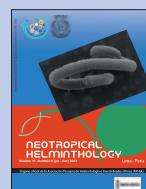


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ORIGINAL ARTICLE / ARTÍCULO ORIGINAL

A NEW SPECIES OF *UROCLEIDOIDES* (MONOGENOIDEA: DACTYLOGYRIDAE) PARASITE OF *PSECTROGASTER AMAZONICA* (CHARACIFORMES: CURIMATIDAE) AND *CAENOTROPUS LABYRINTHICUS* (CHARACIFORMES: CHILODONTIDAE) FROM TOCANTINS RIVER, MARANHÃO STATE, BRAZIL WITH CHECKLIST OF THE GENUS

UNA NUEVA ESPECIE DE PARÁSITO *UROCLEIDOIDES* (MONOGENOIDEA: DACTYLOGYRIDAE) DE *PSECTROGASTER AMAZONICA* (CHARACIFORMES: CURIMATIDAE) Y *CAENOTROPUS LABYRINTHICUS* (CHARACIFORMES: CHILODONTIDAE) DEL RÍO TOCANTINS, ESTADO DE MARANHÃO, BRASIL Y UNA LISTA DE VERIFICACIÓN DEL GÉNERO

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ABSTRACT

Parasites are important components of global biodiversity and among them, the Monogenoidea stands out as a parasites of fishes, commonly affecting the gills of their hosts. The present study aimed to analyze the presence of species of *Urocleidoides* parasitizing characiform fishes from the Tocantins River. During the study, specimens of *Psectrogaster amazonica* Eigenmann & Eigenmann and *Caenotropus labyrinthicus* (Kner) were collected from the urban zone of the municipality of Imperatriz, state of Maranhão. The gills of the fish were removed and placed in vials containing hot

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water (65°C), and posteriorly, absolute ethanol was added to reach a concentration of 70%. A new species of *Urocleidoides* was described parasitizing both hosts. *Urocleidoides psectrogasteri* n. sp. can be distinguished by its congeners species principally by the morphology of the MCO. Besides, the known species *U. tocantinensis* also was found parasitizing *C. labyrinthicus*, which was reported as a new host for this species. In addition, a checklist containing all species of *Urocleidoides* is presented to compile the known data on this monogenoid genus.

Keywords: Fish parasites – Monogenoidean – Neotropical Region – Tocantins-Araguaia Basin – *Urocleidoides psectrogasteri* n. sp.

RESUMEN

Los parásitos son componentes importantes de la biodiversidad global y entre ellos, se destacan los Monogenoidea como parásitos de los peces, afectando comúnmente las branquias de sus hospederos. El objetivo del presente estudio fue analizar la presencia de especies de *Urocleidoides* que parasitan peces Characiformes del río Tocantins. Durante el estudio, se recolectaron ejemplares de *Psectrogaster amazonica* Eigenmann & Eigenmann y *Caenotropus labyrinthicus* (Kner) de la zona urbana del municipio de Imperatriz, estado de Maranhão, Brasil. Se extrajeron las branquias de los peces y se colocaron en viales con agua caliente (65°C), y posteriormente se añadió etanol absoluto hasta alcanzar una concentración del 70%. Se describió una nueva especie de *Urocleidoides* que parasita a ambos hospedadores. *Urocleidoides psectrogasteri* n. sp. se puede distinguir por sus especies congéneres principalmente por la morfología de la MCO. Además, la especie conocida *U. tocantinensis*, también fue encontrada parasitando a *C. labyrinthicus*, la cual fue reportada como un nuevo hospedero para esta especie. Además, se presenta una lista de verificación que contiene todas las especies de *Urocleidoides* para recopilar los datos conocidos sobre este género monogenoideo.

Palabras clave: Bacia del Tocantins-Araguaia – Monogenoideos – Parásitos de peces – Region Neotropical – *Urocleidoides psectrogasteri* n. sp.

INTRODUCTION

Urocleidoides Mizelle & Price, 1964 was proposed to accommodate the species *U. reticulatus* Mizelle & Price, 1964 from the gills of *Poecilia reticulata* Peters, 1859 (Poeciliidae), which was collected from Capitol Aquarium, Sacramento, California, USA (Mizelle & Price, 1964). Kritsky & Thatcher (1983) listed 30 species of the genus described from four different orders of hosts: Characiformes, Cyprinodontiformes, Gymnotiformes e Siluriformes (Mizelle et al., 1968; Mizelle & Kritsky, 1969; Molnar et al., 1974; Kritsky & Thatcher 1974, 1976, 1983). Kritsky et al. (1986) revised the genus, described two new species, *U. eremitus* Kritsky, Thatcher & Boeger, 1986 and *U. paradoxus* Kritsky, Thatcher & Boeger, 1986 and added new morphological details in species described previously: *U. reticulatus*, *U. anops* Kritsky & Thatcher 1974 and *U. curimatae* Molnar, Hanek & Fernando, 1974. The authors emended the diagnosis of the genus, characterizing the species by the presence of vaginal sclerite, male copulatory organ with counterclockwise ring, tandem gonads, no modified anchors, hook with dilated shank and pairs 1 and 5 of hooks usually reduced in size. Kritsky et al. (1986) considered 22 species as *incertae sedis*, mainly by the

absence of the vaginal sclerite. Posteriorly, Ferreira et al. (2017) added *U. advenai* Mendoza-Franco & Reina, 2008 to this status of *incertae sedis*.

Further studies reallocate some of these species on newly described genera as *Ameloblastella* Kritsky, Mendoza-Franco & Scholz, 2000, *Aphanoblastella* Kritsky, Mendoza-Franco & Scholz, 2000, *Characithecium* Mendoza-Franco, Reina & Torchin, 2009, *Diaphorocleidus* Jogunoori, Kritsky & Venkatanarasaiah, 2004, *Nanayella* Acosta, Mendoza-Palmero, Silva & Scholz, 2019, *Philocorydoras* Suriano, 1986 and *Sciadicleithrum* Kritsky, Boeger & Thatcher, 1989 (Price & Bussing, 1968; Kritsky et al., 1989, 2000; Jogunoori et al., 2004; Mendoza-Franco et al., 2009; Yamada et al., 2015; Acosta et al., 2019).

Recently, Santos-Neto & Domingues (2023) proposed four new species of *Urocleidoides* from Characiformes and Gymnotiformes and revalidate the *incertae sedis* species, *Urocleidoides gymnotus* Mizelle, Kritsky & Crane, 1968 and *Urocleidoides carapus* Mizelle, Kritsky & Crane, 1968, based in molecular sequences. One of the new species, *Urocleidoides vanini* Santos-Neto & Domingues, 2023 did not present vaginal sclerite as the *incertae sedis* revalidated by these authors. From the species previously

assigned as *incertae sedis* by Kritsky *et al.* (1986), six have not yet been relocated to other genera.

