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

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**ABSTRACT.** Three new species of *Urocleidoides* Mizelle & Price, 1964 are described from the gills of characiform fishes in the Tocantins River and its tributaries. *Urocleidoides boulengerellae* sp. nov. is described from *Boulengerella cuvieri* (Spix & Agassiz, 1829) and differs from all its congeners by the dorsal bar with a long posteromedial projection; male copulatory organ with 2–3 counterclockwise rings and a base with a flange; an accessory piece comprising a robust Y-shaped unit and a sheath-like unit; and a highly sclerotized vaginal canal. *Urocleidoides paratriangulus* sp. nov., described from *Psectrogaster amazonica* Eigenmann & Eigenmann, 1889, *Cyphocharax gouldingi* Vari, 1992, *Caenotropus labyrinthicus* Kner, 1858 and *Mylesinus paucisquamatus* Jégu & Santos, 1988, is most similar to *Urocleidoides triangulus* (Suriano, 1981) Rossin & Timi, 2016 based on the shape of the anchors and bars but differs from *U. triangulus* in the morphology of the projection of the dorsal bar, the number of rings of male copulatory organ, and by the smaller size of members of hook pairs 1 and 5 compared with those of the remaining pairs. *Urocleidoides tocantinensis* sp. nov. is easily distinguished from all other species of the genus by the morphology of the vagina, which present a vaginal vestibule with a membranous cap. *Urocleidoides triangulus* is reported from its type host in the Guandu River, state of Rio de Janeiro. The present study increases the number of *Urocleidoides* species to 37 recognized species that fit all the generic characters.

**KEY WORDS.** Ectoparasites, fishes, morphology, Neotropical Region, Platyhelminthes, taxonomy.

**INTRODUCTION**

*Urocleidoides* was proposed by Mizelle and Price (1964) for a new species, *Urocleidoides reticulatus* Mizelle & Price, 1964 from the gills of *Poecilia reticulata* Peters (Poeciliidae), which was collected from Capitol Aquarium, Sacramento, California, USA. A few years later, 12 species were described within this genus, from the gills of fish belonging to the orders Characiformes, Cyprinodontiformes, Gymnotiformes and Siluriformes (Mizelle et al. 1968, Mizelle and Kritsky 1969, Kritsky and Leiby 1972). Subsequently, Molnar et al. (1974) described eight new species from Trinidad and Tobago and transferred to this genus two species from *Cleidodiscus* Mueller, 1934, based on the emended diagnosis provided by Mizelle et al. (1968), which expanded the bounds of *Urocleidoides*. Kritsky et al. (1986) revised the generic diagnosis, described new species and reviewed the material belonging to known species. These authors provided redescriptions and restricted the genus to the species that presented a sinistral vaginal sclerite. Twenty-three species were thus considered incertae sedis, which reduced the number of species in the genus to five. Currently, the genus comprises 34 recognized species described in the Neotropical Region (Argentina, Brazil,
Colombia, El Salvador, Panama, Peru, Trinidad and Tobago and Mexico), that are parasites of Characiformes, Gymnotiformes and Cyprinodontiformes (Kritsky and Thatcher 1974, Molnar et al. 1974, Suriano 1997, Kritsky et al. 1986, Mendoza-Franco et al. 2007, 2015, Mendoza-Franco and Reina 2008, Rosim et al. 2011, Moreira et al. 2015, Rosin and Timi 2016, Ferreira et al. 2017, Oliveira et al. 2020, Zago et al. 2020). Although species of *Urocleidoides* have a wide distribution in the tropics, there are still few studies documenting the diversity of Monogenoidea in the Neotropical Region, considering the great biodiversity of host species. Among the species that were considered incertae sedis, eight remain uncertain and 16 have been allocated to other genera (Kritsky et al. 1986, 1989, 2000, Jogunoiri et al. 2004, Mendoza-Franco et al. 2009, Yamada et al. 2015, Acosta et al. 2019).

During studies on the helminth fauna of fish in the Tocantins River, characiform fish, including *Boulengerella cuvieri* (Spix & Agassiz, 1829) (Ctenoluciidae), *Cyphocharax gouldingi* Vari, 1992 (Curimatidae), *Psectrogaster amazonica* Eigenmann & Eigenmann, 1889 (Curimatidae), *Myxelina paucisquama* Jégú & Santos, 1988 (Serrasalmidae) and *Caenotropus labyrinthicus* (Kner, 1858) (Chilodontidae) were examined. Characiformes is the one of the largest orders of freshwater fish, with at least 2300 valid species distributed in 520 genera (Nelson et al. 2016). These fish harbor a great diversity of helminths. However, no monogenoids have previously been described or reported from *B. cuvieri*, *P. amazonica*, *C. labyrinthicus* or *C. gouldingi*, while *Notozotheicum bethei* Kritsky, Boeger & Jégú, 1996 was reported from *M. paucisquama* collected in the Tocantins River by Kritsky et al. (1996). In the current paper, three new species of *Urocleidoides* are described and a new distributional record for *Urocleidoides triangulatus* (Suriano, 1981) Rossin & Timi, 2016 is presented.

