. uncinus Zago *et al.,* 2020	*Gymnotus sylvius* Albert & Fernandes-Matioli	GYM	Gymnotidae	Zago *et al.* (2020)
U. vaginoclaustrum Jogunoori, Kritsky & Venkatanarasaiah, 2004	*Xiphophorus helleri* Heckel	CYP	Poeciliidae	Jogunoori *et al.* (2004)
U. vaginoclaustroides Mendoza-Franco *et al.,* 2015	*Pseudoxiphophorus bimaculate* (Heckel)	CYP	Poeciliidae	Mendoza-Franco *et al.* (2015)
U. vanini n. sp.	*Erythrinus erythrinus*	CHA	Erythrinidae	Present study
Urocleidoides virescens Mizelle, Kritsky & Crane, 1968	*Eigenmannia virescens* (Valenciennes)	GYM	Sternopygidae	Mizelle *et al.* (1968)
U. visiofortatus Mendoza-Franco & Reina, 2008	*B. occidentalis*	GYM	Hypopomidae	Mendoza-Franco & Reina (2008)
U. xinguensis Moreira, Scholz & Luque, 2015	*H. aimara*	CHA	Erythrinidae	Moreira *et al.* (2015)

CHA=Characiformes; CYP=Cyprinodontiformes; GYM= Gymnotiformes; SIL=Siluriformes.

U. digitabulum Zago *et al.*, 2020) (BI, P = 1 and ML, B =100), parondontids (*Urocleidoides tenuis* Zago *et al.*, 2020; *U. indianensis* Oliveira *et al.*, 2021 and *U. parodoni* Oliveira *et al.*, 2021) (BI, P = 1 and ML, B = 100), and erythrinids (*U. vanini* n. sp. and *U. atilaiamarinoi* n. sp.) (BI, P = 1 and ML, B = 99). The other group is made up of species that parasitize Gymnotiformes (*U. carapus*, *U. gymnotus*, *U. uncinus* Zago *et al.*, 2020 [Gymnotidae], and *U. nataliapasternakae* n. sp. [Hypopomidae]) (BI, P = 1 and ML, B = 100) and *H. malabaricus* (Erythrinidae) (*U. brasiliensis*, *U. naris*, and *U. macrosoma* n. sp.) (BI, P = 1 and ML, B = 99). The group formed by *C. papilionis* and the reported species of *Urocleidoides* from Gymnotiformes and *H. malabaricus* shows low support for BI and ML. Clade B2 (BI, P = 1 and ML, B = 97) appears as a sister group to clade B1 and consists of species of monogenoids that parasitize pimelodids (*Unibarra paranoplatensis* Suriano & Incorvaia, 1995 and *Ameloblastella edentesis* Mendoza-Franco, Mendoza-Palmero & Scholz, 2016), heptapterids (*Ameloblastella chavarriai* (Price, 1936) Kritsky, Mendoza-Franco & Scholz, 2000), and doradids (*Vancleaveus janauacaensis* Kritsky, Thatcher & Boeger, 1986) (Figure 1).

The partial sequences of the COI mtDNA gene were obtained for three new species of *Urocleidoides* (*U. vanini* n. sp. – 695 bp long, *U. macrosoma* n. sp. – 733 bp long, and *U. nataliapasternakae* n. sp. – 764 bp long), as well as for three previously described species (*U. carapus* [hologenophore, CHIOC No. 40202] – 717 bp long, *U. gymnotus* [hologenophore, CHIOC No. 40203] – 765 bp long, and *U. naris* [hologenophore, CHIOC No. 40205] – 679 bp long). The alignment obtained had a length of 347 bp, and both ML and BI analyses recovered similar tree topologies. Clade A of the phylogenetic tree is well-supported by BI analysis (P = 0.98) and divided into the clades A1 and A2 (Figure 2). Clade A1 groups the species that occur in Characiformes (Characidae and Parodontidae) and Gymnotiformes (Hypopomidae and Gymnotidae). Subclade A1', which groups species of *Urocleidoides* found in Characiformes (Characidae) and Gymnotiformes (Hypopomidae and Gymnotidae), was poorly supported by both analyses (BI and ML). However, the subclade within A1' comprised of the species that parasitize Gymnotiformes (Hypopomidae and Gymnotidae) is well-supported by BI analysis (P = 0.95), and groups *Urocleidoides* species that are both *incertae sedis* (*U. gymnotus*, *U. carapus*) and *sensu stricto* (*U. cultellus*, *U. uncinus*, and *U. nataliapasternakae* n. sp.). *Urocleidoides tenuis*, which parasitizes parodontids, appears as a sister species to species parasitizing Characiformes (Characidae) and Gymnotiformes (Hypopomidae and Gymnotidae). Clade A2, however, groups the species that occur in anostomids and erythrinids. In this clade, *Urocleidoides digitabulum* appears as a sister group of *U. sinus* and of the species that parasitize erythrinids. However, this group has low support and does not indicate such a relationship between these species. Likewise, the relationship between *U. sinus* and the species that occur in erythrinids is also not supported due to the low P and B values for both analyses. In contrast, the clade comprising the species that parasitize erythrinids is well-supported by the BI analysis (P = 0.98), but the support values between species are low.

Genetic divergence of 28S rDNA was estimated only for monogenoid species belonging to Clade B1 (Table 3). The genetic divergence between *Urocleidoides* spp. and the other dactylogyrid species in Clade B1 ranges between 18.4 and 25.8% (203–349 bp) (Table 3). *Urocleidoides* spp. and *Cacatuocotyle papilionis* diverge at rates between 20.5 and 25% (208–322 bp); *Urocleidoides* spp. and *Heteropriapulus* spp. between 21.1 and 24.8% (205–328 bp); *Urocleidoides* spp. and *Unilatus unilatus* between 18.4 and 23% (203–315 bp); *Urocleidoides* spp. and *Trinigyrus anthus* between 20.3 and

https://doi.org/10.1017/S0022149X2300041X Published online by Cambridge University Press

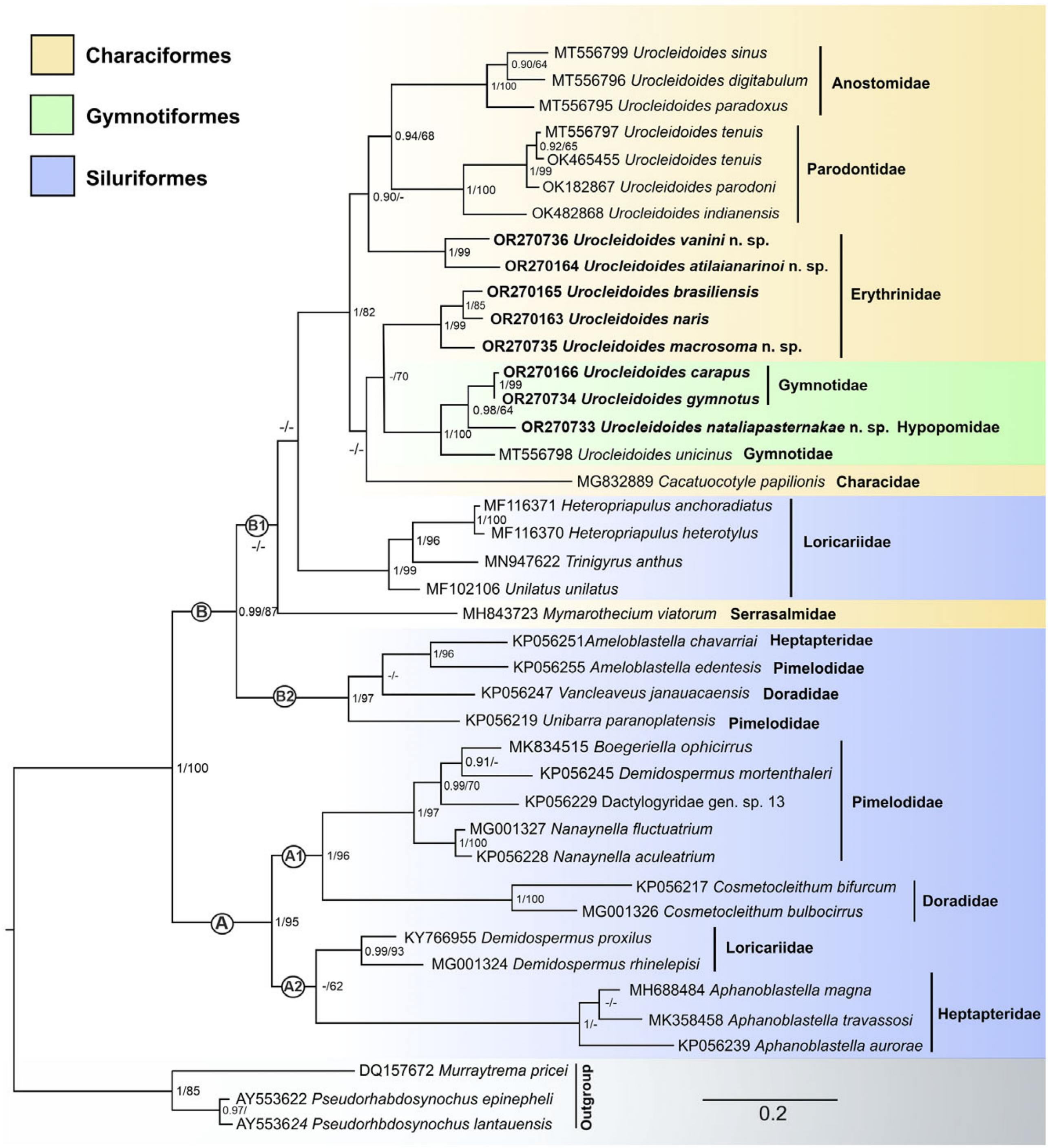

Figure 1. Molecular phylogeny of Dactylogyridae estimated by Bayesian and Maximum Likelihood analyses inferred using the partial 28S rDNA gene (alignment length of 660 bp). The new species sequenced in the present study are presented in bold. The sequences of the other species were retrieved from GenBank. The bootstrap (ML) and posterior probability (BI) supports are presented between branches (values of posterior probability < 0.90 and bootstrap < 60 are not shown). The length of the scale bar indicates the substitution numbers per site.

25.2% (211–349 bp), and *Urocleidoides* spp. and *Mymarothecium viatorum* between 21.3 and 25.8% (212–244 bp).