Species of *Urocleidooides* have been described from *Psectrogaster amazonica* Eigenmann & Eigenmann and *Caenotropus labyrinthicus* (Kner), as *U. tocantinensis* Freitas, Bezerra, Meneses, Justo, Viana & Cohen, 2021 and *U. paratriangulus* Freitas, Bezerra, Meneses, Viana, Justo & Cohen 2021 and the latter also from *C. labyrinthicus* (Freitas *et al.*, 2021).

In this present study, a new species of *Urocleidooides* was found parasitizing *P. amazonica* and *C. labyrinthicus* and is described herein. In addition, *C. labyrinthicus* is reported as new host for *U. tocantinensis* and a checklist of *Urocleidooides* species with all current information about their hosts, localities and validity is presented.

MATERIAL AND METHODS

Fishes were collected in Tocantins River at the urban zone of Imperatriz municipality, state of Maranhão, 129 specimens of *P. amazonica* (standard length 11.5–16.1 cm; total weight 42–100 g) and 20 specimens *C. labyrinthicus* (standard length 12.1–14.5 cm; total weight 38–70 g). The fishes were caught with the aid of local fishermen and were carried to the “Núcleo de Estudos Morfológicos Avançados (NEMO)” at the Universidade Estadual da Região Tocantina do Maranhão (UEMASUL), Maranhão State, Brazil, where they were identified.

The gills of fish were removed and placed in vials containing hot water (65°C), and vigorously shaken to detach the parasites from the gill filaments. Posteriorly, absolute ethanol was added to reach a concentration of 70%. Those vials containing the gills were then sent to the “Laboratório de Helmintos Parasitos de Peixes, Instituto Oswaldo Cruz, FIOCRUZ”, Rio de Janeiro state, Brazil. The gills and sediments were analyzed in Petri dishes. Monogenoids were collected under a stereoscopic microscope, and the specimens mounted in Hoyer’s medium to study the sclerotized structures (Humason, 1979).

Parasitological indexes were calculated as proposed by Bush *et al.* (1997), followed by standard deviation. Measurements are presented in micrometers; range values are followed by mean and number of structures measured in parentheses. Morphometric studies were performed through ImageJ software (Wayne, 2010), distributed by the National Institutes of Health (NIH), and available at <https://imagej.nih.gov/ij/download.html>. The authorship

of the taxa followed the recommendation of Article 50.1 of the International Code of Zoological Nomenclature (ICZN), which deals with the identity of the authors.

A checklist of valid *Urocleidooides* species is presented herein, providing information about hosts and geographical distribution. For construction of this checklist, published papers with original descriptions and/or reports of species, taxonomic revisions, and checklists were used and online biodiversity databases as Taxonomic Catalog of Brazilian Fauna, PubMed, Scopus, Google Scholar and CAB Abstracts.

Postgraduate theses and abstract scientific meetings do not constitute formal publications and were thus not considered.

For Brazilian states, abbreviations are presented as follows:
AC: Acre; **AL:** Alagoas; **AM:** Amazonas; **AP:** Amapá; **BA:** Bahia; **CE:** Ceará; **DF:** Distrito Federal; **ES:** Espírito Santo; **GO:** Goiás; **MA:** Maranhão; **MG:** Minas Gerais; **MS:** Mato Grosso do Sul; **MT:** Mato Grosso; **PA:** Pará; **PB:** Paraíba; **PE:** Pernambuco; **PI:** Piauí; **PR:** Paraná; **RO:** Rondônia; **RJ:** Rio de Janeiro; **RN:** Rio Grande do Norte; **RR:** Roraima; **RS:** Rio Grande do Sul; **SC:** Santa Catarina; **SE:** Sergipe; **SP:** São Paulo; **TO:** Tocantins.

Ethic aspects: The fish sample collection protocol and laboratory procedures were approved by the Research Ethics Committee of “Universidade Estadual do Maranhão” (UFMA), Maranhão State, Brazil under protocol number 43/2021, and the environmental collection license was obtained from the System for Authorization and Information on Biodiversity (SISBIO), under protocol number 79538-1.

RESULTS

TAXONOMY

Class Monogenoidea Bychowsky, 1937

Subclass Polyonchoinea Bychowsky, 1937

Order Dactylogyridea Bychowsky, 1937

Dactylogyridae Bychowsky, 1933

Urocleidooides Mizelle & Price, 1964

Urocleidooides psectrogasteri sp. nov Bezerra, Freitas, Cohen & Justo (Fig. 1)

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

Type locality. Tocantins River ($5^{\circ}27'50''S$; $47^{\circ}33'48''W$), at the urban zone of Imperatriz municipality.

Other hosts: *Caenotropus labyrinthicus* (Kner) (Chilodontidae)

Infestation parameters. *P. amazonica*: Total number of hosts: 129; prevalence: 17%; total number of parasites: 25; mean intensity: 1.14 (± 0.34); mean abundance: 0.19 (± 0.45); range of intensity: 1–2. *C. labyrinthicus*: Total

number of hosts: 20; prevalence: 5%; intensity: 3 (only one host was parasitized); mean abundance: 0.15 (± 0.67).

Deposited material. Holotype CHIOC 40210. Paratypes CHIOC 40211, 40212, 40213, 40214, 40215, 40216, 40217 a-c.

Etymology: The specific name refers to the scientific name of the host *Psectrogaster amazonica*