**MATERIAL AND METHODS**

During expedition carried out in 2010 from the middle part of the Tocantins River, in the states of Maranhão and Tocantins, were collected 32 samples of *B. cuvieri* (14.5–40.8 cm in standard length and 35.3–551.0 g in weight), six of *C. gouldingi* (16.1–17.9 cm in standard length and 50–76 g in weight), six of *M. paucisquama* (12.3–15.5 cm in standard length and 65.2–158.2 g in weight) and seven of *C. labyrinthicus* (11.1–14.1 cm in standard length and 36–71 g in weight). These were identified by the specialists of the Laboratório de Sistemática e Ecologia de Organismos Aquáticos (LASEOA), Universidade Estadual do Maranhão (UEMA). These fish were caught in nets and immediately packed in Styrofoam boxes filled with ice and taken to the Laboratório de Anatomia, Universidade Estadual da Região Tocantina do Maranhão (Uemasul), for material processing. The fish sample collection protocol and laboratory procedures were approved by the Research Ethics Committee of Universidade Estadual do Maranhão, under protocol number 21/2017, and the environmental collection license was obtained from the System for Authorization and Information on Biodiversity (SISBIO), under protocol number 61650–1. The gills were removed from the fish and placed in vials containing hot water (65 °C), which were then shaken. Formalin was added to reach a concentration of 5%.

Parasitological indexes were calculated as proposed by Bush et al. (1997), followed by standard deviation.

Monogenoids were picked out from the sediment and gill filaments in the laboratory with the aid of a stereoscopic microscope. Some specimens were mounted in Hoyer’s medium so that the sclerotized parts could be studied and others were stained with Gomori’s trichrome to study the internal organs of the parasite (Humason 1979). Measurements are presented in micrometers; range values are followed by mean and number of structures measured in parentheses. Measurements on the sclerotized structures of the haptor (bar and anchors) were made in accordance with the scheme shown in Figs 1–3. Morphometric studies were performed through ImageJ (Wayne 2010). This software is distributed by the National Institutes of Health (NIH), available at https://imagej.nih.gov/ij/download.html. Pictures were taken using a digital camera (Sony MPEG Movie EX DSC-S75) coupled to the microscope. The specimens studied were deposited in the ‘Coleção Helmintológica do Instituto Oswaldo Cruz (CHIOC)’ and in the collection of the ‘Instituto Nacional de Pesquisas da Amazônia’ (INPA) in Brazil.

![Figures 1–3. Scheme of measurements of the sclerotized structures of the haptor and male copulatory organ (MCO) of *Urocleidoides* spp.: (1) anchor: (a) base, (b) total length; (2) ventral bar: (a) length, (b) medial projection; (3) dorsal bar: (a) length.](image-url)
TAXONOMY

Class Monogenoidea Bychowsky, 1937
Subclass Polyxenidea Bychowsky, 1937
Order Dactylogyridae Bychowsky, 1937

Urocleidoides Mizelle & Price, 1964

Urocleidoides boulengerellae sp. nov.
Figs 4–11, 31, 32

http://zoobank.org/3E609A35-9326-4217-83FF-37D5C33435D5

Type host. Boulengerella cavieri (Spix & Agassiz) (Cteno-luciidae).

Type locality. Tocantins River (8°22′55.9″ S; 48°07′04.4″ W), near the municipality of Tupiratins, state of Tocantins, Brazil.

Other localities. Arrais River (12°37′52.3″ S; 47°08′11.2″ W), close to the municipality of Babaculândia, state of Tocantins; Tocantins River (6°32′24.53″ S; 47°27′0.75″ W), close to the municipalities of Aguiarimópolis and Estreito; at the mouth of the Itaueiras River (6°29′58.73″ S; 47°25′27.48″ W), in the municipality of Estreito, state of Maranhão, Brazil.

Infestation parameters. Total number of hosts: 32; prevalence: 91%; total number of parasites: 876; mean intensity: 30.2±26.5; range of intensity: 2–113.

Deposited material. Holotype: CHIOC: 39560, paratypes: CHIOC 39561, 39562a-c, 39563a-b, 39564a-b, 39565, 39566; INPA 833, 834.

