Dactylogyrids (Platyhelminthes, Monogenoidea) from the gills of Hoplias malabaricus (Characiformes: Erythrinidae) from coastal rivers of the Oriental Amazon Basin: species of Urocleidoides and Constrictoanchoratus n. gen.

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Abstract

Five species of Urocleidoides (one new) and two new species of Constrictoanchoratus n. gen. are described in this study. All were collected from the gills of Hoplias malabaricus (Characiformes: Erythrinidae) captured in six localities of coastal rivers of the north-eastern sector the State of Pará (Oriental Amazon): Urocleidoides brasiliensis Rosim, Mendoza-Franco & Luque, 2011; Urocleidoides bulbophallus n. sp.; Urocleidoides cuiabai Rosim, Mendoza-Franco & Luque, 2011; Urocleidoides eremitus Kritsky, Thatcher & Boeger, 1986; Urocleidoides malabaricusi Rosim, Mendoza-Franco & Luque, 2011; Constrictoanchoratus lemmyi n. gen. n. sp.; and Constrictoanchoratus ptihonphallus n. gen. n. sp. This is the first reported occurrence of the four previously described species of Urocleidoides parasitizing H. malabaricus from streams in the Oriental Amazon Basin. The analysis of voucher specimens of the four previously described species of Urocleidoides parasitizing H. malabaricus from the Upper Paraná River floodplain in the limits of States of Paraná and Mato Grosso do Sul, Brazil, indicates that these specimens are members of a new species of Urocleidoides, described here as Urocleidoides paranae n. sp. Constrictoanchoratus n. gen. is proposed for the species with a male copulatory organ sclerotized, coiled, clockwise; ventral anchor with elongate superficial root, inconspicuous deep root; dorsal anchor with inconspicuous roots, and a constriction at the intersection between the shaft and the point. The host–parasite diversity scenario and host specificity of the species of Constrictoanchoratus n. gen. and Urocleidoides from the gills of H. malabaricus are also discussed in this study.

Introduction

One hundred and eighty species of monogenoids have been reported to infest characiform fish from Brazil.
(Cohen et al., 2013). However, among these, only ten species have been reported to be members of Erythrinidae (Cohen et al., 2013; Moreira et al., 2015; Santos-Neto et al., 2015): six species of monogenoids are known to parasitize the gills and body surfaces of Hoplias malabaricus (Bloch) (trahira), two species were collected from the gills of Hoplias aimaara (Valenciennes) (trahira) and the two remaining species were from the gills of Hoploerythрус unitaeniatus (Agassiz) (trahira pixuna, jeju). Additionally, two undescribed species of dactylogyrids were found on the gills of H. malabaricus from the Paraná Basin (table 1).

During a survey of the parasites infecting H. malabaricus, which inhabit the streams of the coastal drainage ecosystem of the State of Pará, Brazil, one new species of Urocleidoides and two new species of a new genus of dactylogyrid were encountered on the gills of H. malabaricus. Descriptions of the new species and the proposal of the genus are presented herein. Urocleidoides brasiliensis Rosim, Mendoza-Franco & Luque, 2011, U. cuiabai Rosim, Mendoza-Franco and Luque, 2011, U. eremitus Kritsky, Thatcher & Boeger, 1986 and U. malabaricus Rosim, Mendoza-Franco & Luque, 2011, are reported for the first time parasitizing H. malabaricus from the coastal rivers of the Oriental Amazon Basin. Urocleidoides eremitus reported by Graça et al. (2013) from the Upper Paraná River floodplain is now considered by the authors as a new species of Urocleidoides. We also address the importance of host distributional range, especially in ‘species complex’ cases (e.g. H. malabaricus) in order to understand the patterns of morphological variation in parasites and their species delimitation.