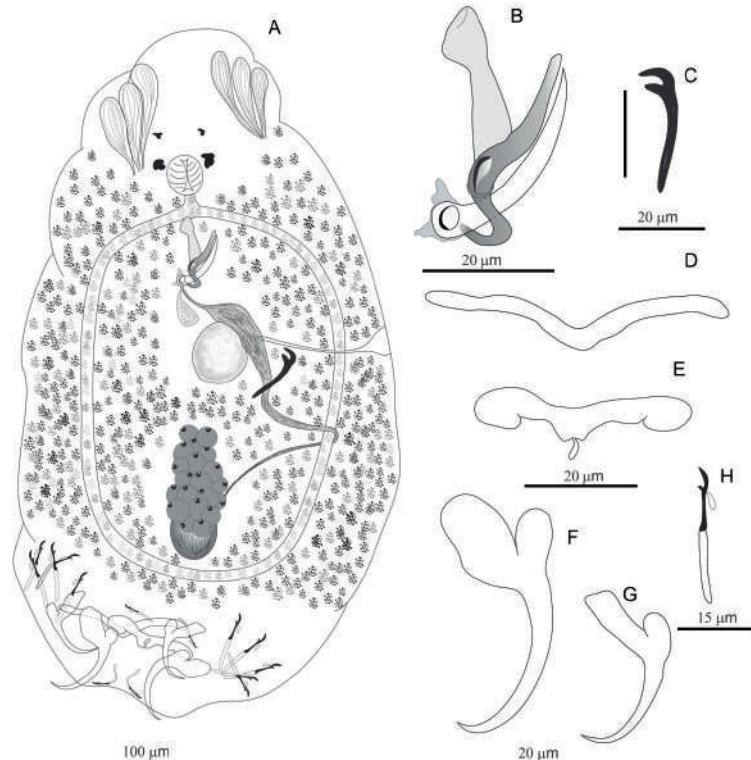


Figure 1. *Urocleidooides psectrogasteri* sp. nov from *Psectrogaster amazonica* (Curimatidae) from Tocantins River, at the urban zone of Imperatriz municipality. A. Total, ventral view (composite). B. Copulatory complex; C. Vaginal sclerite; D. Dorsal bar; E. Ventral Bar; F. Ventral anchor; G. Dorsal anchor; H. Hook.

Description based on 23 specimens mounted in Hoyer's medium: Body fusiform, 250–564 (384, n= 23) long by 97–201 (139, n= 23) wide. Three pairs of cephalic glands. Two pairs of eyespots, equidistant, anterior pair smaller than posterior. Pharynx 14–22 (18, n=5) ovate and muscular. Peduncle short. Haptor sub-hexagonal 75–184 (117, n= 22) wide. Anchors robust, dissimilar in shape. Ventral anchor with well-developed roots, protruding superficial root, semi-circular shape, rounded deep root, evenly curved shaft and short point, 24–53 (39, n=46) long and base 15–22 (18, n=46); Dorsal anchor with rectangular-shaped superficial root and deep root distally round, evenly curved shaft and acute point 23–34 (29, n= 44) long and base 12–19 (16, n= 44). Ventral bar robust, slightly curved, with enlarged

extremities, concave posteromedial 27–77 (46, n=9) and drop-like shaped posteromedian projection, short and thin 5–14 (8, n= 21) long. Dorsal bar slender V-shaped, slightly curved, 37–70 (54, n= 23) long. Seven pairs of marginal hooks, with distribution of ancyrocephaline, five pairs ventral and two dorsal. Hooks similar in shape, divided in two subunits, protruded thumb, curved point, shank straight with proximal dilation, comprising $\frac{2}{3}$ of shank length; FH loop $\frac{1}{4}$ of shank length; pairs 1 and 5 slightly smaller than others, pair 1 12–27 (19, n = 34); pair 2 19–30 (25, n= 35); pair 3 19–34 (26, n= 33); pair 4 19–39 (28, n= 33); pair 5 14–28 (21, n= 28); pair 6 19–35 (27, n= 32); pair 7 19–34 (27, n= 34) long. Copulatory complex composed of male copulatory organ (MCO) with auriculate base, sickle shape, 28–44

(36, n=18) and accessory piece bifurcated, with two elongated parts, articulated to MCO base, 27–41 (33, n=18) long. Testis dorsal to germarium; seminal vesicle a distal dilation of vas deferens; single prostatic reservoir present. Germarium elongated. Vaginal pore sinistral; vagina comprising a vaginal vestibule cup-shaped, sclerotized and a vaginal canal long; seminal receptacle round. Vaginal sclerite present in the middle of the body, with a longitudinal groove in the middle, erected thumb, 18–44 (29, n= 18) long. Eggs not observed. Vitellaria present, heavily distributed throughout the body, except in reproductive organs.

Remarks: The new species is allocated in *Urocleidoides* by the presence of vaginal sclerite, vagina in sinistral position, and hook pairs 1 and 5 reduced in size. The MCO of the new species is similar to those of some species by the absence of coils on the MCO, as observed in *U. surianoae* Rossin & Timi, 2016, *U. falkus* Zago, Yamada, Yamada, Franceschini, Bongiovani & Silva, 2020 and *U. tocantinensis*. The new species is evidently distinguished from these species by the morphology of the male copulatory organ, which is pincer-shaped (reverse J-shaped, with expanded proximal end in *U. surianoae*, male copulatory organ appearing to twist into itself and resembling the shape of a sickle and base enlarged in *U. falkus* and straight tube with enlarged base in *U. tocantinensis*). The new species also resembles *U. tocantinensis* considering the bifurcation of the accessory

piece and morphology of vagina. Considering the projection of the ventral bar, the new species is similar to *Urocleidoides boulengerelae* Freitas, Bezerra, Meneses, Justo, Viana & Cohen, 2021, *Urocleidoides piriati* Mendoza-Franco & Reina, 2008 and *U. tocantinensis*, differing that in *Urocleidoides psectrogasteri* sp. nov. the posteromedian projection is reduced in size. Despite the projection in *Urocleidoides surianoae* Rossim & Timi, 2016 is similar in shape and size, it differs from *U. psectrogasteri* sp. nov. by the anteromedial position.

Checklist of *Urocleidoides* spp. from Neotropical Region

Urocleidoides spp. have been recorded from 3 different orders (34 in Characiformes, eight in Gymnotiformes and four in Cyprinodontiformes), associated with 14 families and 48 species of fishes (Fig. 2). Most of them were reported from fishes belonging to Characiformes, from eight different families with predominance of Erythrinidae, mainly from *Hoplias malabaricus* (Bloch). Regarding the geographical distribution, most species are reported from Brazil, followed by Mexico and Panama, and records in Argentina, Colombia, El Salvador, Honduras and Trinidad and Tobago, thus presenting a broad host and locality spectrum. Until now, thirty-one species of *Urocleidoides* are referred from Brazil in different localities, rivers and basins within the country.