Description. Based on 137 specimens: 9 mounted in Gomori’s trichrome and 128 mounted in Hoyers’ medium: Body fusiform, delicat, 310–530 (363; n = 24) long, 63–140 (102; n = 27) wide. Tegument smooth. Cephalic region with 2 lateral lobes and 2 anterolateral slightly developed; four bilateral pairs of head organs. Eyespots absent; accessory chromat granules present in cephalic area, Mouth subterminal, midventral; Pharynx muscular, spherical; esophagus short; two intestinal caeca, posteriorly confluent to gonads, lacking diverticula. Haptor sub-hexagonal, presenting ventral anchors connected by ventral bar and dorsal anchors connected by dorsal bar, 62–112 (94; n = 13) wide (Fig. 4). Ventral anchor with well-developed roots: protruding superficial root, rectangular in shape, deep root distally round, straight shaft and acute point, 26–44 (35; n = 43) long, base 13–26 (17; n = 31) (Fig. 8); dorsal anchor with developed roots, straight shaft and long point, 23–30 (28; n = 33) long, base 10–21 (12; n = 30) (Fig. 9). Ventral bar straight and robust, with anteromedian groove and slight protuberances at the end, 35–45 (39; n = 27) long (Fig. 10). Dorsal bar recurved, 32–40 (37; n = 14) long, with a long postmedian projection, 9–15 (12; n = 24) long (Fig. 11). Seven pairs of marginal hooks present, ancyrocephaline distribution, five pairs ventral and two dorsal. Hooks similar in shape; pairs 1 and 5 slightly smaller than other pairs: each with protruded thumb, curved point, straight shank, and very short filamentous hook loop about 1/6 shank length (Fig. 7). Pair 1, 10–22 (16; n = 15) long, pair 2, 18–30 (23; n = 24) long, pair 3, 19–38 (24; n = 37) long, pair 4, 16–36 (24; n = 38) long, pair 5, 15–25 (19; n = 9) long, pair 6, 20–33 (29; n = 23) long, pair 7, 16–27 (18; n = 10) long. Copulatory complex comprising male copulatory organ (MCO) and non-articulated accessory piece. MCO with 2–3 counterclockwise rings, base with flange, 61–131 (95; n = 17). Accessory piece comprising a robust Y-shaped unit and a sheath-like unit (Figs 6, 31). Testes dorsal to germarium; seminal vesicle a distal dilation of vas deferens; single prostatic reservoir present. Germarium elongated (Fig. 4). Vaginal canal a highly sclerotized tube, which coils around vaginal acrite, connected with seminal receptacle, located anteriorly to germarium; vaginal opening ventrolateral, sinistral; vaginal acrites present, robust, sinistral, composed of straight rod distally hooked, with a short subterminal projection, 38–50 (41; n = 11) (Figs 5, 32). Eggs, Mehlis′ glands and ootype not observed. Vitellaria present, distributed throughout the body, except in area of reproductive organs (Fig. 4).

Etymology. The specific name refers to the scientific name of the host.

Remarks. The new species is allocated in Urocleidoides by the presence of vaginal acrite, MCO with counterclockwise rings and pairs 1 and 5 reduced in size. Urocleidoides boulengerellae sp. nov. can be differentiated from all other species of the genus mainly by the morphology of the copulatory complex and through the highly sclerotized vaginal canal. Urocleidoides boulengerellae sp. nov. is most similar to Urocleidoides neotropicalis Mendoza-Franco & Reina, 2008 and Urocleidoides piratiti Mendoza-Franco & Reina, 2008, by the long posteroanterior projection in the dorsal bar. However, the new species differs from U. neotropicalis by the morphology of the male copulatory organ (2–3 rings in U. boulengerellae sp. nov. and a coil of about 5½ counterclockwise rings in U. neotropicalis), while it differs from U. piratiti by the shape of the subunits of the accessory piece (an Y-shaped, robust and a sheath-like unit in U. boulengerellae sp. nov. and dextral subunit terminally acute; sinistral subunit bottle-shaped in U. piratiti).

Urocleidoides paratriangulus sp. nov.
Figs 12–21, 33, 34

http://zoobank.org/3C18E487-2368-4587-B800-2A7F03AAE9AA

Type host. Psectrogaster amazonica Eigenmann & Eigenmann (Curimatidae).

Type locality. Tocantins River (5°27′50″S; 47°33′48″W), close to the municipality of Embiral, state of Maranhão.

Other hosts and localities. Psectrogaster amazonica: Tocantins River (5°32′08.6″S; 47°29′41.1″W), close to the urban perimeter of Imperatriz, state of Maranhão. Cyphocharax Gouldingi (Curimatidae): Tocantins River (6°32′24.53″S; 47°27′0.75″W), close to the municipalities of Aguiarimópolis and Estreito; at the mouth of the Itaueiras River (6°29′58.73″S; 47°25′27.48″W), in the municipality of Estreito, state of Maranhão.