Materials and methods

Host sample collection

Fish hosts were collected by trammel net, and line and hook from the Caeté River (North/North-east Atlantic Basin; Gurupi, Turiáçu Sub-basin), Municipality of Bragança, Pará State, Brazil (1°3’54.82″S, 46°41’37.60″W) in April 2013, October 2013 and August 2014; Itabocal River (North/North-east Atlantic Basin; Meruu, Acrá, Guamá Sub-basin), Municipality of Irituía, Pará State, Brazil (1°51’59.82″S, 47°24’17.15″W) in November 2013 and July 2014; Maracanã River (North/North-east Atlantic Basin; Gurupi, Turiáçu Sub-basin), Municipality of Nova Timbóteua, Pará State, Brazil (1°7’46.32″S, 47°21’11.64″W) in July 2013; Maparaimi River (North/North-east Atlantic Basin; Gurupi, Turiáçu Sub-basin), Municipality of Terra Alta, Pará State, Brazil (1°5’0.10″S, 47°55’43.98″W) in July 2013; Gurupi River (North/North-east Atlantic Basin; Gurupi, Turiáçu Sub-basin), Municipality of Viseu, Pará State, Brazil (1°17’37.6″S, 46°11’0.49″W) in May 2014; and Pirá River (North/North-east Atlantic Basin; Gurupi, Turiáçu Sub-basin), Municipality of Viseu, Pará State, Brazil (1°12’44.65″S, 46°17’36.72″W) in March 2014. Host scientific names were validated according to Oyakawa (2003) and Oyakawa & Mattos (2009). The nomenclature of basins and sub-basins follows the Agência Nacional de Águas, Ministério do Meio Ambiente, Brazil (http://hidroweb.ana.gov.br/).

Parasitological procedures

Gill arches were removed and placed in vials containing heated water (~65°C). Each vial was shaken vigorously and formalin was added to obtain a 5% solution. In the laboratory, the contents of each vial were examined under a dissecting microscope (Leica S6D; Leica Microsystems, Canada) and helminths were removed from the gills or sediment using small probes. Some specimens were stained with Gomori trichrome (Humason, 1979; Boeger & Vianna, 2006) or DAPI and mounted in Damar Gum or Canada balsam to determine internal soft structures, and others were mounted in Hoyer’s medium or Gray & Wess medium (Humason, 1979; Boeger & Vianna, 2006) for the study of sclerotized structures. The measurements,
Monogenoids from *Hoplias malabaricus*

all in micrometres, were obtained according to the procedures of Mizelle & Klucka (1953). Dimensions of organs and other structures represent the greatest measurement in dorso-ventral view; lengths of curved or bent structures (anchors, bars and accessory piece) represent the straight-line distances between extreme ends; total lengths of the male copulatory organ were carried out using ImageJ (Rasband, 1997–2016) on drawing-tube images. Each average measurement is followed by the range and the number (n) of specimens measured in parentheses. Illustrations were prepared with the aid of a drawing tube on a Leica DM 2500 microscope with differential interference contrast and phase contrast optics. Illustrations of soft structures were prepared using pen and ink; illustrations of hard structures were scanned and redrawn on a digitizing tablet using Adobe Illustrator and Corel Draw software. Plates were prepared using Photoshop software. Definitions of prevalence and mean intensity followed Bush et al. (1997). Type specimens and vouchers were deposited in the following collections: Helminthological Collection of the Instituto Oswaldo Cruz (CHIOC), Rio de Janeiro, RJ, Brazil; Invertebrate Collection of the Instituto de Pesquisas da Amazônia (INPA), Manaus, AM, Brazil; Invertebrate Collection of the Museu Paraense Emílio Goeldi (MPEG), Belém, PA, Brazil. The following museum specimens were examined: 20 specimens of *U. eremitus* (INPA PA260 1–3, CHIOC 37471), 2 specimens of *U. malabaricus* (CHIOC 37467a–b), 4 specimens of *U. cuiabai* (CHIOC 37469b–e) and 5 specimens of *U. brasiliensis* (CHIOC 37470b–f). Historical review of species containing relevant taxonomic contributions, such as description (descr.), redescription (redes.), citation (citat.) and figure (fig.), are included after valid species’ names.

**Results**

Class Monogonoidea Bychowsky, 1937

Subclass Polyonchoinea Bychowsky, 1937

Order Dactylogyridae Bychowsky, 1937

Dactylogyridae Bychowsky, 1933

_Urocoidoidea_ Mizelle & Price, 1964

_Urocoidoidea bulbophallus_ n. sp.