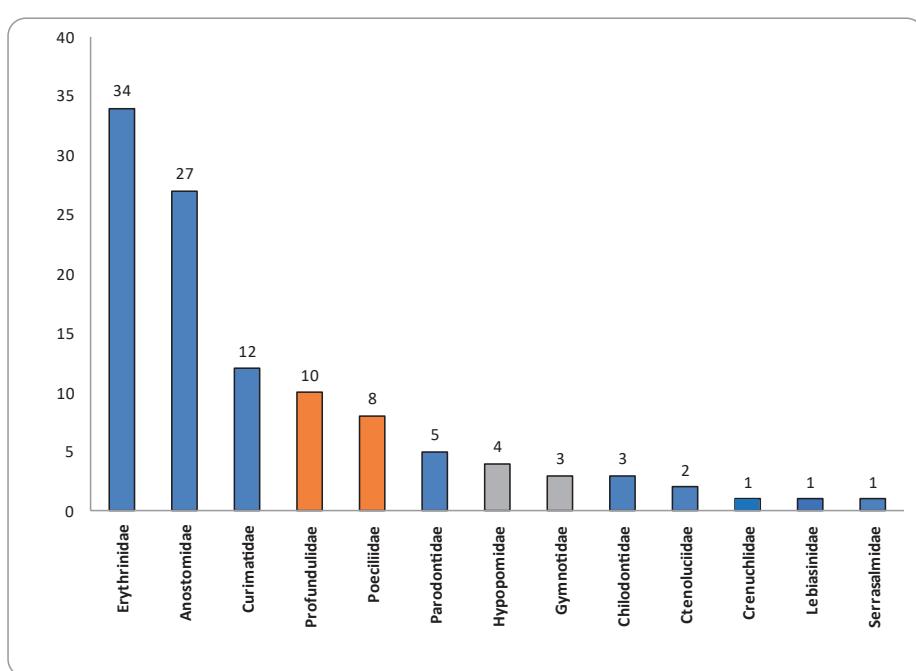


Figure 2. Distribution of *Urocleidoides* spp. within host families of three orders of freshwater fishes. Blue: Characiformes, Orange: Cyprinodontiformes, Grey: Gymnotiformes.

***Urocleidoides aimarai* Moreira, Scholz & Luque, 2015**

Type-host and locality: *Hoplias aimara* (Valenciennes) (Characiformes: Erythrinidae) [Xingu River, around Altamira, PA, **Brazil**].

Other hosts and locality: *Hoplias malabaricus* (Characiformes: Erythrinidae); *Leporinus friderici* (Bloch) (Characiformes, Anostomidae) [Batalha River, SP, **Brazil**].

Records: Moreira et al. (2015); Dias et al. (2017); Gião et al. (2020).

***Urocleidoides anops* Kritsky & Thatcher, 1974**

Type-host and locality: *Characidium caucanum* Eigenmann (Characiformes: Crenuchidae) [Pance River, Cali, Valle, **Colombia**].

Other host and locality: *Psalidodon fasciatus* (Cuvier) (Characiformes: Characidae) [Noc-choncunche and Dzonot Cervera cenotes, **Mexico**].

Record: Kritsky & Thatcher (1974); Mendoza-Franco et al. (1999).

***Urocleidoides atilaamarinoi* Santos-Neto & Domingues, 2023**

Type host and locality: *Hoplerythrinus unitaeniatus* (Agassiz) (Characiformes: Erythrinidae) [Igarapé Maratininha (Moju River Basin), municipality of Tailândia, PA, **Brazil**].

Other locality: Balneário Aracu (Guamá River Basin), municipality of Ourém, Pará, **Brazil**.

Record: Santos-Neto & Domingues (2023).

***Urocleidoides boulengerellae* Freitas, Bezerra, Meneses, Justo, Viana & Cohen, 2021**

Type-host and locality: *Boulengerella cuvieri* (Spix & Agassiz) (Characiformes: Ctenoluciidae) [Tocantins River, near the municipality of Tupyatins, TO, **Brazil**].

Other localities: Arraias River, close to the municipality of Babaçulândia; Tocantins River, close to the municipalities of Aguiarnópolis and Estreito; at the mouth of the Itaueiras River, in the municipality of Estreito, MA, **Brazil**.

Record: Freitas et al. (2021).

***Urocleidoides brasiliensis* Rosim, Mendoza-Franco & Luque, 2011**

Type-host and locality: *Hoplias malabaricus* (Characiformes: Erythrinidae) [Cuiabá River, MT, **Brazil**].

Other localities: Cristalino River, MT; Caeté River, Bragança; Maracaná River, Nova Timboteua; Piriá and Guripi Rivers, Viseu; Maparanim River, Municipality of Terra Alta; Itabocal River, Irituia, PA; Upper Paraná River Floodplain, PR, MS; Paraná River, PR; Guandú River, RJ, **Brazil**.

Records: Rosim et al. (2011); Graça et al. (2013); Ferreira et al. (2017).

***Urocleidoides bulbophallus* Ferreira, Rodrigues, Cunha & Domingues, 2017**

Type-host and locality: *Hoplias malabaricus* (Characiformes: Erythrinidae) [Caeté River, Bragança, PA, **Brazil**].

Other localities: Itabocal River, Irituia; Piriá River, Viseu; Maparanim River, Terra Alta; Gurupi River, Viseu, PA, **Brazil**.

Records: Ferreira et al. (2017).

***Urocleidoides carapus* Mizelle, Kritsky & Crane, 1968**

Type-host and locality: *Gymnotus carapo* (Linnaeus) (Gymnotiformes, Gymnotidae) [Amazon Basin, **Brazil**].

Other host and locality: *Sternopygus macrurus* (Bloch & Schneider) (Gymnotiformes, Gymnotidae) [Guamá River, Ourém, PA, **Brazil**].

Records: Mizelle et al. (1968); Santos-Neto & Domingues (2023).

***Urocleidoides cuiabai* Rosim, Mendoza-Franco & Luque, 2011**

Type host and locality: *Hoplias malabaricus* (Characiformes: Erythrinidae) [Cuiabá River, MT, **Brazil**].

Other localities: Maracaná River, Nova Timboteua; Gurupi and Piriá Rivers, Viseu, PA; Araguaia River, MT; Jaguari-Mirim River, MG, SP; Upper Paraná River Floodplain, PR, MS; Paraná River, PR; Guandu River, RJ; Batalha River, SP, **Brazil**.

Records: Rosim et al. (2011); Graça et al. (2013); Gasques et al. (2016); Ferreira et al. (2017); Dias et al. (2017); Gião et al. (2020).

***Urocleidoides cultellus* Mendoza-Franco & Reina, 2008**

Type-host and locality: *Brachyhypopomus occidentalis* (Regan) (Gymnotiformes: Hypopomidae) [Águas Claras River at its confluence with the Bayano Lake, **Republic of Panama**].

Record: Mendoza-Franco & Reina (2008).

***Urocleidoides curimatae* Molnár, Hanek & Fernando, 1974**

Type-host and locality: *Steindachnerina argentea* (Gill) (= *Curimata argentea*) (Characiformes: Curimatidae) [Arouca River near D'Abadie] after **Trinidad**.

Record: Molnar *et al.* (1974).