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of Estreito, state of Maranhão. *Caenotropus labyrinthicus* (Chilo-
dontidae): Arraias River (12°37'52.3''S; 47°08'11.2''W), close to
the municipality of Babaçulândia, state of Tocantins; Tocantins
River (6°32'24.53''S, 47°27'0.75''W), close to the municipalities of
Aguiarnópolis and Estreito; at the mouth of the Itaueiras River
(6°29'58.73''S; 47°25'27.48''W), municipality of Estreito, state of
Maranhão; João Aires River (7°51’10.6’’S; 47°55’57.3’’W), close to
the municipality of Palmeirantes, state of Tocantins; Farinha River
(6°50’30.5’’S; 47°30’05.8’’W), close to the municipality of Estreito,
state of Maranhão, Brazil. *Mylesinus paucisquamatus* Jégu & Santos
(Serrasalmidae): Arraias River (12°37’52.3’’S; 47°08’11.2’’W), close
to the municipality of Babaçulândia, state of Tocantins; Farinha
River (6°50’30.5’’S; 47°30’05.8’’W), close to the municipality of
Estreito, state of Maranhão, Brazil.

Figures 4–11. *Urocleidoides boulengerellae* sp. nov. from *Boulengerella cuvieri* from Tocantins River: (4) total, ventral view; (5) vaginal sclerite
and vagina; (6) copulatory complex, ventral view; (7) hook; (8) ventral anchor; (9) dorsal anchor; (10) ventral bar; (11) dorsal bar. Scale
bars: 4 = 100 µm, 5 = 20 µm, 6 = 30 µm, 7 = 10 µm, 8–11 = 20 µm.
Figures 12–21. *Urocleidoides paratriangulus* sp. nov. from *Psectogaster amazonica* from Tocantins River: (12) copulatory complex, ventral view; (13) vaginal sclerite; (14) vagina; (15, 16) dorsal bar; (17) ventral bar; (18) ventral anchor; (19) dorsal anchor; (20) hook pairs 1, 5; (21) hook pairs 2–4, 6, 7. Scale bars: 12 = 10 µm, 13–14 = 10 µm, 15–17 = 20 µm, 18–19 = 20 µm, 20 = 5 µm, 21 = 10 µm.
Infestation parameters. *Psectrogaster amazonica*: total number of hosts: 97; prevalence: 11.3%; total number of parasites: 37, mean intensity: 3.1 ± 2.5, range of infection: 1–9; *Caenotropus labirynthicus*: total number of hosts: 8; number of infected hosts: 3; total number of parasites: 4; *Cyphocharax gouldingi*: total number of hosts: 8; number of infected hosts: 1; total number of parasites: 2; *Mylesinus paucisquamatus*: total number of hosts: 7; number of infected hosts: 1; total number of parasites: 10.

Deposited material. Holotype: *Psectrogaster amazonica*: CHIOC: 39567a; paratypes CHIOC 39567b, 39571, 39572, 39573, 39574, INPA 836, 837. *Cyphocharax gouldingi*: CHIOC: 39568a-b. *Caenotropus labirynthicus*: CHIOC: 39570, *Mylesinus paucisquamatus*: CHIOC: 39569a-c, INPA 835.

Description. Based on 51 specimens mounted in Hoyers’ medium: Body fusiform, robust 195–402 (290; n = 15) long by 65–132 (103; n = 15) wide. Cephalic region with cephalic lobes poorly developed; four bilateral pairs of head eyes. Eyespots absent; accessory chromatic granules dispersed in the cephalic region. Mouth subterminal, midventral; pharynx spherical, esophagus short; two intestinal caeca, confluent posteriorly to testes. Haptor sub-hexagonal, 60–105 (83; n = 15) wide (Fig. 34). Ventral anchor with superficial root elongated, round deep root knob-like, straight shaft and short point, 60–105 (83; n = 15) long, base 13–31 (22; n = 38) (Fig. 18). Dorsal anchor with well-developed elongated superficial root and inconspicuous deep root, short shaft and long point, 26–50 (36; n = 27) in length and base 15–30 (22; n = 28) (Fig. 19). Ventral bar straight, with an anteromedian groove and rounded extremities, anteriorly directed, 24–45 (33; n = 15) long (Fig. 17). Dorsal bar V-shaped, postero-median projection 19–38 (24; n = 12) long, with two variations: a slender or a more robust projection with lateral allae in the new species; the number of rings of MCO (2.5 to 3 in *U. triangulus* and about two in the new species); and by the reduced size of hooks (pairs 1, 5 and 7 reduced in size in *U. triangulus* and 1 and 5 only in *U. paratriangulus* sp. nov.). Only five species of *Urocleidoides* possess a medial projection on the posterior margin of the dorsal bar: *Urocleidoides curimatae* Molnar, Henek & Fernando, 1974; *U. neotropicalis*; *U. piria-tius*; *Urocleideoa tenus* Zago, Yamada, Yamada, Franceschini, Bongiovani & Silva, 2020; and *U. boulengerellae* sp. nov. The medial projection is slender than the bar arms in the five species, whereas in *U. triangulus* and in some specimens of *U. paratriangulus* sp. nov., the projection is thicker than the arms. *Urocleidoides paratriangulus* is similar to *U. curimatae* and *U. tenis* also in terms of the triangular shape of the ventral anchor, but it can be differentiated by the number of coils and the length of the MCO (3 coils in *U. paratriangulus* sp. nov. vs 1.5 coils in *U. curimatae* and 7.5 in *U. tenis*), as well as through the morphology of the accessory piece (curved shaft in *U. paratriangulus* sp. nov., straight in *U. curimatae* and pincer-shaped in *U. tenis*). During a study carried out in the Guandu River by the laboratory team, specimens of *U. triangulus* were found parasitizing *Cyphocharax gibert* (Quoy & Gaimard, 1824). The morpomery of the specimens studied herein were used to make comparisons with those of *U. paratriangulus* sp. nov. This was the first record in this host in Brazil.