Among the species of *Urocleidoides* parasitizing Gymnotiformes (*U. caparus*, *U. gymnotus*, *U. uncinus*, and *U. nataliapasternakae* n. sp.), the genetic divergence ranges from 2 to 12.7% (32–154 bp). Among the species that parasitize anostomids (*U. paradoxus*, *U. sinus*, and *U. digitabulum*), the divergence varies between 7.8 and 11.3% (142–157 bp). For the species that parasitize *H. malabaricus* (Characiformes: Erythrinidae) (*U. naris*, *U. brasiliensis*, and *U. macrosoma* n. sp.), divergence ranges from 3.9 to 9% (43–87 bp). *Urocleidoides atilaiamarinoi* n. sp. reported for *H. unitaeniatus* (Agassiz) (Characiformes: Erithrinidae) diverges from the other species that parasitize *H. malabaricus* by between 19 and 21% (207–214 bp). *Urocleidoides vanini* n. sp. from *Erythrinus*

https://doi.org/10.1017/S0022149X2300041X Published online by Cambridge University Press

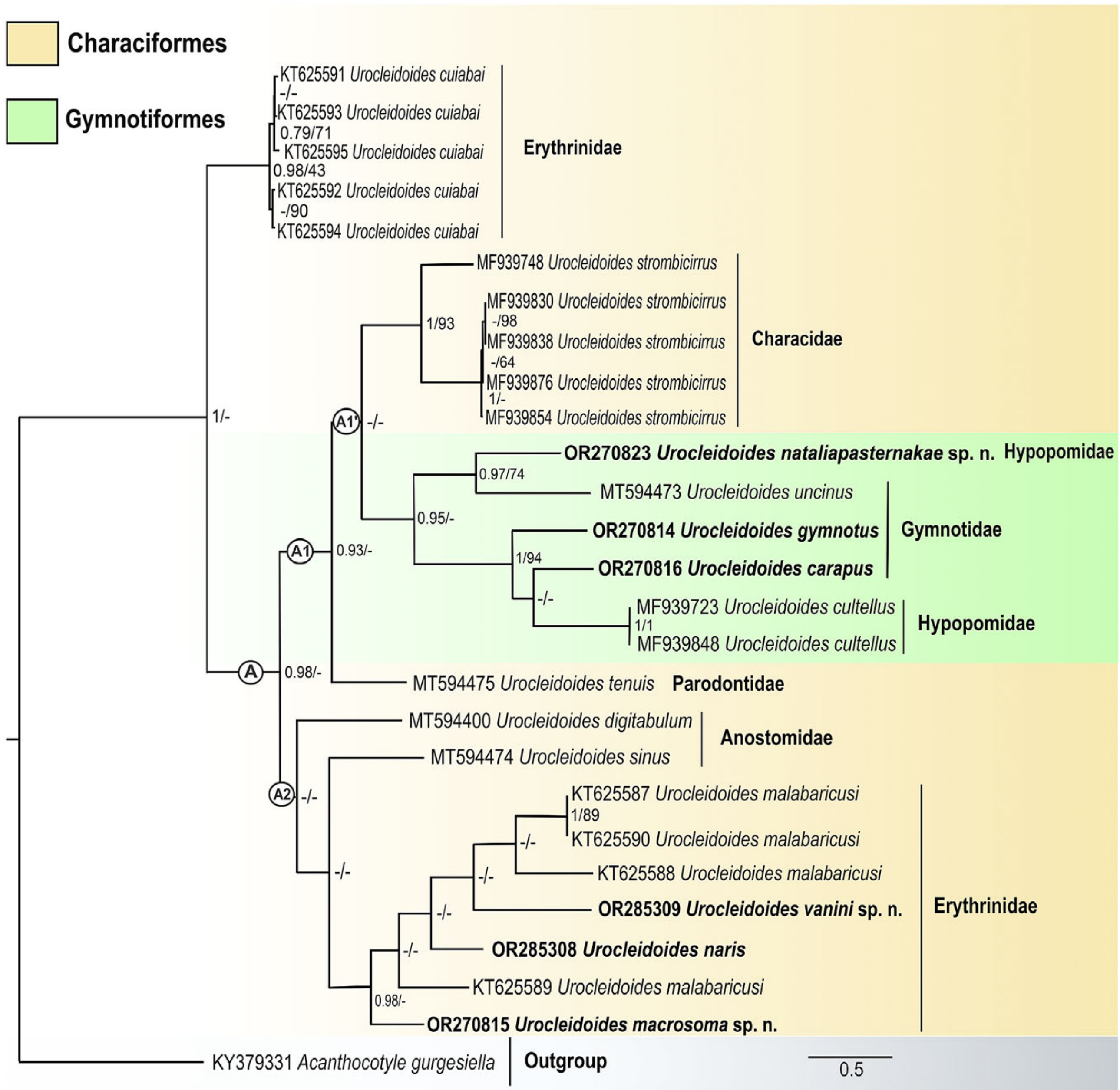

Figure 2. Molecular phylogeny of Dactylogyridae estimated by Bayesian and Maximum Likelihood analyses inferred using the partial COI mtDNA gene (alignment length 347 bp). The new species sequenced in the present study are presented in bold. The sequences of the other species were retrieved from GenBank. The bootstrap (ML) and posterior probability (BI) supports are presented between branches (values of posterior probability < 0.90 and bootstrap < 60 are not shown). The length of the scale bar indicates the substitution numbers per site.

erythrinus (Bloch & Schneider) (Characiformes: Erythrinidae) differs from the remaining species of *Urocleidoides* from *H. malabaricus* by between 20.7 and 21.5% (192–202 bp), and *U. vanini* n. sp. differs 8% (90 bp) from *U. atilaiamarinoi* n. sp. The species that parasitize characiform fish from the family Parodontidae (*U. tenuis*, *U. indianensis*, and *U. parodoni*) diverge from each other from 2.1 to 10.4%. (28–158 bp). For COI mtDNA, genetic divergence was estimated and compared for the species of *Urocleidoides,* varying between 14.7 and 30.8% (50–102 bp) (Table 4).

Taxonomic summary

Class Monogenoidea Bychowsky, 1937
Order Dactylogyridea Bychoswky, 1937
Dactylogyridae Bychowsky, 1933
Urocleidoides Mizelle & Price, 1964

Urocleidoides vanini n. sp. (Figure 3)
Type host. Erythrinus erythrinus (Bloch & Schneider)

https://doi.org/10.1017/S0022149X2300041X Published online by Cambridge University Press

https://doi.org/10.1017/S0022149X2300041X Published online by Cambridge University Press

Table 3. Pairwise genetic identities of 28S rDNA sequences selected from Dactylogyridae species of Clade B1

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22
1. *U. paradoxus* MT556795	–	157	142	257	258	270	265	206	223	204	240	222	247	281	244	239	308	317	317	299	338	239
2. *U. sinus* MT55699	9.8	–	142	271	267	273	256	193	220	202	239	223	238	280	238	244	316	322	323	315	349	240
3. *U. digitabulum* MT556796	11.3	7.8	–	271	268	275	258	212	233	202	238	225	243	278	228	239	314	328	330	311	338	244
4. *U. tenuis* MT556797	19.7	20	20.5	–	28	57	150	189	201	188	227	214	214	261	235	228	321	300	302	278	332	214
5. *U. tenuis* OK465455	19.7	19.7	20.3	0.8	–	71	155	191	203	191	236	221	219	267	235	227	322	303	305	282	334	212
6. *U. parodoni* OK482867	19.1	19.9	20	2.5	2.1	–	158	184	212	194	239	226	228	277	239	235	322	306	309	287	340	220
7. *U. indianensis* OK482868	19.3	18.4	18.6	10.4	10.4	10.0	–	183	206	180	232	217	235	257	242	241	316	293	297	293	326	221
8. ***U. brasiliensis***	20.3	19.1	20.7	18	18.4	18	17	–	43	84	195	198	185	151	214	202	208	218	221	199	218	220
9. ***U. naris***	21.5	20.7	21.9	17.4	17.8	18	17.6	3.9	–	87	203	196	196	159	213	202	218	219	220	206	213	213
10. ***U. macrosoma* n. sp.**	20.5	20.7	20.3	19.5	19.9	19.5	18	8.0	9	–	177	178	179	141	207	192	213	205	209	203	211	216
11. ***U. carapus***	20.7	20.5	20.7	19.9	20.7	20	19	17.4	18	16.2	–	32	88	138	167	185	236	227	232	228	229	242
12. ***U. gymnotus***	20.9	21.3	21.7	19.7	20.5	20	20	18.8	18.8	17.6	2	–	91	131	166	178	223	218	224	215	217	241
13. ***U. nataliapasternakae* n. sp.**	21.7	20.5	22	16.6	17.4	17.2	18.2	16.6	17.8	17	7	7.8	–	154	167	175	238	239	240	218	245	224
14. *U. uncinus* MT556798	21.3	19.3	20	18.2	18.2	18.6	18.2	15.0	15.8	14.8	10.4	10.7	12.7	–	222	217	273	261	267	267	278	218
15. ***U. atilaiamarinoi* n. sp.**	20.3	21.7	20	18.8	18.6	18.6	20.5	20.7	21	19	18.4	19.3	18.2	20.5	–	90	258	238	241	224	242	235
16. ***U. vanini* n. sp.**	21.5	21.3	19.9	19.5	19.5	18.9	19.9	21.5	21.5	20.7	17.6	18.6	172	21.7	8.0	–	249	232	234	211	232	230
17. *C. papilionis* MG832889	22.1	21.9	21.5	23.6	24	23.2	21.3	20.5	21	21.5	22	22	22.3	20.5	24.6	25	–	306	309	297	313	240
18. *H. anchoradiatus* MF116371	24.8	23.6	24.8	22	22	22.3	21.1	22.9	22.3	21.3	21.3	21.7	22.3	21.3	23.2	22.7	23.0	–	24	142	169	227
19. *H. heterotylus* MF116370	24.4	23.2	24.6	22.3	22.7	22.9	21.7	23	22.3	21.5	21.7	22	22.1	21.5	23.2	23	23.4	2	–	141	174	229
20. *U. unilatus* MF102106	21.1	23	22.7	19.3	19.3	18.4	21.3	20.9	20.9	20.3	20.7	20.9	19.5	21.3	19.7	20	23.4	11.7	11.7	–	160	218
21. *T. anthus* MN947622	24.8	25.2	24.4	24.6	24.2	25	24	22.7	21.5	21.5	20.3	20.9	23.6	21.7	22.5	23.2	23.6	11.3	11.5	13.3	–	227
22. *M. viatorum* MH843723	25.8	25.4	25.2	21.7	21.7	22	22.9	22	21.5	21.9	24.4	24.6	23.2	21.3	24	24.2	25	22.9	23.6	22.9	23	–

The upper triangular matrix shows the number of nucleotide differences, and the lower triangular matrix shows the differences in terms of percentage of nucleotides. Sequences obtained in the present work are in bold.