***Urocleidoides digitabulum* Zago, Yamada, Yamada, Franceschini, Bongiovani & Silva, 2020**

Type-host and locality: *Leporinus friderici* (Characiformes: Anostomidae) [Sapucaí-Mirim River, Upper Parana River Basin, SP, **Brazil**].

Other hosts and localities: *Leporinus octofasciatus* Steindachner; *Megaleporinus elongatus* (Valenciennes) (Characiformes: Anostomidae) [Jurumirim Reservoir, Paranapanema River, Upper Paraná River Basin, SP, **Brazil**].

Record: Zago *et al.* (2020).

***Urocleidoides eremitus* Kritsky, Thatcher & Boeger, 1986**

Type-host and locality: *Hoplias malabaricus* (Characiformes: Erythrinidae) [Janauaca Lake near Manaus, AM, **Brazil**].

Other hosts and localities: *Leporinus friderici*; *Megaleporinus macrocephalus* (Garavello & Britski) (Characiformes: Anostomidae) [Chascomus Lake, Buenos Aires province, **Argentina**; fish farms in Cruzeiro do Sul and Rio Branco, AC; Igarapé Fortaleza basin, in the municipality of Macapá, AP; Jaguari Mirim River, MG and SP; Machado River, MG; Cuiabá River, MT; Maracaná River, Nova Timboteua; Piriá River, Viseu; Caeté River, Bragança, PA; Upper Paraná River Floodplain in the PR, MS; Guandu River, RJ; Batalha River, Peixe River; Pirassununga lagoons, SP, **Brazil**; Tambopata River, Madre de Dios, **Perú**].

Records: Kritsky *et al.* (1986); Iannaccone & Luque (1993); Suriano (1997a); Rosim *et al.* (2011); Corrêa *et al.* (2013), Alcântara & Tavares-Dias (2015); Dias *et al.* (2017); Ferreira *et al.* (2017); Martins *et al.* (2017 a, b); Gião *et al.* (2020); Negreiros *et al.* (2021).

***Urocleidoides falkus* Zago, Yamada, Yamada, Franceschini, Bongiovani & Silva, 2020**

Type-host and locality: *Megaleporinus elongatus* (Characiformes: Anostomidae) [Sapucaí-Mirim River,

Upper Paraná River basin, SP, **Brazil**].

Other locality: Jurumirim Reservoir, Paranapanema River, Upper Paraná River basin, SP, **Brazil**.

Record: Zago *et al.* (2020).

***Urocleidoides flegomai* Mendoza-Franco, Aguirre-Macedo & Vidal-Martínez, 2007**

Type-host and locality: *Piabucina panamensis* Gill (Characiformes: Lebiasinidae) [Frijolito River, **Panama**].

Record: Mendoza-Franco *et al.* (2007).

***Urocleidoides gymnotus* Mizelle, Kritsky & Crane, 1968**

Type-host and locality: *Gymnotus carapo* (Gymnotiformes, Gymnotidae) [Amazon Basin, **Brazil**].

Other host and locality: *Sternopygus macrurus* (Gymnotiformes, Gymnotidae) [Guamá River, Ourém, PA, **Brazil**].

Records: Mizelle *et al.* (1968); Santos-Neto & Domingues (2023).

***Urocleidoides hypopomi* Suriano, 1997**

Type-host and locality: *Brachyhypopomus brevirostris* (Steindachner) (Gymnotiformes: Hypopomidae) [Paraná River, Puerto Italia, Corrientes Province, **Argentina**].

Record: Suriano (1997a).

***Urocleidoides indianensis* Oliveira, Silva, Vieira & Acosta, 2021**

Type-host and locality: *Parodon nasus* Kner (Characiformes: Parodontidae) [Indiana stream (Capivara River, Tietê River, Upper Paraná River basin), Botucatu, SP, **Brazil**].

Record: Oliveira *et al.* (2021).

***Urocleidoides jariensis* Oliveira, Santos-Neto, Tavares-Dias & Domingues, 2020**

Type-host and locality: *Schizodon fasciatus* Spix & Agassiz (Characiformes: Anostomidae) [Lower Jari River, near Jarilândia district, in municipality of Vitória do Jari, AP, **Brazil**].

Record: Oliveira *et al.* (2020).

***Urocleidoides macrosoma* Santos-Neto & Domingues, 2023**

Type host and locality: *Hoplias malabaricus* (Characiformes: Erythrinidae) [Vila Segredo – Segredo

River (Quatipuru River Basin), Tauari, municipality of Capanema, PA, **Brazil**].

Record: Santos-Neto & Domingues (2023).

***Urocleidoides malabaricus* Rosim, Mendoza-Franco & Luque, 2011**

Type-host and locality: *Hoplias malabaricus* (Characiformes: Erythrinidae) [Cuiabá River, MT, **Brazil**].

Other localities: Caeté River, Bragança; Gurupi River, Viseu; Maracaná River, Nova Timboteua; Maparanim River, Terra Alta; Piriá River, Viseu; Itabocal River, Irituia, PA; Upper Paraná River Floodplain PR, MS; Batalha River, SP; Paraná River, PR, **Brazil**.

Records: Rosim et al. (2011); Graça et al. (2013); Gasques et al. (2016); Ferreira et al. (2017); Dias et al. (2017); Gião et al. (2020).

***Urocleidoides naris* Rosim, Mendoza-Franco & Luque, 2011**

Type-host and locality: *Hoplias malabaricus* (Characiformes: Erythrinidae) [Cuiabá River, MT, **Brazil**].

Other localities: Guandu River, RJ; Jaguari-Mirim River, MG and SP; Machado River, MG, **Brazil**.

Record: Rosim et al. (2011).

***Urocleidoides nataliapasternakae* Santos-Neto & Domingues, 2023**

Type host and locality: *Brachyhypopomus brevirostris* (Steindachner) (Gymnotiformes: Hypopomidae) [Balneário Aracu (Guamá River Basin), municipality of Ourém, PA, **Brazil**].

Record: Santos-Neto & Domingues (2023).

***Urocleidoides neotropicalis* Mendoza-Franco & Reina, 2008**

Type-host and locality: *Saccodon dariensis* Meek & Hildebrand (Characiformes: Parodontidae) [Piriati River at its confluence with the Chagres River Basin, **Republic of Panama**].

Record: Mendoza-Franco & Reina (2008).

***Urocleidoides paradoxus* Kritsky, Thatcher & Boeger, 1986**

Type-host and locality: *Rhytidodus microlepis* Kner (Characiformes, Anostomidae) [Solimões River near Ilha Marchantaria, Manaus, AM, **Brazil**].