*Urocleidoides tocantinensis* sp. nov.

Figs 22–30, 35, 36

http://zoobank.org/96A69E56-0836-4AC2-85A3-3C486B873C33

Type host. *Psectrogaster amazonica* Eigenmann & Eigenmann (Curimatidae).

Type locality. Tocantins River (5°27’50’’ S; 47°33’48’’ W), close to the municipality of Embiral, state of Maranhão.

Other hosts and localities. *Psectrogaster amazonica*: Tocantins River (5°32’08.6’’ S; 47°29’41.1’’ W), close to the urban perimeter of Imperatriz, state of Maranhão. *Mylesinus paucisquamatus* (Serrasalmidae): Arraiças River (12°37’ 52.3’’ S; 47°08’11.2’’ W), close to the municipality of Baciaulândia, state of Tocantins; Fariinha River (6°50’30.5’’ S; 47°30’05.8’’ W), close to the municipality of Estreito, state of Maranhão, Brazil.

Infestation parameters. *Psectrogaster amazonica*: total number of hosts: 97; prevalence: 9.3%; total number of parasites: 11; mean intensity: 1.22 ±0.44; range of infection: 1–2; *Mylesinus paucisquamatus*: total number of hosts: 7; number of infected hosts: 2; total number of parasites: 12.

Etymology. The specific name refers to the similarity with *Urocleidoides triangulus*.

Remarks. *Urocleidoides paratriangulus* sp. nov. is similar to *U. triangulus* considering the shape of the anchors and bars. The new species differs from *U. triangulus* by the projection of the dorsal bar (prominent postero-median process in *U. triangulus* and slender or a more robust projection with lateral allae in the new species); the number of rings of MCO (2.5 to 3 in *U. triangulus* and about two in the new species); and by the reduced size of hooks (pairs 1, 5 and 7 reduced in size in *U. triangulus* and 1 and 5 only in *U. paratriangulus* sp. nov.).
Figures 22–30. *Urocleidoides tocantinensis* sp. nov. from *Psectogaster amazonica* from Tocantins River: (22) copulatory complex, ventral view; (23) vagina; (24) ventral bar; (25) vaginal sclerite; (26) dorsal bar; (27) ventral anchor; (28) dorsal anchor; (29) hook pairs 2–4, 6, 7; (30) hook pairs 1, 5. Scale bars: 22, 23, 27, 28 = 20 µm, 24–26, 29 = 10 µm, 30 = 5 µm.
Deposited material. *Psectrogaster amazonica*: Holotype CHIOC 39575: paratypes 39577, 39578; INPA 838; *Mylesinus paucisquamatus*: CHIOC 39576a-b, INPA 839.

Description. Based on 15 specimens: 2 mounted in Gomori’s trichrome and 13 mounted in Hoyers’ medium. Body fusiform, robust, 200–317 (278; n = 8) long by 68–103 (89; n = 9). Cephalic lobes poorly developed; two pairs of eyespots, posterior pair larger than anterior; accessory chromatic granules dispersed in the cephalic region. Pharynx spherical; esophagus short; two intestinal caeca, posteriorly confluent to gonads.