**Description**

Based on eight specimens (fig. 1); one mounted in Gomori’s trichrome, seven mounted in Gray & Weiss medium. Body fusiform, total length excluding haptor 268 (225–275; n = 7) long, 101 (72–130; n = 8) wide at level of germarium. Testis smooth. Cephalic margin tapered; moderately developed terminal lobes; three bilateral pairs of head organs with rod-shaped secretion; cephalic glands unicellular, posterolateral to pharynx. Four eyes, posterior pair larger than anterior pair; accessory granules present in cephalic area, elliptical. Mouth subterminal, midventral; pharynx muscular, glandular; oesophagus short. Two intestinal caeca, confluent posteriorly to gonads, lacking diverticula. Genital pore opening midventral; genital atrium muscular. Testis, vas deferens, prostatic reservoir not observed. Copulatory complex comprising male copulatory organ (MCO), accessory piece; MCO

sclerotized, coiled, counterclockwise, with approximately 1½ rings, 75 (75; n = 3) long, base with sclerotized cap; circular sclerotized tandem brim associated with the base of the male copulatory organ; proximal portion of the MCO slightly expanded, bulb-shaped, distal aperture acute (fig. 1b). Accessory piece sclerotized, non-articulated with the MCO, comprising a bent sheath, ‘e’ shape. Germainium, seminal receptacle, Mehlis’ glands, ootype not observed. Vagina single, muscular; vaginal aperture sinistro-ventral, marginal; vagina comprising vaginal vestibule with soft-tissue canal, elongated, sigmoid, slightly sclerotized. Vaginal sclerite 31 (28–35; n = 6) long, robust, with longitudinal superficial groove, distally hooked (fig. 1a). Vitellaria dense throughout trunk, except in region of reproductive organs. Eggs not observed. Peduncle short. Haptor subtriangular, 52 (47–54; n = 3) long, 67 (54–77; n = 3) wide. Anchors similar; each with well-developed superficial root, short deep root, evenly curved shaft and point; point acute, extending just past level of tip of superficial root. Ventral anchor (fig. 1g), base 18 (17–20; n = 4) long, superficial root with small sclerotized cap, 35 (33–38; n = 7) long; shaft and point, forming angle of approximately 115°. Dorsal anchor more delicate than ventral anchor (fig. 1h) 19 (17–22; n = 8) in length, base 10 (9–12; n = 4) long; shaft and point, forming angle of approximately 110°. Ventral bar (fig. 1c) 35 (30–40; n = 5) long, slightly curved or straight rod with small terminal enlargements, ends curved in anterior direction. Dorsal

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Fig. 1. *Urocoidoidea bulbophallus* n. sp. (a) Vaginal sclerite; (b) copulatory complex; (c) ventral bar; (d) dorsal bar; (e, f) hooks; (g) ventral anchor; (h) dorsal anchor. Scale bars in μm.
bar (fig. 1d) 22 (18–25; n = 4) long, narrow, broadly U-shaped, slightly curved in posterior direction. Hooks similar in shape (fig. 1e, f), shank with inflation, erected thumb, lightly curved long shaft, delicate point, filamentous hook; loop of hook extending to union of shank sub-units; hook pair 1, 12 (11–13; n = 6) long; pairs 2–4 and 6–7, 21 (18–25; n = 8) long; hook pair 5 not observed.

**Taxonomic summary**

**Type host.** *Hoplias malabaricus* (Bloch).

**Site of infection.** Gill filaments.

**Type locality.** Caeté River, Municipality of Bragança, Pará State, Brazil (1°3′54.82″S, 46°41′37.60″W).

**Other records.** *Hoplias malabaricus*, Itabocal River, Municipality of Irituia, Pará State, Brazil (1°51′59.82″S, 47°24′17.15″W); Pirí River, Municipality of Viseu, Pará State, Brazil (1°12′44.65″S, 46°17′36.72″W); Maparanim River, Municipality of Terra Alta, Pará State, Brazil (1°5′0.10″S, 47°55′43.98″W); Gurupi River, Municipality of Viseu, Pará State, Brazil (1°17′37.6″S, 46°11′0.49″W).

**Specimens deposited.** Holotype: CHIOC no. 38621a. Six paratypes: CHIOC nos 38620a–b, 38621b; INPA no. 706; MPEG nos 0081–0082. Thirteen vouchers: CHIOC nos 38616–38619, 38635a–b, 38639; INPA nos 707–708; MPEG nos 0083–0085.

**Etymology.** The specific name refers to the presence of a bulb in the proximal portion of the male copulatory organ of this species.