Other hosts and localities: *Leporinus friderici*; *Leporinus lacustris* Amaral Campos; *Megaleporinus elongatus*; *Megaleporinus macrocephalus*, *Megaleporinus obtusidens* (Valenciennes) (Characiformes, Anostomidae) [Parana River, Puerto Italia, Corrientes province, **Argentina**; fish farms in Cruzeiro do Sul and Rio Branco, AC; Furo do Catalão, near Encontro das Aguas, Manaus; Coari Manaus section, Lake Baixio; Lake Ananá, Lake Preto and Lake Catalão, Irandauba, AM; lower Jari River, near Jarilândia district, in municipality of Vitória do Jari, AP; Upper Paraná River floodplain, PR; Lake Guaiba, RS; Batalha River, SP; **Brazil**].

Records: Kristsky et al. (1986); Suriano (1997a); Guidelli et al. (2006, 2011); Takemoto et al. (2009); Souza et al. (2017); Martins et al. (2017a,b); Wendt et al. (2018); Oliveira et al. (2020); Negreiros et al. (2021).

***Urocleidoides paranae* Ferreira, Rodrigues, Cunha & Domingues, 2017**

Type-host and locality: *Hoplias malabaricus* (Characiformes: Erythrinidae) [Upper Paraná River floodplain (Paraná River Basin; Paraná, Paranapanema Sub-basin), PR and MS, **Brazil**].

Records: Graça et al. (2013); Ferreira et al. (2017).

Remarks: The authors examined vouchers of *U. eremitus* collected from *H. malabaricus* from the Upper Paraná River floodplain of Graça et al. (2013) and indicated that these specimens are members of *U. paranae*.

***Urocleidoides paratriangulus* Freitas, Bezerra, Meneses, Justo, Viana & Cohen, 2021**

Type host and locality: *Psectrogaster amazonica* (Characiformes: Curimatidae) [Tocantins River, close to the municipality of Embiral, MA, **Brazil**].

Other hosts and localities: *Cyphocharax gouldingi* Vari (Characiformes: Curimatidae); *Caenotropus labyrinthicus* (Chraciformes: Chilodontidae); *Mylesinus paucisquamatus* Jégu & Santos (Characiformes: Serrasalmidae) [Farinha River, close to the municipality of Estreito, MA; Tocantins River, close to the urban perimeter of Imperatriz, MA; Tocantins River, close to the municipalities of Aguiarnópolis and Estreito, MA; at the mouth of the Itaueiras River, in the municipality of Estreito, MA; Tocantins River, close to the municipalities of Aguiarnópolis and Estreito, MA; at the mouth of the Itaueiras River, municipality of Estreito, MA; João Aires River, close to the municipality of Palmeirantes, TO; Arraias River, close to the municipality of Babaçulândia, TO, **Brazil**].

Record: Freitas et al. (2021).

***Urocleidoides parodoni* Oliveira, Silva, Vieira & Acosta, 2021**

Type-host and locality: *Parodon nasus* (Characiformes: Parodontidae) [Indiana stream (Capivara River, Tietê River, Upper Paraná River basin), Botucatu, SP, Brazil].

Record: Oliveira *et al.* (2021).

***Urocleidoides piriatiu* Mendoza-Franco & Reina, 2008**

Type-host and locality: *Ctenolucius beani* (Fowler) (Characiformes: Ctenoluciidae) [Piriati River at its confluence with the Chagres River Basin, Republic of Panama].

Record: Mendoza-Franco & Reina (2008).

***Urocleidoides psectrogasteri* Bezerra, Freitas, Cohen & Justo 2023**

Type-host and locality: *Psectrogaster amazonica* (Characiformes: Curimatidae); [Tocantins River, at the urban zone of Imperatriz municipality, MA; Brazil].

Other hosts: *Caenotropus labyrinthicus* (Chraciformes: Chilodontidae)

Record: Present study

***Urocleidoides ramentacuminatus* Oliveira, Santos-Neto, Tavares-Dias & Domingues, 2020**

Type-host and locality: *Schizodon fasciatus* (Characiformes: Anostomidae) [Lower Jari River, near Jarilândia district, in municipality of Vitória do Jari, AP, Brazil].

Other host: *Laemolyta proxima* Garman (Characiformes: Anostomidae).

Record: Oliveira *et al.* (2020).

***Urocleidoides reticulatus* Mizelle & Price, 1964**

Type-Host and locality: *Poecilia reticulata* (Peters) [= *Lebistes reticulatus* (Peters)] (Cyprinodontiformes: Poeciliidae) [Host obtained from Capitol Aquarium, Sacramento, California, United States].

Other hosts and localities: *Belonesox belizanus* Kner; *Poecilia mexicana* Steindachner; *Poecilia petenensis* Gunther; *Xiphophorus helleri* Heckel; *Xiphophorus maculatus* (Günther) (Cyprinodontiformes: Poeciliidae) [Private Aquaria, Prague and Ceske Budejovice, Czech Republic; imported freshwater ornamental fish, Australia; Imported freshwater ornamental fish, Sri Lanka].

Records: Mizelle & Price (1964); Evans & Lester (2001); Pineda-López *et al.* (2005); Trujillo-González *et al.* (2018).

***Urocleidoides sapucaiensis* Zago, Yamada, Yamada, Franceschini, Bongiovani & Silva 2020**

Type-host and locality: *Megaleporinus elongatus* (Characiformes: Anostomidae) [Sapucaí-Mirim River, Upper Paraná River basin, SP, Brazil].

Other locality: Jurumirim Reservoir, Paranapanema River, Upper Paraná River basin, SP, Brazil.

Record: Zago *et al.* (2020).

***Urocleidoides similuncus* Mendoza-Franco, Aguirre-Macedo, & Vidal-Martínez, 2007**

Type-host and locality: *Poecilia gillii* (Cyprinodontiformes, Poeciliidae) [Frijolito River, Panama].

Record: Mendoza-Franco *et al.* (2007).

***Urocleidoides simonae* Mendoza-Franco, Caspeta-Mandujano, Salgado-Maldonado & Matamoros, 2015**

Type-host and locality: *Profundulus punctatus* (Günther) (Cyprinodontiformes: Profundulidae) [Nandalumi River, Chiapa de Corso, Chiapas, Mexico].