Table 4. Pairwise genetic identities of COI mtDNA sequences selected from Dactylogyridae species of Clade B1

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27
1. *U. cultellus* MF939723	–	0	61	63	86	82	82	82	82	81	84	97	91	98	99	100	98	93	95	93	95	94	96	82	91	90	94
2. *U. cultellus* MF939848	0	–	61	63	86	82	82	82	82	81	84	97	91	98	99	100	98	93	95	93	95	94	96	82	91	90	94
3. *U. carapus*	18.7	18.6	–	56	85	78	78	78	78	86	80	90	87	101	95	94	97	90	92	90	92	92	90	89	86	76	97
4. *U. gymnotus*	19	19.2	17	–	80	83	83	83	83	88	85	89	86	102	100	99	99	85	88	86	88	88	88	90	93	79	87
5. *U. nataliapasternakae* n. sp.	26.9	26.9	25.5	24.2	–	88	88	88	88	86	77	77	73	90	95	94	79	88	85	83	83	83	84	79	80	67	95
6. *U. strombicirrus* MF939830	24.9	24.9	22.9	23.9	27.2	–	0	0	1	57	71	79	80	92	90	89	90	79	90	88	92	90	91	83	84	83	92
7. *U. strombicirrus* MF939876	24.9	24.9	22.9	23.9	27.2	0	–	0	1	57	71	79	80	92	90	89	90	79	90	88	92	90	91	83	84	83	92
8. *U. strombicirrus* MF939838	24.9	24.9	22.9	23.9	27.2	0	0	–	1	57	71	79	80	92	90	89	90	79	90	88	92	90	91	83	84	83	92
9. *U. strombicirrus* MF939854	24.9	24.9	22.9	23.9	27.2	0	0	0	–	57	70	78	80	91	89	88	89	78	90	88	92	90	91	83	83	83	91
10. *U. strombicirrus* MF939748	25.2	25.2	26.2	27.2	26.2	16.7	16.7	16.7	16.7	–	71	85	84	82	86	85	92	81	86	84	88	87	85	78	93	97	99
11. *U. macrosoma* n. sp.	30.1	26.2	24.2	25.5	23.9	21.6	21.6	21.6	21.3	21.3	–	57	63	82	68	67	68	55	74	72	74	73	74	77	70	80	87
12. *U. naris*	30.8	30.8	28.5	27.2	23.6	24.2	24.2	24.2	23.9	26.2	17.7	–	59	83	60	59	70	50	79	77	77	76	78	83	65	78	88
13. *U. vanini* n. sp.	28.5	28.5	26.5	26.5	21.9	23.9	23.9	23.9	23.9	26.2	20	18.3	–	91	67	66	61	69	85	83	83	82	84	79	86	84	89
14. *U. digitabulum* MT594400	30.1	30.1	30.8	31.4	26.9	27.5	27.5	27.5	27.2	25.9	24.9	25.5	28.5	–	77	78	78	78	83	81	83	82	84	76	78	108	106
15. *U. malabaricusi* KT625587	30.8	30.8	30.1	30.5	28.5	27.2	27.2	27.2	26.9	26.5	19.3	17.7	19	23.2	–	1	56	58	82	80	82	81	82	78	79	86	91
16. *U. malabaricusi* KT625590	31.1	31.1	29.8	30.1	28.2	26.9	26.9	26.9	26.5	26.2	19	17.3	18.6	23.6	0	–	57	58	83	81	83	82	83	79	80	87	92
17. *U. malabaricusi* KT625588	29.8	29.8	29.5	29.8	23.6	28.2	28.2	28.2	27.9	29.1	20.6	20.9	18.3	23.6	16.3	16.7	–	68	82	80	82	81	83	81	86	90	94
18. *U. malabaricusi* KT625589	28.8	28.8	27.8	25.8	26.2	22.6	22.6	22.6	22.3	24.6	16	14.7	20.6	23.9	17	17	19.3	–	82	80	80	79	84	83	63	90	84
19. *U. cuiabai* KT625591	29.1	29.1	27.5	26.5	25.9	27.2	27.2	27.2	27.2	26.2	22.3	24.2	25.9	25.9	24.5	24.9	23.9	24.9	–	2	6	6	8	86	86	97	89
20. *U. cuiabai* KT625593	28.5	28.5	26.8	25.9	25.2	26.6	26.5	26.5	26.5	25.6	21.6	23.6	25.2	25.2	23.9	24.2	23.2	24.2	0	–	4	4	6	84	84	95	88
21. *U. cuiabai* KT625592	29.5	29.5	27.8	26.8	25.5	27.5	27.5	27.5	27.5	26.5	22.6	23.9	25.5	25.5	24.2	24.5	23.6	24.6	1	0	–	2	10	84	84	95	91
22. *U. cuiabai* KT625594	29.1	29.1	27.8	26.8	25.5	26.9	26.9	26.9	26.9	26.2	22.3	23.6	25.2	25.2	23.9	24.2	23.2	24.2	1	0	0	–	10	83	82	95	89
23. *U. cuiabai* KT625595	29.1	29.1	26.5	26.2	25.2	27.2	27.2	27.2	27.2	25.5	21.9	23.6	25.2	25.2	23.6	23.9	23.9	24.6	1	0	1	1	–	85	86	95	89
24. *U. tenuis* MT594475	25.2	25.2	28.2	27.2	23.9	25.2	25.2	25.2	25.2	22.6	24.2	25.9	24.2	21.9	23.9	23.9	24.6	24.6	25.2	24.6	24.9	24.6	24.6	–	88	90	96
25. *U. sinus* MT594474	28.8	28.8	26.56	28.5	23.9	24.9	24.9	24.9	24.6	28.8	20.9	19.3	26.2	22.9	23.9	24.2	25.9	18.7	25.9	25.2	25.6	24.9	25.6	26.6	–	86	87
26. *U. uncinus* MT594473	28.2	28.2	23.2	23.2	20.6	25.5	25.5	25.5	25.6	29.8	24.9	24.6	26.2	32.7	26.2	26.5	27.9	26.9	29.1	28.5	28.8	28.8	28.2	28.2	26.2	–	89
27. *A. gurgesiella* KY379331	30.8	30.8	31.8	28.5	31.1	30.1	30.1	30.1	29.8	32.4	28.5	28.8	29.1	34.7	29.8	30.1	30.8	27.5	29.1	28.8	29.8	29.1	29.1	31.5	28.5	29.2	–

The upper triangular matrix shows the number of nucleotide differences, and the lower triangular matrix shows the differences in terms of percentage of nucleotides. Sequences obtained in the present work are in bold.

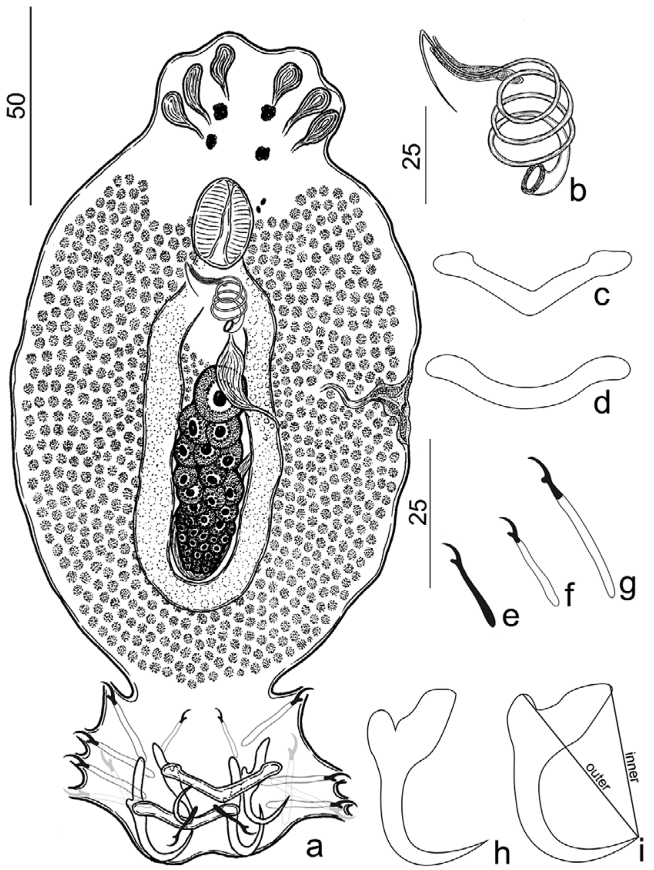

Figure 3. *Urocleidoides vanini* n. sp. **a.** Holotype, whole body; **b.** copulatory complex; **c.** ventral bar; **d.** dorsal bar; **e.** hook pair 5; **f.** hook pair 1; **g.** hook pairs 2, 3, 4, 6, and 7; **h.** dorsal anchor; **i.** ventral anchor. Scales: **a.** 50µm scale, **b–i.** 25µm scale.

Type locality. Vila Perseverança, Palheta River (Guamá River Basin), municipality of São Domingos do Capim, Pará, Brazil (1° 51'41.8"S, 47°38'26.5"W).
Site of infestation. Gills.
Prevalence. 100% of 2 hosts examined.
Average intensity. 4.5 parasites per host.
Specimens deposited. Holotype (CHIOC No. 40208a); 9 paratypes (CHIOC No. 40208b–f, 40209a–d), 1 hologenophore (CHIOC No. 40208g).
Molecular sequence data. The partial 28S rDNA (773 bp) and COI mtDNA (695 bp) sequences obtained from one specimen (GenBank accession numbers OR270736 and OR285309, respectively).
Etymology. The specific name of the species is a tribute to zoologist Sergio Antonio Vanin (1948–2020), a lover of zoology who dedicated his life to the studies of systematics and taxonomy and contributed to the education of new generations of Brazilian zoologists.
Number of ZooBank. C053980D-B95E-4FC1-80F0-85932FF1B3CD.
Description. (Based on 10 adult specimens – 5 mounted on Gomori Trichrome, 5 mounted on Hoyer's medium). Body elongated, robust, foliform, total length excluding haptor 157 (135–167; n=5), total width at level of germarium 112 (92–150; n=5) (Figure 3a). Cephalic lobes (4) moderately developed, 2 terminal and 2 bilateral; 3 pairs of head organs; cephalic glands not observed (Figure 3a). Eyes (2 pairs) equidistant; accessory chromatic granules distributed near pharynx (Figure 3a). Pharynx suboval, muscular, 21 (19–23; n=5) long, 16 (15–17; n=5) wide; esophagus short (Figure 3a). Genital pore midventral, anterior to copulatory complex. Genital atrium non-sclerotized. Gonads overlapping, testis dorsal to germarium (Figure 3a). Oviduct, Mehlis' glands, uterus, egg, prostatic reservoir, seminal receptacle not observed. Testis oval 22 (19–24; n=3) long, 16 (14–17; n=3) wide. Copulatory complex comprising MCO, accessory piece. MCO sclerotized, tubular with three and a half counterclockwise rings, 194 (187–213; n=4) long, base with sclerotized cap; proximal portion of MCO slightly expanded, distal aperture acute. Accessory piece located in distal portion of MCO, not articulated with base of MCO, comprising an elongated sheath (Figure 3b). Seminal vesicle sigmoid (Figure 3a). Vaginal pore sinistral, ventro-marginal; vaginal vestibule broad, slightly sclerotized; vaginal canal muscular, sigmoid (Figure 3a). Vaginal sclerite absent. Germarium elongated 50 (42–60; n=5) long, 25 (22–27; n=5) wide. Vitellaria dense coextensive with gut, absent in regions of reproductive organs. Haptor hexagonal 38 (31–44; n=5) long, 76 (71–79; n=5) wide (Figure 3a). Anchors similar; each with well-developed superficial root, depressed at distal surface; short deep root, rounded at distal surface; shaft evenly curved, point; point extending past level of tip of superficial root; ventral anchor base 11 (11–12; n=5) long, inner 28 (25–33; n=5) long, outer 29 (27–31; n=5) long, (Figure 3i); dorsal anchor base 12 (11–13; n=5) long, inner 19 (18–20; n=5) long, outer 26 (24–26; n=5) long, (Figure 3h). Ventral bar 29 (25–35; n=7) long, open V-shaped with enlarged ends (Figure 3c); dorsal bar 28 (24–34; n=7) long, open U-shaped with rounded ends (Figure 3d). Hook pairs 2, 3, 4, 6, and 7 26 (24–29; n=6) long (Figure 3g) similar in morphology with shank divided into two subunits, thumb slightly depressed, slightly curved shaft, delicate point; hook pairs 1 and 5 reduced in size 13 (11–14; n=7) long; hook pair 1 with shank divided into two subunits, thumb erect, curved shaft, delicate point (Figure 3f); hook pair 5 with erected thumb, curved shaft, delicate point, lacking dilated shank portion (Figure 3e).