**Remarks**

Most specimens of *U. bulbophallus* n. sp. were mounted in Gray & Wess medium. Measurements and description of internal organs are therefore limited. The new species resembles *U. visiortatus* Mendoza-Franco & Reina 2008 mainly by the dissimilarity in the size of anchors (ventral anchors twice as large as dorsal anchors) and *U. neotropicalis* Mendoza-Franco & Reina 2008 by having a male copulatory organ with bulbous base. It differs from *U. visiortatus* mainly by possessing a male copulatory organ with bulbous base proximal (bulbous base absent in *U. visiortatus*) and a vaginal aperture marginal (midventral position in *U. visiortatus*). It is easily distinguished from *U. neotropicalis* by the comparative size of anchors and shape of the accessory piece. In *U. neotropicalis*, the anchors are approximately similar in size (ventral anchors twice as large as dorsal anchors in *U. bulbophallus* n. sp.), and the accessory piece comprising a variable sheath along the distal portion of male copulatory organ (a bent sheath, ‘e’ shape in *U. bulbophallus* n. sp.).

**Urocleidoides paranae** n. sp.

**Description**

Based on two specimens mounted in Hoyers’s medium (fig. 2). Body fusiform, total length excluding haptor 361 (346–377; n = 2) long, 156 (155–158; n = 2) wide at level of germarium. Testum smooth. Cephalic margin tapered; moderately developed terminal lobes; three bilateral pairs of head organs with rod-shaped secretion; cephalic glands unicellular, posterolateral to pharynx. Four eyes, posterior pair larger than anterior pair; accessory granules present in cephalic area, elliptical. Mouth subterminal, midventral; pharynx muscular, glandular 29 (n = 2) in diameter; oesophagus, intestinal caeca not observed. Genital pore, gonads, ooty, uterus, eggs, seminal receptacle not observed. Copulatory complex comprising MCO, accessory piece; MCO sclerotized, coiled, counterclockwise, with approximately 2½ rings, 108 (105–110; n = 2) long, base with sclerotized cap; circular sclerotized tandem brim associated with the base of the MCO present; distal aperture acute (fig. 2a). Accessory piece sclerotized, non-articulated with the MCO, comprising variably flattened sheath along distal shaft of MCO. Vagina single; vaginal aperture sinistro-ventral, marginal; vagina comprising vaginal vestibule with slightly sclerotized funnel; vaginal canal heavily sclerotized at proximal portion with a dilatation at middle portion, distal portion an elongate tube slightly sclerotized (fig. 2b). Vaginal sclerite 29 (n = 1) long, robust, with longitudinal superficial groove, distally hooked. Vitellaria dense throughout trunk, except in region of reproductive organs. Peduncle short. Haptor subtriangular, 95 (85–105; n = 2) long, 107 (104–111; n = 2) wide. Anchors similar. Ventral anchor (fig. 2h) 47.5 (47–48; n = 2) in length, base 22.5 (22–23; n = 2) long with depressed, moderately short superficial root, non-existent deep root, elongate shaft and short point, forming angle of approximately 98°. Dorsal anchor (fig. 2i) 39 (n = 1) in length, base 16 (n = 1) long with elongate superficial root, poorly developed deep root, evenly curved shaft and point, forming angle of approximately 95°. Ventral and dorsal bars slightly curved rods with enlarged ends; ventral bar (fig. 2d) 46 (45–47; n = 2) long; dorsal bar (fig. 2e) 41.5 (41–42; n = 2) long. Hooks similar in shape (fig. 2f, g), shank with inflation, erected thumb, lightly curved long shaft, delicate point; hook pairs 1 and 5, 17 (16–18; n = 2) long; pairs 2–4 and 6–7, 28 (n = 2) long.

**Taxonomic summary**

**Type host.** *Hoplias malabaricus* (Bloch).

**Type locality.** Upper Paraná River floodplain (Paraná River Basin; Paraná, Paranapanema Sub-basin), Paraná and Mato Grosso do Sul State, Brazil (22°43′00″S, 53°10′00″W).

**Specimens studied.** Holotype: CHIOC no. 37789. One paratype: CHIOC no. 37790.

**Etymology.** The specific name refers to the Paraná River, from which the type host was collected.

**Remarks**

Examination of the vouchers of *U. eremitus* collected from *H. malabaricus* from the Upper Paraná River floodplain (see Graça et al., 2013) indicates that these specimens are members of a new species of *Urocleidoides*, described above as *U. paranae* n. sp. The new species could be confused with *U. eremitus* by having similar hooks, bars
and dorsal anchors. However, examination of the type series of *U.* eremitus (INPA PA260 1–3) allowed us to differentiate both species. The new species differs from *U.* eremitus by possessing a ventral anchor with a depressed, moderately short superficial root and non-existent deep root, whereas the latter species has a well-developed superficial root and small deep root in the ventral anchor. Also, the accessory piece in *U.* paranae n. sp. is a variable sheath along the distal shaft of MCO (fig. 2a), whereas in *U.* eremitus, the accessory piece is represented by an elongate proximal portion and expanded distal portion, ventrally bent (see figs 3a and 4a).