Other hosts and localities: *Profundulus punctatus* (= *Profundulus balsanus*); *Profundulus guatemalensis* (Günther), *Profundulus kreiseri* Matamoros, Shaefer, Hernández & Chakrabarty, *Tlaloc labialis* (= *Profundulus labialis*) (Günther), *Profundulus oaxacae* (Meek); *Profundulus* sp. 1, *Profundulus* sp. 2. (Cyprinodontiformes: Profundulidae) [Cauta River (Lempa River Basin); Cauca River, Nonoalpa River, Quebrada Los Tecomates (Lempa River Basin), El Salvador; Nil River (Guacalate River Basin); El Cantil River (Guacalate River Basin); Creek El Platanar (Guacalate River basin), Guatemala; River at rancho San Antonio, Chicoasén; Arroyo Ojo de Agua, El Canelar, La Frailesca, Chiapas, Creek Tres Picos, Copainalá and River Nandalumi, Chiapa de Corso, Chiapas State; Ahl from La Laca River (Papagayo River Basin); Cahapan River, Tamarindo River (Nexpa River basin), Guerrero State; Creek Los Sabinos (Atoyac-Verde River Basin), Chicaguaxtla River, Concepción del Progreso (Atoyac-Verde River Basin), Chico River, San Lorenzo Albarradas (Atoyac-Verde basin), Aguacate River, Juquilá, Maniatépec River Basin, Oaxaca State; Mexico].

Record: Mendoza-Franco *et al.* (2015).

***Urocleidoides sinus* Zago, Yamada, Yamada, Franceschini, Bongiovani & Silva, 2020**

Type-host and locality: *Schizodon nasutus* Kner (Characiformes: Anostomidae) [Sapucaí-Mirim River, Upper Paraná River basin, SP, Brazil].

Other hosts and localities: *Leporinus striatus* Kner, *Schizodon intermedius* Garavello & Britski (Characiformes: Anostomidae) [Jurumirim Reservoir, Paranapanema River, Upper Paraná River basin, SP, Brazil].

Record: Zago et al. (2020).

***Urocleidoides solarivaginatus* Zago, Yamada, Yamada, Franceschini, Bongiovani & Silva, 2020**

Type-host and locality: *Leporinus friderici* (Characiformes: Anostomidae) [Sapucaí-Mirim River, Upper Paraná River basin, SP, Brazil].

Other hosts and locality: *Leporinus octofasciatus*, *Leporinus striatus* (Characiformes: Anostomidae) [Jurumirim Reservoir, Paranapanema River, Upper Paraná River basin, SP, Brazil].

Record: Zago et al. (2020).

***Urocleidoides surianae* Rossin & Timi, 2016**

Type-host and locality: *Cyphocharax voga* (Hensel) (Characiformes: Curimatidae) [Chascomus Lake, Buenos Aires province, Argentina].

Record: Rossin & Timi (2016).

***Urocleidoides tenuis* Zago, Yamada, Yamada, Franceschini, Bongiovani & Silva 2020**

Type-host and locality: *Apareiodon piracicabae* (Eigenmann) (Characiformes: Parodontidae) [Streams of the Middle Paranapanema River, Upper Paraná River basin, SP, Brazil].

Other hosts and localities: *Apareiodon affinis* (Steindachner), *Parodon nasus* (Characiformes: Parodontidae) [Jurumirim Reservoir, Paranapanema River, Upper Paraná River basin; Indiana stream (Capivara River, Tietê River, Upper Paraná River basin), Botucatu, SP, Brazil].

Records: Zago et al. (2020); Oliveira et al. (2021).

***Urocleidoides tocantinensis* Freitas, Bezerra, Meneses, Justo, Viana & Cohen, 2021**

Type host and locality: *Psectrogaster amazonica* (Characiformes, Curimatidae) [Tocantins River, close to the municipality of Embiral, MA, Brazil].

Other host and localities: *Caenotropus labyrinthicus* (Characiformes, Chilodontidae); *Mylesinus paucisquamatus* (Characiformes, Serrasalmidae) [Farinha River, close to the municipality of Estreito, MA; Tocantins River, close to the urban perimeter of Imperatriz; Tocantins River, at the urban zone of Imperatriz municipality, MA; Arraias River, close to the municipality of Babaçulândia, TO; Brazil].

Records: Freitas et al. (2021); Present study.

***Urocleidoides triangulus* (Suriano, 1981) Rossin & Timi, 2016**

Type host and locality: *Cyphocharax gilbert* (Quoy & Gaimard) (Characiformes: Curimatidae) [Chascomus Lake, Buenos Aires province, Argentina].

Other hosts and localities: *Cyphocharax modestus* (Fernández-Yépez); *Cyphocharax nagelii* (Steindachner); *Cyphocharax voga* (Characiformes: Curimatidae) [Guandu River, RJ; Batalha River and Peixe River, Anhembi, SP, Brazil].

Records: Suriano (1981); Suriano (1997b); Vieira et al. (2013); Abdallah et al. (2015); Rossin & Timi (2016); Dias et al. (2017); Freitas et al. (2021).

***Urocleidoides uncinus* Zago, Yamada, Yamada, Franceschini, Bongiovani & Silva 2020**

Type-host and locality: *Gymnotus sylvius* Albert & Fernandes-Matioli (Gymnotiformes: Gymnotidae) [Sapucaí-Mirim River, Upper Paraná River basin, SP, Brazil].

Other locality: Jurumirim Reservoir, Paranapanema River, Upper Paraná River basin, SP, Brazil.

Record: Zago et al. (2020).

***Urocleidoides vaginoclaustroides* Mendoza-Franco, Caspeta-Mandujano, Salgado-Maldonado & Matamoros, 2015**

Type-host and locality: *Pseudoxiphophorus bimaculatus* (Heckel) (Cyprinodontiformes: Poeciliidae) [Danta River, a tributary of the Río Lacantún basin in the Biosphere Reserve of Montes Azules (BRMA), Chiapas, Mexico].

Other host and locality: *Poeciliopsis retropinna* (Regan) (Cyprinodontiformes: Poeciliidae) [Arroyo Jose, Chiriquicito River, Panama].

Record: Mendoza-Franco et al. (2015).

***Urocleidoides vaginoclastrum* Jogunoori, Kritsky & Venkatanarasaiah, 2004**

Type-host and locality: *Xiphophorus hellerii* (Cyprinodontiformes: Poeciliidae) [Aquarium fishes in the twin cities of Hyderabad and Secunderabad, **India**].