Figures 31–36. Light photomicrographs of *Urocleidoides* spp.: (31, 32) *Urocleidoides boulengerellae*: (31) copulatory complex; (32) vaginal sclerite; (33, 34) *Urocleidoides paratriangulus*: (33) copulatory complex; (34) haptor; (35, 36) *Urocleidoides tocantinensis*: (35) copulatory complex; (36) vagina. Scale bars: 31–33, 35–36 = 20 µm, 34 = 40 µm.
lacking diverticula. Haptor sub-hexagonal, 62–86 (68; n = 12) wide. Ventral anchor with developed superficial root and inconspicuous deep root, evenly curved shaft and point, 21–44 (33; n = 22) long and base 13–20 (17; n = 22) (Fig. 27). Dorsal anchor, smaller than ventral, with well-defined and long superficial root, shorter deep root, evenly curved shaft and robust point, passing from the level of tip of superficial root, 15–29 (22; n = 18) long and base 10–19 (13; n = 16) (Fig. 28). Ventral bar straight, with extremities directed toward posterior extremity, with a median projection arising from the middle portion of the bar, 23–34 (30; n = 9) long (Fig. 24). Dorsal bar straight, 25–41 (30; n = 6) long (Fig. 26). Marginal hooks present, dissimilar in shape: pairs 1 and 5 with straight shank, erected thumb and curved point; filamentous hook (FH) loop about 1/3 of shank length (Fig. 30), pairs 2–4, 6, 7 with dilated shank composed of two subunits, erected thumb and point, FH loop about 1/3 shank length (Fig. 29). Pair 1, 9–16 (13; n = 15); pair 2, 15–27 (19; n = 19); pair 3, 14–22 (18; n = 18); pair 4, 15–27 (17; n = 17); pair 5, 10–15 (13; n = 14); pair 6, 15–25 (20; n = 6); pair 7, 13–25 (20; n = 14). Copulatory complex composed of male copulatory organ (MCO), which is a straight tube, 23–40 (33; n = 14) long and by bifurcated accessory piece, serving as guide to MCO; accessory piece 41–70 (53; n = 15) long (Figs 22, 35). Gonads overlapping. Vaginal pore sinistral, vaginal vestibule, with a membranous cap (Fig. 23, 36). Vaginal sclerite composed of a grooved rod, distal hook and a long subterminal projection, 22–35 (27; n = 11) (Fig. 25). Eggs, Mehlis’ glands and ootype not observed. Vitelline follicles distributed throughout the body, except in the region of reproductive organs.

Etymology. The specific name refers to the locality, Tocantins River.

Remarks. Urocleidoides tocantinensis sp. nov. resembles Urocleidoides falxus. Zago, Yamada, Yamada, Franceschini, Bongiovani & Silva, 2020 by the absence of coils on the MCO and Urocleidoides surinamica Rosin & Timi, 2016 in the shape of accessory piece, but differs in the morphology of the MCO (MCO reverse J-shaped, with expanded proximal end in U. surinamica and a straight tube in the new species). The new species differs from all other species of the genus by the morphology of the vagina, which present a vaginal vestibule with a membranous cap.

**DISCUSSION**

To date, 34 species of *Urocleidoides* are known, described from 44 different host species. *Urocleidoides* is mainly characterized by the presence of a sclerotized structure located in the median region of the body, named vaginal sclerite. At present, species of *Urocleidoides* are found in fishes from Argentina, Brazil, Colombia, El Salvador, Guatemala, Mexico, Panama and Trinidad and Tobago. Although there is not enough information to reconstruct the historical associations of *Urocleidoides* spp., there is plenty of evidence that their lineages can parasitize a diverse range of host, from the fact that they are parasites of 10 different families belonging to three orders (Characiformes, Cyprinodontiformes and Gymnotiformes) (Mizelle and Price 1964, Kritsky et al. 1986, Moreira et al. 2015, Ferreira et al. 2017). A phylogenetic analysis using morphological and molecular data has suggested that Characiformes is a sister group of Gymnotiformes (Briggs 2005). However, the parasite data is still at too early a stage to be able to say whether divergence between these two latter fish groups in South America might also represent the earliest phylogenetic split of *Urocleidoides* in the tropics (Saitoh et al. 2003, Briggs 2005, Mendoza-Franco and Reina 2008).

Species of *Urocleidoides* have also been found in aquarium fishes, generally those collected from the native habitats in the Neotropical Region, such as *U. reticulatus* from *Poeclia reticulata* and *Urocleidoides vaginolastrum* Jogunoori, Kritsky & Venkatnarasiah, 2004, from *Xiphophorus hellerii* Heckel, 1848 (type host). Hosts of these two species have been introduced into aquaria and ponds in Israel, Czech Republic, India, California (USA), and central Mexico (see Kritsky et al. 1986, Jogunoori et al. 2004, Mendoza-Palmero & Aguilar-Aguilar 2008).

*Urocleidoides boulengerellae* sp. nov. was found only in one host species, *B. cuvieri*, with a high prevalence, mean intensity, and abundance. In Brazil, the distribution of *B. cuvieri* is restricted to the Amazon and Tocantins-Araguaia basins, in the states of Pará, Amapá, and north of Mato Grosso. The new species was not found in any other host examined in the present study, and thus can be considered to be a specialist, as the majority species of the genus. On the contrary, *U. tocantinensis* sp. nov. was found in host species belonging to different families: *M. paucisquamatus* (Serrasalmidae) and *P. amazonica* (Curimatidae), likewise, *U. paratriangulus* sp. nov. was found in hosts of different families, thus demonstrating that these species are more generalist. This scenario is similar to what has been observed for a few other species of this genus, such as *Urocleidoides eremitus* Kritsky, Thatcher & Boeger, 1986 which was found parasitizing hosts belonging to Anostomidae and Erythrinidae. All of the remaining species that occur in more than one host species are restricted to a single host family.