Remarks. The molecular results in the present study support the validity of *U. vanini* n. sp. as well as *U. carapus* and *U. gymnotus* as members of *Urocleidoides* (see Molecular data and phylogenetic inferences section). These three species differ from their cogeners by lacking the vaginal sclerite. The new species differs from *U. carapus* mainly by possessing a uniform dorsal anchor, whereas *U. carapus* has a dorsal anchor with point presenting ornamentation as sclerotized shredded filaments. *Urocleidoides vanini* n. sp. also can be distinguished from *U. gymnotus* mainly by having a MCO with three and a half rings (seven to nine rings in *U. gymnotus*).

Urocleidoides atilaiamarinoi n. sp. (Figure 4)
Type host. Hoplerythrinus unitaeniatus (Agassiz) (Characiformes: Erythinidae).
Type locality. Igarapé Maratininga (Moju River Basin), municipality of Tailândia, Pará, Brazil (02°27'55.7"S, 48°53'27.6"W).
Site of infestation. Gills.
Prevalence. 43% (3 of 7 hosts examined).
Average intensity. 5 parasites per host.
Other hosts and locations. Hoplerythrinus unitaeniatus (prevalence: 33% [1 of 3 hosts]; average intensity: 7 parasites per host), Balneário Aracu (Guamá River Basin), municipality of Ourém, Pará, Brazil (1°34'1.02"S, 47° 9'52.35"W).
Specimens deposited. Holotype (CHIOC No. 39995a); 14 paratypes (CHIOC No. 39995b–f, 39996a–c, 39997a–f), 1 hologenophore (CHIOC No. 40000); 7 vouchers (CHIOC No. 39998a–c, 39999a–d).

https://doi.org/10.1017/S0022149X2300041X Published online by Cambridge University Press

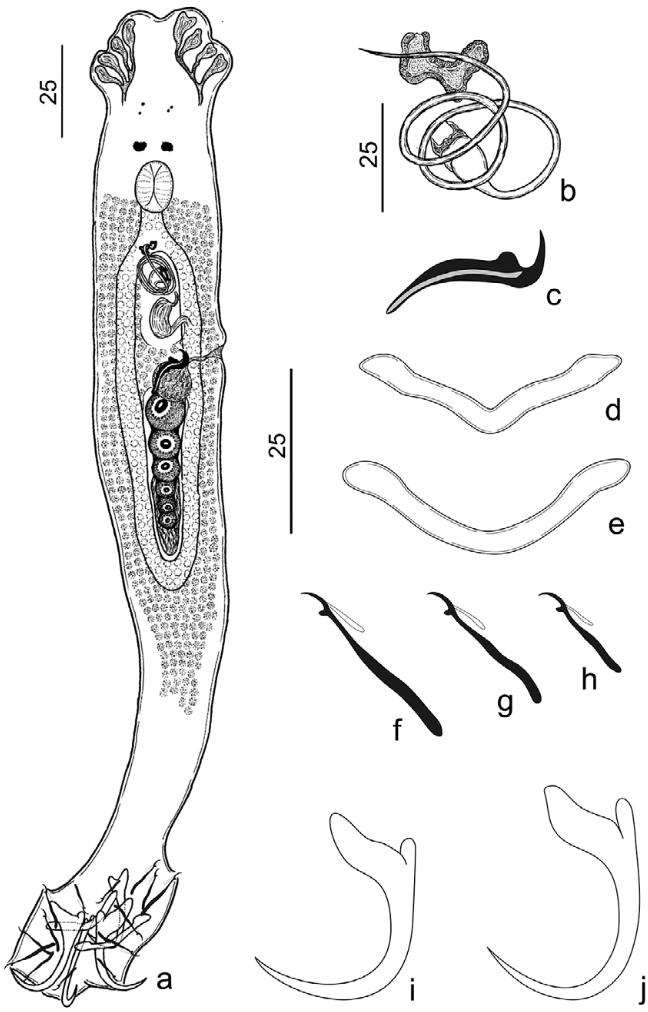

Figure 4. *Urocleidoides atilaiamarinoi* n. sp. **a.** Whole body – composite (ventral); **b.** copulatory complex; **c.** vaginal sclerite; **d.** ventral bar; **e.** dorsal bar; **f.** pair hook 7; **g.** hook pairs 2, 3, 4, and 6; **h.** hook pair 1; **i.** dorsal anchor; **j.** ventral anchor. Scales: **a.** 25µm scale, **b–j**. 25µm scale.

Molecular sequence data. The partial 28S rDNA (767 bp) sequence obtained from one specimen (GenBank accession number OR270164).

Etymology. The specific name of the species is a tribute to the biologist and science communicator Atila Iamarino, who is dedicated to studies related to genetics of microorganisms and works tirelessly to communicate scientific research to the general population.

Number of ZooBank. 8684EAB5-4587-44E1-9F25-9255CDE5-FEE4.

Measurements. Table 5.

Description. (Based on 16 adult specimens – 2 mounted on Gomori's Trichrome, 11 mounted on Hoyer's medium, 3 mounted on Gray & Wess medium). Body elongated, fusiform, total length excluding haptor 209 (175–237; n=12), total width at level of germarium 75 (57–97; n=13) (Figure 4a). Cephalic lobes (4) well-developed, 2 terminal and 2 bilateral; 4 pairs of head organs; cephalic glands not observed (Figure 4a). Eyes (2 pairs) equidistant, posterior pair greater than anterior; anterior pair with few granules observed, accessory chromatic granules present or absent (Figure 4a). Pharynx oval, muscular 16 (15–18; n=8) long, 16 (12–17; n=8) wide; esophagus short (Figure 4a). Genital pore midventral, anterior to copulatory complex. Genital atrium non-sclerotized. Gonads overlapping, testis dorsal to germarium (Figure 4a). Oviduct, Mehlis' glands, uterus, egg, prostatic reservoir

Table 5. Measurements (µm) of *Urocleidoides atilaiamarinoi* n. sp., gill parasite of *Hoplerythrinus unitaeniatus* from two locations

Structures	Tailândia*	N	Ourém	N
Body				
Length	209 (175–237)	12	238 (192–317)	6
Width	75 (57–97)	13	65 (37–112)	6
Haptor				
Length	48 (32–55)	12	50 (32–65)	6
Width	68 (47–90)	12	60 (37–82)	6
Pharynx				
Length	16 (15–18)	8	20 (16–25)	6
Width	16 (12–17)	8	16 (11–22)	6
MCO	120 (96–129)	11	114 (111–117)	2
Germarium				
Length	37	1	32 (25–36)	3
Width	10	1	12 (11–14)	3
Seminal receptacle				
Length	12	1	–	–
Width	11	1	–	–
Testis				
Length	23	1	–	–
Width	8	1	–	–
Vaginal sclerite	30 (22–38)	9	22 (18–26)	2
Ventral anchor				
Base	12 (11–14)	12	13 (12–15)	3
Inner	26 (23–28)	12	30 (29–31)	3
Outer	24 (22–27)	12	27 (24–32)	3
Dorsal anchor				
Base	10 (10–11)	11	11 (10–11)	3
Inner	23 (21–24)	11	27 (27–28)	3
Outer	22 (20–24)	11	24 (21–27)	3
Ventral bar				
Length	34 (29–40)	12	38 (28–44)	4
Dorsal bar				
Length	34 (28–40)	12	36 (27–45)	3
Hooks				
Pair 1	14 (12–16)	12	16 (15–18)	3
Pairs 2, 3, 4, 6	22 (20–23)	12	21 (21–22)	3
Pair 5	15 (14–16)	10	16	1
Pair 7	27 (25–29)	13	28 (27–30)	3

*Type-locality; MCO = male copulatory organ.

https://doi.org/10.1017/S0022149X2300041X Published online by Cambridge University Press

not observed. Testis elongated 23 (n=1) long, 8 (n=1) wide. Copulatory complex comprising MCO, accessory piece. MCO sclerotized, tubular with two and a half counterclockwise rings, 120 (96–129; n=11) long, bulbous base with sclerotized cap, distal aperture acute (Figure 4b). Accessory piece located in distal portion of MCO, not articulated with base of MCO, dumbbell-shaped (Figure 4b). Vaginal pore ventro-marginal, vaginal vestibule slightly sclerotized, vaginal canal muscular, slightly sigmoid. Vaginal sclerite 30 (22–38; n=9) long, sickle-shaped with longitudinal superficial groove, thumb short, point curved, elongated (Figure 4c). Germarium elongated 37 (n=1) long, 10 (n=1) wide. Seminal receptacle spherical 12 (n=1) long, 11 (n=1) wide. Vitellaria dense coextensive with gut, absent in regions of reproductive organs. Haptor hexagonal 48 (32–55; n=12) long, 68 (47–90; n=12) wide (Figure 4a). Ventral anchor with elongate slightly depressed tip of superficial root; elongate deep root, rounded at distal surface; evenly curved shaft, point; point extending past level of tip of superficial root, base 12 (11–14; n=12) long, inner 26 (23–28; n=12) long, outer 24 (22–27; n=12) long (Figure 4j). Dorsal anchor with elongate superficial root; short deep root, rounded at distal surface; evenly curved shaft, point; point extending past level of tip of superficial root, base 10 (10–11; n=11), inner 23 (21–24; n=11) long, outer 22 (20–24; n=11) long (Figure 4i). Ventral bar 34 (29–40; n=12) long, open V-shaped, with ends slightly tapered (Figure 4d); dorsal bar 34 (28–40; n=12) long, open U-shaped with rounded ends (Figure 4e). Hook pairs similar in morphology with shank divided into two subunits, proximal dilation comprising 2/3 of shank length, thumb erect, elongated slightly curved shaft, delicate point, filament hook loop extended to near beginning of shank dilation. Hook pairs 1 and 5 reduced in size, pair 1 14 (12–16; n=12) long (Figure 4h); pair 5 15 (14–16; n=10) long; pairs 2, 3, 4, 6 22 (20–23; n=12) long (Figure 4g); pair 7 27 (25–29; n=13) long (Figure 4f).

Remarks. Urocleidoides atilaiamarinoi n. sp. resembles *Urocleidoides bulbophallus* Ferreira *et al.*, 2017 since they share a MCO with bulbous base. However, the new species differs from *U. bulbophallus* due the numbers of MCO rings (2 ½ rings in *U. atilaiamarinoi* n. sp. and 1 ½ in *U. bulbophallus*) and the morphology of the accessory piece (dumbbell-shaped in *U. atilaiamarinoi* n. sp., and a bent sheath, 'e' shape in *U. bulbophallus*). Also, they differ on the comparative size of anchors and bars. In *U. atilaiamarinoi* n. sp., the anchors and bars are approximately similar in size, whereas *U. bulbophallus* has ventral anchors and ventral bar twice as large as dorsal anchors and dorsal bar.