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


**Taxonomic summary**

**Type host.** *Hoplias malabaricus* (Bloch).

**Site of infection.** Gill filaments.

**Type locality.** Baía das Pedras, Cuiabá River (Paraná River Basin; Paraguay, São Loureço Sub-basin), Mato Grosso State, Brazil (16°58′S, 56°25′W).

**Comparative measurements**

The comparative measurements of specimens of *U. brasiliensis* from three localities are listed in table 2.

**Other records.** *Hoplias malabaricus,* Guandú River (East Atlantic Basin; Macaé, São João Sub-basin), Municipality of Rio de Janeiro, Rio de Janeiro State, Brazil (22°48′N, 43°37′W); Upper Paraná River floodplain, Parana and Mato Grosso do Sul State, Brazil (22°43′00″S, 53°10′00″W); Cristalino River (Tocantins River Basin; Araguaia, Mortes Javaés Sub-basin), Mato Grosso State, Brazil (13°22′00″S, 50°52′00″W); Caeté River, Municipality of Bragança, Pará State, Brazil (1°54.82′S, 46°41′37.60″W); Maracanã River, Municipality of Nova Timboteua, Pará State, Brazil (1°35.62′S, 47°21′11.64″W); Pirá River, Municipality of Viseu, Pará State, Brazil (1°12′44.65″S, 46°17′36.72″W); Gurupi River, Municipality of Viseu, Pará State, Brazil (1°17′37.6″S, 46°11′0.49″W); Maparanã River, Municipality of Terra Alta, Pará State, Brazil (1°50′10″S, 47°35′43.98″W); Itabocal River, Municipality of Itaituba, Pará State, Brazil (1°51′59.82″S, 47°24′17.15″W).

**Specimens studied.** Five paratypes: CHIOC nos 37470b–f. Fourteen vouchers: CHIOC nos 38612–38615, 38648a–c, 38654; INPA nos 721a–b; MPEG nos 0096–0099.
morphometrically from specimens from the type locality (Cuiabá River) and voucher specimens from Cristalino River.

Uroleioides cuiabai Rosim, Mendoza-Franco & Luque, 2011


Taxonomic summary

Type host. Hoplias malabaricus (Bloch).

Site of infestation. Gill filaments.

Type locality. Baía das Pedras Cuiabá River, Mato Grosso State, Brazil (16°58′S, 56°25′W).

Other records. Hoplias malabaricus, Maracanã River, Municipality of Nova Timboteua, state of Pará, Brazil (1°7′46.32″S, 47°21′11.64″W); Gurupi River, Municipality of Viseu, Pará State, Brazil (1°17′37.6″S, 46°11′0.49″W); Piria River, Municipality of Viseu, Pará State, Brazil (1°12′44.65″S, 46°17′36.72″W).

Specimens studied. Four paratypes: CHIOC nos 37469b–e. Eleven vouchers: CHIOC nos 38622–38624, 38645, 38647; INPA nos 720a–b; MPEG nos 0103.

Comparative measurements

The comparative measurements of specimens of U. cuiabai from two localities are listed in table 3.

Remarks

The comparative analysis of the type material of U. brasiliensis (CHIOC 37470) and specimens of Uroleioides parasitizing the gills of H. malabaricus from the streams of the coastal drainages of the State of Pará indicated that they are conspecific, mainly by sharing the morphology of anchors and vagina. The specimens studied here differ

![Fig. 4. Uroleioides eremitus Kritsky, Thatcher & Boeger, 1986, voucher (CHIOC 37471). (a) Copulatory complex; (b) vaginal region showing vaginal sclerite, vaginal canal and muscular pad; (c) ventral bar; (d) dorsal bar; (e) hook pair 1; (f) hook pair 2; (g) ventral anchor; (h) dorsal anchor. Scale bars in μm.](image)

Table 2. Comparative measurements (in μm) of specimens of Uroleioides brasiliensis Rosim, Mendoza-Franco & Luque, 2011 from three localities.