Other hosts and localities: *Pseudoxiphophorus bimaculatus* (=*Heterandria bimaculata*), *Xiphophorus birchmanni*; *Xiphophorus malinche* (Cyprinodontiformes, Poeciliidae), *Tlaloc labialis* (=*Profundulus labialis*); *Tlaloc portillorum* (=*Profundulus portillorum*) (Cyprinodontiformes, Profundulidae) [Creek at Ojojona, Francisco Morazán (Nacaome River basin); Lepaterique, Francisco Morazán (Nacaome River basin), **Honduras**. Danta River, a tributary of the Lacantún River, Chiapas; River at rancho San Antonio, Chicoasén, Chiapas; Los Berros Spring, San Pedro River Mezquital basin, Durango; Arroyo Xontla and Conzintla River, Pánuco drainage, Hidalgo; Benito Juárez, part of Zontecomatlán River; La Antigua River basin, Veracruz, **Mexico**].

Records: Jogunoori *et al.* (2004); Salgado-Maldonado *et al.* (2014, 2016) Mendoza-Palmero & Aguilar-Aguilar (2008); Mendoza-Franco *et al.* (2015); Bautista-Hernández *et al.* (2014; 2019); Mendoza-Garfias *et al.* (2017).

Remarks: This species was referred by Rodríguez-Santiago *et al.* (2016) parasitizing *Pterygoplichthys pardalis* (Siluriformes, Loricariidae). Considering that *Urocleidoides* spp. are not reported from Siluriformes and these authors stated that only three specimens were collected, we did not consider this report.

***Urocleidoides vanini* Santos-Neto & Domingues, 2023**

Type host and locality: *Erythrinus erythrinus* (Bloch & Schneider) (Characiformes, Erythrinidae) [Vila Perseverança, Palheta River (Guamá River Basin), municipality of São Domingos do Capim, PA, **Brazil**].

Record: Santos-Neto & Domingues (2023).

***Urocleidoides visiofortatus* Mendoza-Franco & Reina, 2008**

Type-host and locality: *Brachyhypopomus occidentalis* (Regan) (Gymnotiformes: Hypopomidae) [Águas Claras River at its confluence with the Bayano Lake, **Panama**].

Record: Mendoza-Franco & Reina (2008).

***Urocleidoides xinguensis* Moreira, Scholz & Luque, 2015**

Type-host and locality: *Hoplias aimara* (Characiformes, Erythrinidae) [Xingu River, near Altamira, PA, **Brazil**].

Record: Moreira *et al.* (2015).

DISCUSSION

Urocleidoides was originally described by Mizelle & Price (1964) to accommodate the type species, *U. reticulatus*. The authors proposed that species of the genus are restricted to those that present, besides vaginal sclerite, overlapping (tandem) gonads, counterclockwise cirrus rings, unmodified anchors and hooks (pairs 1, 5 usually reduced) with enlarged shanks. Afterwards, some authors identified different characteristics to the genus, Rosim *et al.* (2011) stated that the ventral bar with enlarged extremities may be considered a generic character for this genus. Zago *et al.* (2020) added an amended diagnosis, considering the recent discovery of new species of *Urocleidoides*, including “vagina lateral (dextral or sinistral) sclerotized; receptacle seminal present”. Besides these characteristics, Rossim & Timi (2016), Zago *et al.* (2020) and Freitas *et al.* (2021) described species with absence of coils in the male copulatory organ, and this character may be included as diagnostic for the genus, according to the amendment made by Zago *et al.* (2020). Santos-Neto & Domingues (2023) postulated that, although the presence of vaginal sclerite is a differential character for *Urocleidoides*, it cannot be considered a main characteristic for the species of the genus. According to these authors, the species described from gymnotiform hosts, even without vaginal sclerite, share some morphological characteristics.

The type species of *Urocleidoides* have been described from aquarium fishes, found in native habitats in the Neotropical Region, as *U. reticulatus* from *Poecilia reticulata* from Capitol Aquarium, Sacramento, California, USA, and another species of this genus was also reported from aquarium fishes, *U. vaginoclastrum*, described from *Xiphophorus hellerii*. The hosts from both species were collected from Neotropical Region and are available in aquarium in different countries: Israel, Czech Republic, India, California (USA) and in Central Mexico (Kritsky *et al.*, 1986; Jogunoori *et al.*, 2004; Mendoza-Palmero & Aguilar-Aguilar, 2008).

From the total number of species, 27 were reported parasitizing a single host species, while 19 species are

found in more than one host species, ranging from 2 to 6 species, belonging or not to the same family. All species of *Urocleidoides* found in more than one host species are specific to the fish order that they parasitize, and within the order, 12 species are restricted to one family, while 7 were recorded in more than one family, mainly in 2 different families from the same order, with emphasis in *U. paratriangulus* and *U. tocantinensis*, the only species recorded in 3 different families. This demonstrated that, despite the generalist behavior of *Urocleidoides*, in which all known species are found in 3 different orders, each species shows a specificity to the host.

Hoplias malabaricus is the host species which present the highest diversity in species: seven species from *Urocleidoides* were described from different river basins in Brazil (Rosim *et al.* 2011; Ferreira *et al.*, 2017; Santos-Neto & Domingues, 2023). Variations in size and shape of haptoral structures were observed by Rosim *et al.* (2011) from different river basins and were considered to be intraspecific variation. According to Ferreira *et al.* (2017), this is probably due to geographic distance, phenotypic plasticity of parasites or host induced morphological change. Rosim *et al.* (2011) found their new species in *H. malabaricus* from different basins. Nevertheless, *H. malabaricus* appears to be a species complex when comparing cytogenetic and molecular studies. Thus, the diversity of species presented in this host may be artificial, considering that they represent different *Hoplias* species that may harbour different *Urocleidoides* spp. Considering *Hoplias*, nine species were reported in 10 associations from *H. malabaricus* and *H. aimara*.

Anostomidae is the most representative family housing *Urocleidoides* spp., represented by 12 different species in 23 associations host-parasite, followed by Poeciliidae, with 11 species in 13 associations and Curimatidae, with 8 species and 10 associations.

Previous studies reported *Urocleidoides* spp. as parasites of *P. amazonica* and *C. labyrinthicus*. In the present study, besides the new species, *Urocleidoides tocantinensis* were found parasitizing *C. labyrinthicus*, amplifying the host spectrum of this monogenoidean.

In this paper, the number of valid species in genus *Urocleidoides sensu stricto* was increased to 46, as well as that of monogenoids in the Tocantins River basin, contributing to knowledge of the diversity of these parasites in this important region, which includes an endemic diversity of fish and consequently, monogenoideans parasites. Further studies on other

host species from this basin, whose fauna of parasites is underestimated, will provide interesting and valuable information about biogeographical and evolutionary research on dactylogyrids in the Neotropics.

Author contributions: CRediT (Contributor Roles Taxonomy)

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Formal Analysis: SCC, MCNJ

Funding acquisition: SCC, MCNJ, DCV

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