Urocleidoides macrosoma n. sp. (Figure 5)

Type host. Hoplias malabaricus (Bloch) (Characiformes: Erythrinidae).

Type locality. Vila Segredo – Segredo River (Quatipuru River Basin), Tauari, municipality of Capanema, Pará, Brazil (1°5'32.44"S, 47°5'37.02"W).

Site of infestation. Gills.

Prevalence. 66% (2 of 3 hosts examined).

Average intensity. 1.5 parasites per host.

Specimens deposited. Holotype (CHIOC No. 40204a);2 paratypes (CHIOC No. 40204b–c), 1 hologenophore (CHIOC No. 40204d) .

Molecular sequence data. The partial 28S rDNA (731 bp) and COI mtDNA (733 bp) sequences obtained from one specimen (GenBank accession numbers OR270735 and OR270815, respectively).

Etymology. The specific name of the species derives from the Greek (*macro* = large + *soma* = body) and refers to the size of the parasite's body.

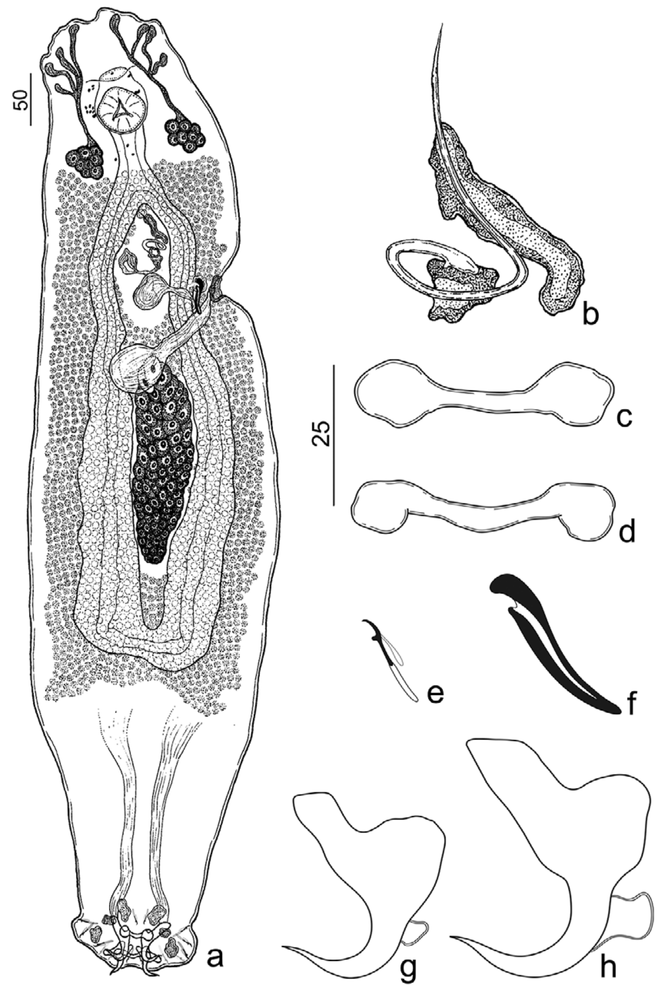

Figure 5. *Urocleidoides macrosoma* n. sp. **a.** Holotype, whole body (ventral); **b.** copulatory complex; **c.** ventral bar; **d.** dorsal bar; **e.** hooks; **f.** vaginal sclerite; **g.** dorsal anchor; **h.** ventral anchor. Scales: **a.** 50μm scale, **b–h**. 25μm scale.

Number of ZooBank. 8A13B412-E0B8-41B3-BE31-F9ED7F409EB5.

Description. (Based on 3 adult specimens – 1 mounted on Gomori's Trichrome, 1 mounted on Hoyer's medium, 1 mounted on Gray & Wess). Body elongated, fusiform, robust, total length excluding haptor 795 (737–827; n=3), total width at level of germarium 274 (215–347; n=3) (Figure 5a). Cephalic lobes (4) poorly developed, 2 terminal, 2 bilateral; 4 pairs of head organs; cephalic glands unicellular, posterolateral to pharynx (Figure 5a). Eyes absent; accessory chromatic granules distributed in cephalic region and esophagus (Figure 5a). Pharynx subspherical, muscular, 58 (55–60; n=3) long, 58 (56–62; n=3) wide; esophagus elongated (Figure 5a). Genital pore midventral, anterior to copulatory complex. Genital atrium non-sclerotized. Gonads apparently overlapping. Oviduct, Mehlis' glands, uterus, egg, testis, prostatic reservoir not observed. Copulatory complex comprising MCO, accessory piece. MCO sclerotized, tubular with one counterclockwise ring, 94 (82–103; n=3) long, base with sclerotized cap, proximal portion of MCO slightly expanded, distal aperture acute (Figure 5b). Accessory piece located in distal portion of MCO, not articulated with base of MCO, comprising an elongated sheath with a groove, which serves as a guide for MCO (Figure 5b). Seminal vesicle with dilated proximal portion, with descending loop followed by ascending loop, distal

https://doi.org/10.1017/S0022149X2300041X Published online by Cambridge University Press

portion tapered connecting base of MCO. Vaginal pore sinistral, ventro-marginal; vaginal vestibule heavily sclerotized, cup-shaped; vaginal canal muscular. (Figure 5a). Vaginal sclerite 40 (36–46; n=3) long, with longitudinal superficial groove, thumb short, point rounded (Figure 5f). Germarium elongated, fusiform 168 (n=1) long, 55 (n=1) wide. Seminal receptacle subspherical 43 (n=1) long, 46 (n=1) wide. Vitellaria dense, extending from esophagus to confluence of intestinal cecum. Haptor trapezoidal 65 (57–77; n=3) long, 145 (118–162; n=3) wide (Figure 5a). Anchors similar in morphology, robust with elongate superficial root, slightly depressed tip; short deep root, rounded; short shaft; wavy point, extending past level of tip of superficial. Ventral anchor base 31 (29–36; n=3) long, inner 38 (30–42; n=3) long, outer 42 (38–45; n=3) long (Figure 5h). Dorsal anchor base 25 (24–27; n=3) long, inner 34 (32–36; n=3) long, outer 30 (24–37; n=3) long (Figure 5g). Bars similar in morphology, dumbbell-shaped. Ventral bar 38 (36–39; n =3) long (Figure 5c). Dorsal bar 39 (37–39; n=3) long (Figure 5d). Hook pairs similar in morphology with shank divided into two subunits, proximal dilation comprising ½ of shank length, thumb erect, slightly curved shaft, delicate short point, filament hook loop extended to near beginning of shank dilation. Hook pairs 1 and 5 reduced in size, 13 (12–14; n=2) long; pairs 2, 3, 4, 6, 7 17 (17–18; n=2) long (Figure 5e).

Remarks: *Urocleidoides macrosoma* n. sp. resembles *Urocleidoides aimarai* Moreira, Scholz & Luque, 2015 by the general morphology of the copulatory complex and anchors. However, they differ from one another mainly due to the morphology of the anchor's point, bars, germarium, and vaginal sclerite. In *U. macrosoma* n. sp., anchors have a wavy point, and both bars are dumbbell-shaped, whereas *U. aimarai* has anchors with evenly curved shaft, point, and a V-shaped ventral bar and rod-shaped dorsal bar with a smooth anteromedial projection. In addition, *Urocleidoides macrossoma* n. sp. exhibits an elongated and fusiform germarium (bacilliform germarium in *U. aimarai)* and a vaginal sclerite with a short and rounded point (tapered distal portion of the vaginal sclerite and robust rod in *U. aimarai*).

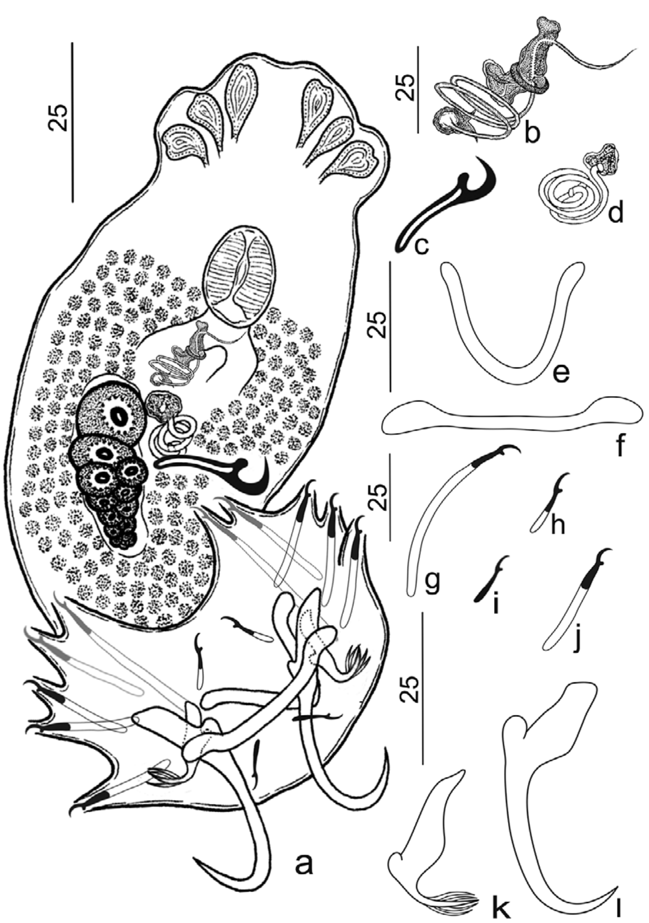

Figure 6. *Urocleidoides nataliapasternakae* n. sp. **a.** Holotype, whole body (ventral); **b.** copulatory complex; **c.** vaginal sclerite; **d.** vagina; **e.** dorsal bar; **f.** ventral bar; **g.** hook pair 6; **h.** hook pair 1; **i.** hook pair 5; **j.** hook pairs 2, 3, 4, and 7; **k.** dorsal anchor; **l.** ventral anchor. Scales: **a.** 25μm scale, **b–l.** 25μm scale.