<table>
<thead>
<tr>
<th>Coastal Rivers of north-east Pará</th>
<th>*Cuiabá River</th>
<th>Cristalino River</th>
</tr>
</thead>
<tbody>
<tr>
<td>Body length</td>
<td>375 (348–430; n = 5)</td>
<td>565 (520–618; n = 5)</td>
</tr>
<tr>
<td>Greatest width</td>
<td>104 (90–120; n = 4)</td>
<td>79 (66–97; n = 5)</td>
</tr>
<tr>
<td>Haptor length</td>
<td>81 (76–88; n = 4)</td>
<td>71 (66–75; n = 3)</td>
</tr>
<tr>
<td>Ventral anchor length</td>
<td>38 (36–43; n = 8)</td>
<td>50 (48–52; n = 6)</td>
</tr>
<tr>
<td>Base width</td>
<td>22 (24–20; n = 8)</td>
<td>35 (34–37; n = 4)</td>
</tr>
<tr>
<td>Dorsal anchor length</td>
<td>32 (30–35; n = 10)</td>
<td>37 (36–47; n = 10)</td>
</tr>
<tr>
<td>Base width</td>
<td>20 (18–21; n = 8)</td>
<td>26 (23–30; n = 4)</td>
</tr>
<tr>
<td>Ventral bar length</td>
<td>42 (40–45; n = 9)</td>
<td>37 (32–46; n = 4)</td>
</tr>
<tr>
<td>Dorsal bar length</td>
<td>32 (31–34; n = 9)</td>
<td>39 (32–49; n = 4)</td>
</tr>
<tr>
<td>Hook pair 1</td>
<td>15 (14–16; n = 9)</td>
<td>19 (18–22; n = 4)</td>
</tr>
<tr>
<td>Hook pairs 2–4, 6–7</td>
<td>23 (22–25; n = 9)</td>
<td>24 (21–26; n = 9)</td>
</tr>
<tr>
<td>MCO length</td>
<td>33 (23–44; n = 6)</td>
<td>44 (40–55; n = 6)</td>
</tr>
<tr>
<td>Vaginal sclerite</td>
<td>32 (31–34; n = 8)</td>
<td>17 (15–18; n = 5)</td>
</tr>
</tbody>
</table>

*Type locality; MCO, male copulatory organ.
Table 3. Comparative measurements (in μm) of specimens of *Urocleidoides cuiabai* Rosim, Mendoza-Franco & Luque, 2011 from two localities. MCO = Male copulatory organ.

<table>
<thead>
<tr>
<th></th>
<th>Coastal Rivers of north-east Pará</th>
<th>*Cuibá River</th>
</tr>
</thead>
<tbody>
<tr>
<td>Body length</td>
<td>350 (311–389; n = 6)</td>
<td>304 (180–453; n = 7)</td>
</tr>
<tr>
<td>Greatest width</td>
<td>113 (127–98; n = 6)</td>
<td>61 (53–76; n = 6)</td>
</tr>
<tr>
<td>Haptor length</td>
<td>109 (85–126; n = 5)</td>
<td>64 (57–70; n = 5)</td>
</tr>
<tr>
<td>Ventral anchor</td>
<td>39.5 (41–58; n = 7)</td>
<td>46 (40–52; n = 19)</td>
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<tr>
<td>Dorsal anchor length</td>
<td>31 (28–34; n = 7)</td>
<td>48 (42–52; n = 21)</td>
</tr>
<tr>
<td>Ventral bar length</td>
<td>43 (37–50; n = 7)</td>
<td>41 (38–48; n = 9)</td>
</tr>
<tr>
<td>Dorsal bar length</td>
<td>31 (25–36; n = 8)</td>
<td>31 (28–35; n = 7)</td>
</tr>
<tr>
<td>Hook pair 1</td>
<td>14 (n = 1)</td>
<td>18 (17–19; n = 3)</td>
</tr>
<tr>
<td>Hook pairs 2–4, 6–7</td>
<td>25 (23–28; n = 2)</td>
<td>24 (22–28; n = 8)</td>
</tr>
<tr>
<td>MCO length</td>
<td>54 (40–70; n = 7)</td>
<td>42 (33–70; n = 9)</td>
</tr>
<tr>
<td>Vaginal sclerite</td>
<td>30 (26–34; n = 7)</td>
<td>45 (34–48; n = 10)</td>
</tr>
</tbody>
</table>

* Type locality: MCO, male copulatory organ.