Rosin et al. (2011) postulated that the presence of a ventral bar with enlarged extremities may be also a characteristic that can be considered to be diagnostic for *Urocleidoides*, in addition to those proposed by Kritsky et al. (1986) in the revision of the genus. Zago et al. (2020) proposed an amended diagnosis for the genus, considering the recent discovery of new *Urocleidoides* species. Among these features considered was the absence of coil in the MCO, which groups together *U. falxus* and *Urocleidoides tocantinensis* sp. nov.

*Urocleidoides triangulus* was originally described from *C. gilbert*, as *Andropira triangula* from the Chascomús lagoon, Argentina, by Suriano (1981). Suriano (1997) provided a redescription of the species and proposed a new combination, allocating the species in *Palombitrema*, as *P. triangula*. Rosin and Timi (2016) studied the monogenoidean fauna of *Cyphochilax voga*.
1870): they found this species and proposed a new combination, U. triangulus, based on having identical morphology of the copulatory complex, hooks and internal organs, specially by the presence of a vaginal sclerite. Urocleidoides triangulus has been reported parasitizing different species of Cyphochilarax: C. voga (Rosin and Timi 2016), C. gibert in Argentina (Suriano 1981, 1997), C. modestus (Fernández-Yépez) (Abdallah et al. 2015) and C. nagellii in Brazil (Steindachner) (Vieira et al. 2013, Abdallah et al. 2015). The present report provides the first record in the type host in Brazil.

The data obtained in the present study increases the number of Urocleidoides species to 37 and shows that further studies are necessary to clarify the morphological characteristics that limits the diagnosis of this genus.

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**LITERATURE CITED**

Abdallah VD, Azevedo RK, Luque JL (2015) First record of Palombitrema triangulum (Suriano, 1981) Suriano, 1997 (Monogenea: Dactylogyridae) from freshwater fishes in Brazil. Brazilian Journal of Biology 75: 229–233. https://doi.org/10.1590/1519-6984.12913

Acosta AA, Mendoza-Palmero CA, Silva RJ, 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: 004. https://doi.org/10.14411/fp.2019.004

Briggs JC (2005) The biogeography of otophysan fishes (Ostariophysi: Otophysi): A new appraisal. Journal of Biogeography 32: 287–294. https://doi.org/10.1111/j.1365-2699.2004.01170.x

Bush AO, Lafferty KD, Lotz JM, Shostak AW (1997) Parasitology meet ecology on its own terms: Margolis et al. revisited. Journal of Parasitology 83: 575–583.

Ferreira KDC, Rodrigues ARO, Cunha JM, Domingues MV (2017) Dactylogyrids (Platyhelminthes, Monogeneida) from the gills of Hoplias malabaricus (Characiformes: Erythrinidae) from coastal rivers of the Oriental Amazon Basin: species of Urocleidoides and Constrictoanchorhatus n. gen. Journal Helminthology 92: 3535–368. https://doi.org/10.1017/S0022149X17000384

Humason GL (1979) Animal Tissue Techniques. W.H. Freeman, San Francisco, 4th ed., 468 pp.

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

Kritsky DC, Boeger WA, Jego M (1996) Neotropical Monogenea. 28. Anocyrocephalinae (Dactylogyridae) of piranha and their relatives (Teleostei, Serrasalmidae) from Brazil and French Guiana: species of Notozothecium Boeger and Kritsky, 1988, and Myxentriophycus gen. n. Journal of Helminthological Society of Washington 63: 153–175.

Kritsky DC, Leiby PD (1972) Dactylogyridae (Monogenea) from the freshwater fish, Astyanax fasciatus (Cuvier), in Costa Rica, with descriptions of Jainus hexops sp. n., Urocleidoides costaricensis, and U. heterocephylus n. combs. n. Proceedings of the Helminthological Society of Washington 39: 227–230

Kritsky DC, Mendoza-Franco EF, Scholz T (2000). Neotropical Monogenea. 36. Dactylogyrids from the gills of Rhamdia guatemalensis (Siluriformes: Pimelodidae) from cenarios of the Yucatan Peninsula, Mexico with proposal of Ameloblastella gen. n. and Aphanoblastella gen. n. (Dactylogyridae, Anocyrocephalinae). Comparative Parasitology 67: 76–84.

Kritsky DC, Thatcher V (1974) Monogeneric trematodes (Mono- pisthocotylea: Dactylogyridae) from freshwater fishes of Colombia, South America. Journal of Helminthology 48: 59–66.

Kritsky DC, Thatcher VE, Boeger WA (1986) Neotropical Monogenea. 8. Revision of Urocleidoides (Dactylogyridae, Anocyrocephalinae). Proceedings of the Helminthological Society of Washington 53: 1–37.