Urocleidoides nataliapasternakae n. sp. (Figure 6)
Type host. Brachyhypopomus brevirostris (Steindachner) (Gymnotiformes: Hypopomidae).
Type locality. Balneário Aracu (Guamá River Basin), municipality of Ourém, Pará, Brazil (1°34'1.02"S, 47° 9'52.35"W).
Site of infestation. Gills.
Prevalence. 50% (2 of 4 hosts examined).
Average intensity. 6.5 parasites per host.
Specimens deposited. Holotype (CHIOC No. 40206a); 9 paratypes (CHIOC No. 40206b–f, 40207a–d), 1 hologenophore (CHIOC No. 40206g) .
Representative DNA sequence. The partial 28S rDNA (766 bp) and COI mtDNA (764 bp) sequences obtained from one specimen (GenBank accession numbers OR270733 and OR270823, respectively).
Etymology. The specific name of the species is a tribute to the biologist and writer Natalia Pasternak Taschner in recognition and admiration for her valuable work of scientific dissemination and communication.
Number of ZooBank. BF8B6560-747D-43CC-B6E6-08FAD-CE6FA86.
Description. (Based on 10 adult specimens – 4 mounted on Gomori's Trichrome, 6 mounted on Hoyer's medium). Body elongated, fusiform, total length excluding haptor 145 (97-201; n=8), total width at level of germarium 56 (44–71; n=9) (Figure 6a). Cephalic lobes (4) moderately developed, 2 terminal, 2 bilateral; 3 pairs of head organs; cephalic glands not observed (Figure 6a). Eyes, accessory chromatic granules absent. Pharynx oval, muscular 16 (14–17; n=4) long, 13 (10–15; n=4) wide; esophagus short (Figure 6a). Genital pore midventral, anterior to copulatory complex. Genital atrium non-sclerotized. Gonads apparently overlapping. Oviduct, Mehlis' glands, uterus, seminal receptacle, seminal vesicle, testis, prostatic reservoir not observed. Copulatory complex comprising MCO, accessory piece. MCO sclerotized, tubular with two and a half counterclockwise rings,102 (92–119; n=5) long, base with sclerotized cap, proximal portion of MCO slightly expanded, distal aperture acute (Figure 6b). Accessory piece located in distal portion of MCO serving as a guide to MCO, not articulated with base of MCO, comprising a dumbbell-shaped elongated sheath (Figure 6b). Vaginal pore medial, ventral; vaginal vestibule heavily sclerotized; vaginal canal sclerotized, convoluted (Figure 6d). Vaginal sclerite with longitudinal superficial groove, thumb erect, point elongated, slightly straight 28 (20–34; n=6) long (Figure 6c). Germarium elongated, fusiform 29 (27–20; n=3) long, 12 (11–12; n=3) wide. Vitellaria dense, extending from esophagus to confluence of intestinal cecum. Haptor hexagonal 44 (30–54; n=9) long, 68 (53–86; n=9) wide (Figure 6a). Ventral anchor with well-developed superficial root; short deep root, rounded; slightly curved long shaft; curved point extending past level of tip of superficial root, base 11 (10–12; n=7) long, inner 32 (29–38; n=7) long, outer

https://doi.org/10.1017/S0022149X2300041X Published online by Cambridge University Press

30 (28–34; n=7) long (Figure 6l). Dorsal anchor with long superficial root, slightly depressed at distal surface; short deep root, rounded; shaft short, curved; point with ornaments as shredded sclerotized filaments, base 12 (10–13; n=7) long, inner 22 (20–23; n=6) long, outer 17 (15–18; n=6) long (Figure 6k). Ventral bar 46 (37–52; n=8) long, straight, rod-shaped with enlarged ends (Figure 6f); dorsal bar 41 (31–49; n=8) long, U-shaped with rounded ends (Figure 6e). Hook pair 1 15 (13–16; n=6) long (Figure 6h), shank with proximal dilation comprising ½ of length of shaft, filament hook loop not observed; hook pairs 2, 3, 4, 7 32 (22–37; n=13) long (Figure 6j) with proximal dilation at shank comprising approximately 1/3 of shank length; hook pair 6 55 (47–62; n=6) long (Figure 6g) larger than others, shank with proximal dilation comprising approximately 1/5 of shank length, filament hook loop not observed; hook pair 5 14 (13–15; n=6) long (Figure 6i) reduced, shank without proximal dilation, filament hook loop not observed.

Remarks. Urocleidoides nataliapasternakae n. sp. resembles *Urocleidoides carapus* from *Gymnotus carapo* (Gymnotidae: Gymnotiformes), *Urocleidoides cultellus* from *Brachyhypopomus occidentalis* (Gymnotiformes: Hypopomidae), and *Urocleidoides ramentacuminatus* Oliveira *et al*., 2019 from *Schizodon fasciatus* (Characiformes: Anostomidae) by possessing ornamentations at the point of the dorsal anchor. However, *U. nataliapasternakae* n. sp. is easily distinguished from these species by the combination of the following features: an MCO with two and a half counterclockwise rings (five rings in *U. cultellus* and one ring MCO in *U. ramentacuminatus*), a U-shaped dorsal bar (slightly recurved dorsal bar with enlarged ends in *U. cultellus*), a vagina with a medial aperture (sinistro-marginal vaginal pore in *U. ramentacuminatus* and *Urocleidoides carapus*), a vaginal canal convoluted (sigmoid in *Urocleidoides carapus* and straight in *U. ramentacuminatus*), and the presence of a vaginal sclerite (absence in *U. carapus*).

Discussion

Since the amendment of the diagnosis of *Urocleidoides* proposed by Kritsky *et al.* (1986), the presence of vaginal sclerite has been used to define the species of the genus. However, the presence or absence of the vaginal sclerite used to validate species of *Urocleidoides* is still questioned (Mendoza-Franco & Reina, 2008). According to Mendoza-Franco & Reina (2008), the species of *Urocleidoides incertae sedis* (*i.e., U. advenai* Mendoza-Franco & Reina, 2008, *U. carapus*, *U. gymnotus*, and *U. hypopomi* Suriano, 1997) and *sensu stricto* (*i.e., U. cultellus* and *U. visiofortatus*) described from gymnotiform hosts share some morphological characteristics (*i.e.*, absence of eyes in *U. advenai, U. carapus*, *U. gymnotus*, *U. cultellus*, and *U. visiofortatus*; ornamentations at the point of the dorsal in *U. carapus* and *U. cultellus*; vaginal aperture in the midventral position in *U. cultellus*, *U. gymnotus*, *U. visiofortatus*, and *U. hypopomi*) suggesting that they may be evolutionarily related. However, these authors commented that the main limitation in diagnosing species of *Urocleidoides* is the absence of phylogenetic analysis. Kmentová *et al.* (2022) commented that contradictions in the diagnoses of genera and the morphology of monogenoid species can occur even if the species of a genus exhibit the characteristics listed in the most recent diagnoses. Furthermore, morphological similarities between more distantly related lineages of monogenoids can lead to the erection of several so-called 'catch-all' genera. Thus, the molecular data approach for phylogenetic reconstruction in monogenoid studies has been used to highlight and solve such taxonomic problems.

In the present study, the taxonomic status of some species of *Urocleidoides* with and without vaginal sclerite was evaluated through morphological and molecular data. The phylogenetic analyses based on molecular data support the conclusion that some *Urocleidoides* species considered *incertae sedis* (*sensu* Kritsky *et al.* 1986) are closely related to their *sensu stricto* congeners (*sensu* Kritsky *et al.* 1986) (Figures 1 and 2). For example, the clade formed by species of *Urocleidoides* parasitizing gymnotiform fishes (*U. cultellus*, *U. uncinus*, *U. nataliapasternakae* n. sp., all *sensu stricto* species; *U. carapus, U. gymnotus*, both *incertae sedis* species) is well supported by both analyses (ML and BI) using partial sequences of the 28S rDNA gene (BI, P = 1 and ML, B = 100) (Figure 1) and the COI mtDNA gene (BI, P = 0.95) (Figure 2). We also found that *U. vanini* n. sp. (without vaginal sclerite) and *U. atilaiamarinoi* n. sp. (with vaginal sclerite) parasites of Characiformes (Erythrinidae) are closely related and supported by the 28S rDNA gene analyses (BI, P = 1 and ML, B = 99) (Figure 1).

Zago *et al.* (2020) proposed a phylogenetic hypothesis based on molecular data (COI mtDNA) for species of *Urocleidoides* reported from Characiformes and Gymnotiformes, whose results showed that *Urocleidoides strombicirrus* (Price & Bussing, 1967) (*incertae sedis*) from Characiformes hosts is the sister group of the *sensu stricto* species, *U. cultellus* and *U. uncinus* reported for Gymnotiformes fish. Our results with the inclusion of additional taxa corroborate the findings of Zago *et al.* (2020), which also supports the hypothesis proposed by Mendoza-Franco and Reina (2008) by showing that species with and without vaginal sclerite are closely related. Therefore, although the presence of vaginal sclerite is an important diagnostic characteristic for *Urocleidoides*, it cannot be considered a main characteristic for the species of the genus. Boeger and Vianna (2006) commented that the presence of a vaginal sclerite in *Urocleidoides* spp. may be associated with its reproductive system. However, the absence of sclerite in some species may indicate an evolutionary modification in the reproductive mode that may have arisen independently or have been lost secondarily within the group.

Secondary loss of morphological structures has already been reported in some groups of monogenoids. For example, Domingues and Boeger (2008), reviewing species of the family Diplectanidae observed that some genera (*i.e.*, *Rhabdosynochus* Mizelle & Blatz, 1941, *Rhamnocercus* Monaco, Wood & Mizelle, 1954, and *Rhamnocercoides* Luque & Iannacone, 1991) do not present the accessory adhesive organ, which is considered an important feature of the family. Through morphological phylogenetic analysis, they concluded that the absence of such a structure in species of these genera might have been lost secondarily and that this loss probably occurred several times within the evolutionary history of Diplectanidae (see Domingues & Boeger 2008). Therefore, based on our results using partial sequences of the 28S rDNA and the COI mtDNA genes, we can conclude that *U. carapus*, *U. gymnotus,* and *U. vanini* n. sp., even if devoid of vaginal sclerite, are valid species for the genus.

Oliveira *et al.* (2021) in their phylogenetic analysis based on 28S rDNA have shown that some species of *Urocleidoides* appear nested with species of *Cacatuocotyle* Boeger, Domingues & Kritsky, 1997. The results of our 28S rDNA phylogenetic analysis reveal that the clade formed by *Urocleidoides* spp. has significant support from both analyses (BI and ML). However, an internal clade with low support shows *Cacatuocotyle papilionis* as a sister group of the species of *Urocleidoides* that parasitize gymnotiform and erythrinid

(Characiformes) fishes (*U. brasiliensis*, *U. naris*, and *U. macrosoma* n. sp.) (Figure 1). Given this context, our results corroborate those of Oliveira *et al.* (2021) and provide evidence that *Urocleidoides* may represent a non-monophyletic group.

We detected two clades formed by species of *Urocleidoides* (Figure 1). For species that parasitize Characiformes, we observed four groups related to host families (*i.e.*, Anostomidae, Erythrinidae, and Parodontidae). In contrast, for species that parasitize Gymnotiformes, we found three groups related to the reported species of Hypopomidae and Gymnotidae (Figure 1). The recovery of these clades might be associated with coevolutionary processes that occurred in isolation within each host family. Boeger and Kritsky (1997) and Desdevises *et al.* (2002) observed that, within coevolutionary scenarios, co-speciation events seem to restrict monogenoid lineages to their hosts and that these events occur at higher taxonomic levels (*i.e.*, family or genus), suggesting that broad historical constraints drive close relationships between monogenoids and their hosts.