Specimens studied here differ morphometrically from the other locality where this species was previously reported.

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


**Taxonomic summary**

**Type host.** *Hoplias malabaricus* (Bloch).

**Site of infestation.** Gill filaments.

**Type locality.** Janauacá Lake (Amazon River Basin; Solimões, Negro, Branco Sub-basin) near Manaus, Amazons State, Brazil.

**Other records.** *Hoplias malabaricus*, Maracanã River, Municipality of Nova Timboteua, Pará State, Brazil (1°17′46.0′′S, 47°21′11.64′′W); Piráí River, Municipality of Viseu, Pará State, Brazil (1°12′44.65′′S, 46°17′36.72′′W); Caeté River, Municipality of Bragança, Pará State, Brazil (1°3′54.82′′S, 46°41′37.60′′W).

**Specimens studied.** Holotype: INPA no. 141. Two paratypes: INPA nos 142a–b. Thirty-two vouchers: CHIOC nos 37471–q, 38625a–d, 38636, 38644, 38651; INPA nos 723a–c; MPEG nos 0104–0108.

**Comparative measurements**

The comparative measurements of specimens of *U. eremitus* from three localities are listed in table 4.

**Remarks**

Recently, Rosim et al. (2011) reported *U. eremitus* for specimens collected from *H. malabaricus* from the East Atlantic Basin (Guandú River) and Paraná River Basin (Cuibá, Jaguari-Mirim and Machado rivers). These authors recognized some morphological differences among those specimens when compared with specimens from the type series (i.e. four paratypes, USNPC 78764). Most significantly, these authors reported the presence of a conspicuous muscular pad on the left side of the body midline, at the level of the vaginal sclerite. Most of the available voucher specimens deposited in the CHIOC (37471–q) by Rosim et al. (2011) were, in general, in very poor condition (all specimens stained in Gomori’s trichrome). However, the presence of the muscular pad was confirmed for some specimens (fig. 4b). Nonetheless, examination of the type specimens, particularly the holotype (INPA 141) (stained in Gomori’s trichrome) (fig. 3b) and specimens of *U. eremitus* collected from coastal rivers of the Oriental Amazon Basin, demonstrated that the studied specimens do not possess the muscular pad. Although this feature can be relevant taxonomically, the comparative analysis of studied specimens (type and voucher specimens) allowed us to confirm that they are conspecific by sharing the similar morphology of the copulatory complex and haptoral structures (see figs 3a, c–h and 4a, c–h).

Rosim et al. (2011) recognized morphometrical differences in the length of the male copulatory organ among specimens collected in their study and the type material of *U. malabaricus* (17–30 vs. 136, respectively). These authors considered this feature, besides the presence of the muscular pad, an important characteristic in distinguishing the difference between both morphotypes. However, an examination of Rosim et al.’s (2011) specimens of *U. eremitus* during the present study demonstrated that the authors apparently measured the length of the male copulatory organ incorrectly. The measurements conducted herein demonstrate that those specimens did not differ morphometrically from the type specimens from other localities (table 4).

Iannacone & Luque (1993) reported the same species from *H. malabaricus* captured in the Tambopata River, Madre de Dios, Perú. *Urocleidoides eremitus* was also found parasitizing the same host in Chascomus Lake, Argentina by Suriano (1997). Examination of specimens from both localities will be necessary to determine the identity of the specimens (with or without muscular pad) and whether or not all specimens are conspecific with *U. eremitus*.

The presence of a muscular pad for some specimens assigned as *U. eremitus* from the East Atlantic Basin and Paraná River Basin, for instance, does not seem to be sufficient enough evidence to propose a new species. We agree with Rosim et al. (2011) that in order to prevent future synonyms, those specimens with a muscular pad should be provisionally accepted as conspecific with *U. eremitus* until the impact of a representative sampling of the geographic distribution (East Atlantic and Paraná River Basins vs. Amazon River Basin) on colonization/speciation events within this group of parasites is better understood.

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

Table 4. Comparative measurements (in μm) of specimens of *Urolepides eremitus* Kritsky, Thatcher & Boeger, 1986 from three localities.