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

Mendoza-Franco EF, Aguirre-Macedo ML, Vidal-Martínez VM (2007) New and previously described species of Dactylogyridae (Monogenea) from the gills of Panamanian freshwater fishes (Teleostei). Journal of Parasitology 93: 761–771. https://doi.org/10.1645/GE-1068R.1

Mendoza-Franco EF, Caspeta-Mandujano JM, Salgado-Maldonado G, Maramoros WA (2015) Two new species of Urocleidoides Mizelle et Price, 1964 (Monogenea) from the gill lamellae of profundulids and poecilids from Central America and southern Mexico. Folia Parasitologica 62: 059. https://doi.org/10.14411/fp.2015.059
Mendoza-Franco EF, 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. The Journal of Parasitology 94: 793–802. https://doi.org/10.1645/GE-1438.1

Mendoza-Franco EF, Reina RG, 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 Characichthyes n. gen. The Journal of Parasitology 95: 46–65. https://doi.org/10.1645/GE-1592.1

Mendoza-Palmero CA, Aguilar-Aguilar R (2008) Record of Urocleidoides vaginoclastrum Jorgunooori, Kritsky and Venkatanarasalal, 2004 (Monogenea: Dactylogyridae) from a freshwater fish in Mexico. Parasitology Research 103: 1235–1236. https://doi.org/10.1007/s00436-008-1119-9

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

Mizelle JD, Kritsky DC, 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.

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

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

Moreira J, Scholz T, Luque JL (2015) First data on the parasites of Hoplias aimara (Characiformes): description of two new species of gill monogeneans (Dactylogyridae). Acta Parasitologica 60: 254–260. https://doi.org/10.1515/ap-2015-0036

Nelson JS, Grande TC, Wilson MVH (2016) Fishes of the World. John Wiley & Sons, New York, 5th ed., 707 pp.

Oliveira MSB, Santos-Neto JF, Tavares-Dias M, Domingues MV (2020) New species of Urocleidoides (Monogenoidea: Dactylogyridae) from the gills of two species of Anostomidae from the Brazilian Amazon. Brazilian Journal of Veterinary Parasitology 29: e007820. https://doi.org/10.1590/S1984-296120200039

Rosim DF, Mendoza-Franco EF, 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. The Journal of Parasitology 97: 406–417. https://doi.org/10.1645/GE-2593.1

Rossin MA, Timi JT (2016) Dactylogyrid monogeneans parasitising Cyphocharax voga (Hensel) (Teleostei: Curimatidae) from the Pampas region, Argentina: new and previously described species. Systematic Parasitology 93(7): 701–714. https://doi.org/10.1007/s11230-016-9654-8

Saitoh K, Miya M, Inoue JG, Ishiguro NB, Nishida M (2003) Mitochondrial genomics of Ostariophyan fishes: Perspectives on phylogeny and biogeography. Journal of Molecular Evolution 56: 464–472. https://doi.org/10.1007/s00239-002-2417-y

Suriano DM (1981) Androspira gen. nov. (Monogenea Ancyrocephalinae) parásito branquial de Pseudocurinata gibbert (Quoy & Gaimard, 1824) Fernández-Yepes, 1948 (Pisces: Tetragonopteridae) de la Laguna de Chascomú, República Argentina. Neotropica 27: 67–78.

Suriano DM (1997) Palombitrema heteroancistrium Price and Bussing, 1968 (Monogenea: Ancyrocephalidae) from Astyanax (A.) fasciatus (Cuvier, 1819) (Pisces: Characidae) in Chascomus Lake, Argentina: anatomy and systematic position. Physia 53: 7–10.

Vieira DH, Caramello LE, Abdallah VC, Silva RJ, Azevedo RK (2013) Community ecology of metazoan parasites of the sairú Cyphocharax nagelii from the Peixe River. Revista Brasileira de Parasitologia Veterinaria 22: 611–615. https://doi.org/10.1590/S1984-29612013000400027

Wayne R (2010) NIH: IMAGEJ. https://imagej.nih.gov/ij/download.html

Yamada FH, Brandão H, Yamada POE, Da Silva RJ (2015) Philocorydor longus sp. n. (Monogenea, Dactylogyridae) from the gills of Hoplosternum littorale (Siluriformes, Callichthyidae) in Southeastern Brazil and the reassignment of two species from the genus Urocleidoides to Philocorydor. Helminthologia 52: 331–335. http://dx.doi.org/10.1515/helm-2015-0052

Zago AC, Yamada FH, Yamada POE, Franceschini L, Bongiovani MF, Silva RJ (2020) Seven new species of Urocleidoides (Monogenea: Dactylogyridae) from Brazilian fishes supported by morphological and molecular data. Parasitology Research, https://doi.org/10.1007/s00436-020-06831-z

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