Finally, the species of *Urocleidoides* reported from erythrinid fish in the present study did not represent a monophyletic group (28S rDNA) (Figure 1). We found a clade comprising the species reported from *H. malabaricus* (*U. naris*, *U. brasiliensis*, and *U. macrosoma* n. sp.) and another with the species reported from *E. erythrinus* and *H. unitaeniatus* (*U. vanini* n. sp. and *U. atilaiamarinoi* n. sp., respectively). These two clades showed a significant genetic divergence, ranging from 19 to 21.5% (192–214 bp). The species *U. atilaiamarinoi* n. sp. and *U. vanini* n. sp. are closely related, reflecting proximity with their hosts (see Oliveira *et al.* 2011). The 28S rDNA tree shows that the species of *Urocleidoides* that parasitize *H. malabaricus* are more closely related to the species that occur in gymnotiform fish. However, the relationships between the species of these clades are not supported, as we found low support values in the BI and ML analyses (Figure 1). Therefore, the separation of clades from species that occur in erythrinid fish may be associated with host exchange events, which may be related to diversification events. In addition, the overlapping geographical distribution of their hosts may also contribute to shaping the sharing of these parasites (Braga *et al.* 2015). We suggest that the relationships between the species groups of *Urocleidoides* can be better elucidated in future studies, with the possible inclusion of all species (*i.e.*, *sensu stricto* and *incertae* sedis) in the analyses.

Conclusion

The present study contributes to an understanding of the diversity of species in *Urocleidoides*, expanding the genus to 52 valid species with the description of four new parasitic species of characiform and gymnotiform fishes from South America. Furthermore, the molecular data from partial sequences of the 28S rDNA and COI mtDNA genes used to reconstruct the phylogenetic relationships between species of *Urocleidoides* permit a better understanding of the relationships between the *sensu stricto* species and those considered *incertae sedis.* Moreover, the absence of vaginal sclerite in some species of *Urocleidoides* can be explained by secondary loss events, which may have occurred several times within the evolutionary history of the group. We also suggest that the presence of the vaginal sclerite alone is insufficient for diagnosing the species of the genus. Finally, future studies may clarify the correct taxonomic status of the other species still considered *incertae sedis* and thus generate more robust data for a better understanding of the evolutionary history of this host–parasite system.

Acknowledgements. The authors thank Geusivam Soares (UNICAMP) for reviewing early versions of this manuscript and the members of the Laboratório de Sistemática e Coevolução (UFPA) and J-M.F.L. Cunha for assistance during the collecting trips. We thank the anonymous reviewers for their contributions to this manuscript.

Financial support. The present study was partly supported by research grants from the Conselho Nacional de Desenvolvimento Científico e Tecnológico, CNPq – Brazil (CNPq - PROTAX 001/2015-440526/2015-9) and Fundação Amazônia de Amparo a Estudos e Pesquisas, FAPESPA – Brazil (ICAAF 017-2018) to M.V. Domingues. J.F. Santos-Neto was supported by a doctoral scholarship from the Coordenação de Aperfeiçoamento de Pessoal de Nível Superior, CAPES – Brazil (grant# 88882.460123/2019-01). M.V. Domingues received research productivity grants from the Conselho Nacional de Desenvolvimento Científico e Tecnológico (grant #309896/2019-3). The preparation of this manuscript was supported by Programa de Apoio à Publicação Qualificada (PAPQ 2022) of Pró-Reitoria de Pesquisa e Pós-Graduação (PROPESP) of the Universidade Federal do Pará (UFPA).

Competing interest. None.

Ethical standard. All applicable institutional, national, and international guidelines for the care and use of animals were followed. Specimens were collected under the license for collection of biological material (43381) granted by the Instituto Chico Mendes de Conservação da Biodiversidade (ICMBio).

References

Acosta AA, **Franceschini L**, **Zago AC**, **Scholz T, and da Silva RJ** (2017) Six new species of *Heteropriapulus* (Monogenea: Dactylogyridae) from South American fishes with an amended diagnosis to the genus. *Zootaxa* **4290**, 459–482.

Acosta AA, **Mendoza-Palmero CA**, **da Silva RJ, and Scholz T** (2019) 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.* Folia Parasitologica **66**, 1–12.

Acosta AA, **Scholz T**, **Blasco-Costa I**, **Alves PV, and da Silva RJ** (2018) A new genus and two new species of dactylogyrid monogeneans from gills of Neotropical catfishes (Siluriformes: Doradidae and Loricariidae). *Parasitology International* **67**, 4–12.

Boeger WA and Kritsky DC (1997) Coevolution of the Monogenoidea (Platyhelminthes) based on a revised hypothesis of parasite phylogeny. *International Journal for Parasitology* **27**(**12**), 1495–1511.

Boeger WA, **Piasecki W, and Sobecka E** (2002) Neotropical Monogenoidea. 44. Mymarothecium viatorum sp. n. (Ancyrocephalinae) from the gills of Piaractus brachypomus (Serrasalmidae, Teleostei) captured in a warm-water canal of a power plant in Szczecin, Poland. *Acta Ichthyologica et Piscatoria* **2**(**32**), 157–161.

Boeger WA and Vianna RT (2006) Monogenoidea. pp. 42–116 in Thatcher, VE. (Ed), *Aquatic biodiversity in Latin America: Amazon fish parasites*. Moscow, Pensoft Publishers.

Braga MP, **Razzolini E, and Boeger WA** (2015) Drivers of parasite sharing among Neotropical freshwater fishes. *Journal of Animal Ecology* **84**, 487–497.

Bush AO, **Lafferty KD**, **Lotz JM, and Shostak W** (1997) Parasitology meets ecology on its own terms: Margolis et al. Revisited. *Journal Parasitology* **83**, 575–583.

Bychowsky BE and Nagibina LF (1977) The systematic position of some representatives of lower monogeneans frommarine fish. *Parazitologicheski Sbornik* **27**, 7–17 (in Russian).

Desdevises Y, **Morand S**, **Jousson O, and Legendre P** (2002) Coevolution between *Lamellodiscus* (Monogenea, Diplectanidae) and Sparidae (Teleostei): The study of a complex host–parasite system. *Evolution* **56**(**12**), 2459–2471.

Domingues MV and Boeger WA (2008) Phylogeny and revision of Diplectanidae Monticelli, 1903 (Platyhelminthes: Monogenoidea). *Zootaxa* **1698**, 1–40.

Ferreira KDC, Rodrigues ARO, Cunha JM, and Domingues MV (2018) Dactylogyrids (Platyhelminthes, Monogenoidea) from the gills of Hopliasmalabaricus (Characiformes: Erythrinidae) from coastal rivers of the Oriental Amazon Basin: species of Urocleidoides and Constrictoanchoratus n. gen.. *Journal of Helminthology* May;9 **2**(**3**):353–368. doi: 10.1017/S0022149X17000384. Epub 2017 May 15. PMID: 28502254.

Franceschini L, Zago AC, Müller MI, Francisco CJ, Takemoto RM, and da Silva RJ (2017) Morphology and molecular characterization of *Demidospermus spirophallus* n. sp., *D. prolixus* n. sp. (Monogenea: Dactylogyridae) and a redescription of *D. anus* in siluriform catfish from Brazil. *Journal of Helminthology* **92**, 228 – 243.

Franceschini L, Acosta AA, Zago AA, Müller MI, and da Silva RJ (2020) *Trinigyrus* spp. (Monogenea: Dactylogyridae) from Brazilian catfishes: New species, molecular data and new morphological contributions to the genus. *Journal of Helminthology* **94**, e126, 1–15.

Freitas AJB, Bezerra CAM, Meneses YC, Justo MCN, Viana DC, and Cohen SC (2021) Three new species of *Urocleidoides* (Monogenoidea: Dactylogyridae) parasitizing characiforms (Actinopterygii: Characiformes) in Tocantins River, states of Tocantins and Maranhão, and new record for *U. triangulus* in Guandu River, state of Rio de Janeiro, Brazil. *Zoologia* **38**, 1–11.

Gasques LS, Graça RJ, Prioli SM, Takemoto RM, and Prioli AJ (2016) Molecular characterization of *Urocleidoides cuiabai* and *U. malabaricusi* (Monogenea: Dactylogyridae) from the trahira fish *Hoplias* aff. *malabaricus* in the Paraná River, *Brazil.* Journal Helminthology **90**, 693–697.

Guindon S, Dufayard JF, Lefort V, Anisimova M, Hordijk W, and Gascuel O (2010) New algorithms and methods to estimate maximum-likelihood phylogenies: Assessing the performance of PhyML 3.0. *Systematic Biology* **59**, 307–321.

Humason GL (1979) *Animal tissue techniques*. San Francisco, USA, W. H. Freeman. 661 pp.

Jogunoori W, Kritsky DC, and Venkaranarasaiah J (2004) Neotropical Monogenoidea. 46. Three new species from the gills of introduced aquarium fishes in India, the proposal of *Heterotylus* n. g. and *Diaphorocleidus* n. g., and the reassignment of some previously described species of *Urocleidoides* Mizelle & Price, 1964 (Polyonchoinea: Dactylogyridae). *Systematic Parasitology* **58**, 115–124.

Kearse M, Moir R, Wilson A, Stones-Havas S, Cheung M, Sturrock S, Buxton S, Cooper A, Markowitz S, Duran C, Thierer T, Ashton B, Mentjies P, and Drummond A (2012) Geneious Basic: An integrated and extendable desktop software platform for the organization and analysis of sequence data. *Bioinformatics* **28**, 1647–1649.

Kmentová N, Cruz-Laufer AJ, Pariselle A, Smeets K, Artois T, and Vanhove MPM (2022) Dactylogyridae 2022: A meta-analysis of phylogenetic studies and generic diagnoses of parasitic flatworms using published genetic and morphological data. *International Journal for Parasitology* **52**(**7**), 427–457.

Kritsky DC and Thatcher VE (1974) Monogenetic trematodes (Monopisthocotylea: Dactylogyridae) from freshwater fishes of Colombia, South America. *Journal of Helminthology*, **48**, 59–66.

Kritsky DC and Thatcher VE (1983) Neotropical Monogenea. 5. Five new species from aruana, *Osteoglossum bicirrisum* Vandelli, a freshwater teleost from Brazil, with the proposal of *Gonocleithrum* n. gen. (Dactylogyridae: Ancyrocephalinae). *Proceedings of the Biological Society of Washington* **96**, 581–597.

Kritsky DC, Thatcher VE, and Boeger WA (1986) Neotropical Monogenea. Revision of *Urocleidoides* (Dactylogyridae, Ancyrocephalinae). *Proceedings of the Helminthological Society of Washington* **53**, 1–37.

Kritsky DC, Thatcher VE, and Boeger WA (1989) Neotropical Monogenea. 15. Dactylogyrids from the gills of Brazilian Cichlidae with proposal of *Sciadicleithrum* gen. n. (Dactylogyridae). *Proceeding of the Helminthological Society of Washington* **56**, 128–140.

Kritsky DC, Mendoza-Franco EF, and Scholz T (2000) Neotropical Monogenoidea. 36. Dactylogyrids from the gills of *Rhamdia guatemalensis* (Siluriformes: Pimelodidae) from cenotes of the Yucatan Peninsula, Mexico, with proposal of *Ameloblastella* gen. n. and *Aphanoblastella* gen. n. (Dactylogyridae: Ancyrocephalinae). *Journal of the Helminthological Society of Washington* **67**(**1**), 76–84.

Kumar S, Stecher G, Li M, Knyaz C, and Tamura K (2018) MEGA X: Molecular Evolutionary Genetics Analysis across computing platforms. *Molecular Biology and Evolution* **35**, 1547–1549.

Littlewood DTJ and Olson PD (2001) SSU rDNA and the Platyhelminthes: Signal, noise, conflict and compromise. pp. 262–278 in Littlewood DTJ and Bray RA (Eds), *Interrelationships of the platyhelminthes*. London, UK, Taylor & Francis.

Luque JL and Iannacone J (1991) Rhamnocercidae (Monogenea: Dactylogyroidea) in Sciaenidae fishes from Perú, withdescription of Rhamnocercoides menticirrhi n. gen., n. sp. *and two new species of Rhamnocercus.* Revista de BiologiaTropical **39**, 193–201.

Mendoza-Franco EF and Reina RG (2008) Five new species of *Urocleidoides* (Monogenoidea) (Mizelle and price 1964) Kritsky, Thatcher, and Boeger, 1986 parasitizing the gills of Panamanian freshwater fishes. *Journal of Parasitology* **94**(**4**), 793–802.

Mendoza-Franco EF, Aguirre-Macedo ML, and Vidal-MartÍnez VM (2007) New and previously described species of Dactylogyridae (Monogenoidea) from the gills of Panamanian freshwater fishes (Teleostei). *The Journal of Parasitology* **93**(**4**), 761–771.

Mendoza-Franco EF, Mendoza-Palmero CA, and Scholz T (2016) New species of Ameloblastella Kritsky, Mendoza-Franco & Scholz, 2000 and Cosmetocleithrum Kritsky, Thatcher & Boeger, 1986 (Monogenea: Dactylogyridae) infecting the gills of catfishes (Siluriformes) from the Peruvian Amazonia. *Systematic Parasitology* **93**(**9**), 847–862.

Mendoza-Franco EF, Posel P, and Dumailo S (2003) Monogeneans (Dactylogyridae: Ancyrocephalinae) of freshwater fishes from the Caribbean coast of Nicaragua. *Comparative Parasitology* **70**, 32–41.

Mendoza-Franco EF, Reina RG, and Torchin ME (2009) Dactylogyrids (Monogenoidea) parasitizing the gills of *Astyanax* spp. (Characidae) from Panama and Southeast Mexico, a new species of *Diaphorocleidus* and a proposal for *Characithecium* n. *gen.* Journal Parasitology **95**, 46–55.

Mendoza-Franco EF, Caspeta-Mandujano JM, Salgado-Maldonado G, and Matamoros WA (2015) Two new species of *Urocleidoides* Mizelle et Price, 1964 (Monogenoidea) from the gill lamellae of profundulids and poeciliids from Central America and southern Mexico. *Folia Parasitologica* **62**, 1–7.

Mendoza-Palmero CA and Scholz T (2011) New species of *Demidospermus* (Monogenea: Dactylogyridae) of pimelodid catfish (Siluriformes) from Peruvian Amazonia and the reassignment of *Urocleidoides lebedevi* Kritsky and Thatcher, 1976. *Journal Parasitology* **97**(**4**), 586–592.

Mendoza-Palmero CA, Blasco-Costa I, and Scholz T (2015) Molecular phylogeny of Neotropical monogeneans (Platyhelminthes: Monogenea) from catfishes (Siluriformes). *Parasite & Vector* **8**, 1–11.

Mendoza-Palmero CA, Mendoza-Franco EF, Acosta AA, and Scholz T (2019) *Walteriella* n. g. (Monogenoidea: Dactylogyridae) from the gills of pimelodid catfishes (Siluriformes: Pimelodidae) from the Peruvian Amazonia based on morphological and molecular data. *Systematic Parasitology* **96**, 441–452.

Mizelle JD and Blatz V (1941) Studies on monogenetic trematodes VI. Two new dactylogyrid genera from Floridafishes. *American Midland Naturalist* **26**, 105–109.

Mizelle JD and Klucka AR (1953) Studies on monogenetic trematodes. XVI. Dactylogyridae from Wisconsin fishes. *American Midland Naturalist* **49**, 720–733.

Mizelle JD and Kritsky DC (1969) Studies on monogenetic trematodes. XXXIX. Exotic species of Monopithocotylea with the proposal of *Archidiplectanum* gen. n. and *Longihaptor* gen. n. *American Midland Naturalist* **81**, 370–386.

Mizelle JD and Price CE (1963) Additional haptoral hooks in the genus *Dactylogyrus*. *Journal of Parasitology* **49**, 1028–1029.

Mizelle JD and Price CE (1964) Studies on monogenetic trematodes. XXVII. Dactylogyrid species with the proposal of *Urocleidoides* gen. n. *The Journal of Parasitology* **50**(**4**), 579–584.

Mizelle JD and Kritsky DC (1967) Unilatus gen. n., a unique neotropical genus of Monogenea. *Journal of Parasitology* **53**, 1113–1114.

Mizelle JD, Kritsky DC, and Crane JW (1968) Studies on monogenetic trematodes. XXXVIII. Ancyrocephalinae from South America with the proposal of *Jainus* gen. n. *American Midland Naturalist* **80**, 186–198.

Molmar K, Hanek G, Fernando CH (1974) Ancyrocephalids (Monogenea) from freshwater fishes of Trinidad. *The Journal of Parasitology*, **60**(**6**), 914–920.

Monaco HL, Wood RA, and Mizelle JD (1954) Studies on monogenetic trematodes. XVI. Rhamnocercinae, a new subfamily of Dactylogyridae. *American Midland Naturalist* **52**, 129–132.

Moreira J, **Scholz T, and Luque JL** (2015) First data on the parasites of *Hoplias aimara* (Characiformes): Description of two new species of gill monogeneans (Dactylogyridae). *Acta Parasitologica* **60**(**2**), 254–260.

Moreira J, Luque JL, and Šimková A (2019) The phylogenetic position of *Anacanthorus* (Monogenea, Dactylogyridae) parasitizing Brazilian serrasalmids (Characiformes). *Parasite* **26**, 44.

Ñacari LA, **Sepulveda FA**, **Escribano R, and Oliva ME** (2017) *Acanthocotyle gurgesiella* n. sp. (Monogenea: Acanthocotylidae) from the deepsea skate *Gurgesiella furvescens* (Rajidae) in the south-eastern Pacific. *Journal Helminthology* **92**, 223–227.

Oliveira C, **Avelino GS**, **Abe KT**, **Mariguela TC**, **Benine RC**, **Ortí G**, **Vari RP, and Castro RMC** (2011) Phylogenetic relationships within the speciose family Characidae (Teleostei: Ostariophysi: Characiformes) based on multilocus analysis and extensive ingroup sampling. *BMC Evolutionary Biology* **11**, 275.

Oliveira MSB, **Santos-Neto JF**, **Tavares-Dias M, and Domingues MV** (2020) New species of *Urocleidoides* (Monogenoidea: Dactylogyridae) from the gills of two species of Anostomidae from the Brazilian Amazon, Brazilian. *Journal Veterinary Parasitology* **29**(**3**), e007820.

Oliveira GS, **da Silva RJ**, **Vieira FEG, and Acosta AA** (2021) *Urocleidoides* spp. (Monogenea: Dactylogyridae) from the gills of *Parodon nasus* (Characiformes: Parodontidae) from a Brazilian stream with descriptions of two new species. *Zootaxa* **5081**(**4**), 535–550.

Plaisance L, **Rousset V**, **Morand S, and Littlewood TDJ** (2008) Colonization of Pacific islands by parasites of low dispersal ability: Phylogeography of two monogenean species parasitizing butterflyfishes in the South Pacific Ocean. *Journal of Biogeography* **35**, 65–87.

Posada D (2008) J ModelTest: Phylogenetic model averaging. *Molecular Biology Evolution* **25**, 1253–1256.

Price CE and Bussing WA (1968) Monogenean parasites of Costa Rican fishes. *II. Proposal of* Palombitrema heteroancistrium *n. gen., n. sp.* Proceedings of the Helminthological Society **35**(**1**), 54–57.

Rambaut A (2012) *FigTree v1.4. Molecular evolution, phylogenetics and epidemiology*. Available at http://tree.bio.ed.ac.uk/software/figtree/ (accessed 26 June 2020).

Rambaut A, **Suchard MA**, **Xie D, and Drummond AJ** (2014) Tracer v1.6. World Wide Web electronic publication. http://tree.bio.ed.ac.uk/software/tracer/.

Rasband WS (2016) *ImageJ*. US National Institute of Health, Bethesda, Maryland, USA. Available at http://imagej.nih.gov/ij/ (accessed 02 January 2020).

Ronquist F and Huelsenbeck JP (2003) MrBayes 3: Bayesian phylogenetic inference under mixed models. *Bioinformatics* **19**, 1572–1574.

Rosim DF, **Mendoza-Franco EF, and Luque JL** (2011) New and previously described species of *Urocleidoides* (Monogenoidea: Dactylogyridae) infecting the gills and nasal cavities of *Hoplias malabaricus* (Characiformes: Erythrinidae) from Brazil. *Journal of Parasitology* **97**(**3**), 406–417.

Rossin MA and Timi JT (2016) Dactylogyrid monogeneans parasitising *Cyphocharax voga* (Hensel) (Teleostei: Curimatidae) from the Pampas region, Argentina: New and previously described species. *Systematic Parasitology* **93**, 701–714.

Suriano DM (1997) The genus *Urocleidoides* Mizelle and Price, 1964 (Monogenea: Ancyrocephalidae) parasitizing characoidei fishes in Argentina. *Physis* **53**, 1–6.

Thompson JD, **Higgins DG, and Gibson TJ** (1994) CLUSTAL W: Improving the sensitivity of progressive multiple sequence alignment through sequence weighting, position-specific gap penalties and weight matrix choice. *Nucleic Acids Research* **22**, 4673–4680.

Wu XY, **Zhu XQ**, **Xie MQ, and Li AX** (2006) The radiation of *Haliotrema* (Monogenea: Dactylogyridae: Ancyrocephalinae): Molecular evidence and explanation inferred from LSU rDNA sequences. *Parasitology* **132**, 659–668.

Yamada FH, **Brandão H**, **Yamada POF, and da Silva RJ** (2015) *Philocorydoras longus* n. sp. (Monogenea, Dactylogyridae) from the gills of *Hoplosternum littorale* (Siluriformes, Callichthyidae) in Southeastern Brazil and the reassignment of two species from the genus *Urocleidoides* to *Philocorydoras*. *Helminthologia* **52**, 331–335.

Zago AC, **Franceschini L**, **Müller MI, and da Silva RJ** (2018) A new species of *Cacatuocotyle* (Monogenea, Dactylogyridae) parasitizing *Astyanax* spp. (Characiformes, Characidae) from Brazil, including molecular data and a key to species identification. *Acta Parasitological* **63**(**2**), 261–269.

Zago AC, **Yamada FH**, **Yamada POF**, **Franceschini L**, **Bongiovani MF, and da Silva RJ** (2020) Seven new species of *Urocleidoides* (Monogenea: Dactylogyridae) from Brazilian fishes supported by morphological and molecular data. *Parasitology Research* **119**(**10**), 3255–3283.