<table>
<thead>
<tr>
<th></th>
<th><em>Amazonas</em></th>
<th>Pará</th>
<th>Rio de Janeiro</th>
</tr>
</thead>
<tbody>
<tr>
<td>Body length</td>
<td>546 (536–557; n = 2)</td>
<td>396 (360–432; n = 8)</td>
<td>510 (450–550; n = 15)</td>
</tr>
<tr>
<td>Greatest width</td>
<td>91 (87–95; n = 2)</td>
<td>105 (98–130; n = 6)</td>
<td>61 (50–66; n = 15)</td>
</tr>
<tr>
<td>Haptor length</td>
<td>105 (100–110; n = 2)</td>
<td>79 (69–80; n = 8)</td>
<td>99 (81–110; n = 12)</td>
</tr>
<tr>
<td>Ventral anchor length</td>
<td>46 (45–49; n = 3)</td>
<td>48 (45–50; n = 8)</td>
<td>49 (38–51; n = 15)</td>
</tr>
<tr>
<td>Base width</td>
<td>25 (23–27; n = 3)</td>
<td>22 (20–24; n = 6)</td>
<td>28 (26–30; n = 10)</td>
</tr>
<tr>
<td>Dorsal anchor length</td>
<td>39 (38–41; n = 3)</td>
<td>42 (41–44; n = 8)</td>
<td>39 (34–40; n = 15)</td>
</tr>
<tr>
<td>Base width</td>
<td>20 (19–21; n = 3)</td>
<td>19 (21–18; n = 5)</td>
<td>22 (22–24; n = 10)</td>
</tr>
<tr>
<td>Ventral bar length</td>
<td>34 (31–38; n = 3)</td>
<td>40 (38–44; n = 6)</td>
<td>31 (30–32; n = 11)</td>
</tr>
<tr>
<td>Dorsal bar length</td>
<td>33 (31–37; n = 3)</td>
<td>37 (35–39; n = 6)</td>
<td>30 (30–31; n = 10)</td>
</tr>
<tr>
<td>Hook pair 1</td>
<td>15 (15; n = 2)</td>
<td>17 (16–18; n = 4)</td>
<td>18 (17–18; n = 8)</td>
</tr>
<tr>
<td>Hook pairs 2, 3, 4, 6, 7</td>
<td>25 (23–28; n = 3)</td>
<td>25 (24–27; n = 8)</td>
<td>27 (25–27; n = 15)</td>
</tr>
<tr>
<td>MCO length</td>
<td>118 (104–126; n = 3)</td>
<td>128 (116–133; n = 5)</td>
<td>103 (93–124; n = 14)</td>
</tr>
<tr>
<td>Vaginal sclerite</td>
<td>20 (19–20; n = 2)</td>
<td>27 (26–29; n = 8)</td>
<td>45 (40–50; n = 15)</td>
</tr>
</tbody>
</table>

* Type locality; MCO, male copulatory organ.

**Taxonomic summary**

Type host. *Hoplias malabaricus* (Bloch).

Site of infestation. Gill filaments.

Type locality. Baia das Pedras, Cuiabá River, Mato Grosso State, Brazil (16°58'S, 56°25'W).

Other records. *Hoplias malabaricus*, Caeté River, Municipality of Bragança, Pará State, Brazil (1°3’54.82”S, 46°41’37.60”W); Gurupi River, Municipality of Viseu, Pará State, Brazil (1°17’37.6”S, 46°11’0.49”W); Maracanã River, Municipality of Nova Timboteua, Pará State, Brazil (1°7’46.32”S, 47°21’11.64”W); Maparanim River, Municipality of Terra Alta, Pará State, Brazil (1°5’0.10”S, 47°55’43.98”W); Piriri River, Municipality of Viseu, Pará State, Brazil (1°12’44.65”S, 46°17’36.72”W); Ibá River, Municipality of Irituia, Pará State, Brazil (1°51’59.82”S, 47°24’17.15”W).

Specimens studied. Two paratypes: CHIOC nos 37467a-b. Thirteen vouchers: CHIOC nos 38626–38629, 38641; INPA nos 722a–c; MPEG nos 0109–0113.

Comparative measurements

The comparative measurements of specimens of *U. malabaricus* from two localities are listed in table 5.

Remarks

A comparative analysis of the type material of *U. malabaricus* (CHIOC 37467) and specimens of *Urolepides eremitus* from *H. malabaricus* of the coastal rivers of Pará indicated that they are conspecific, mainly because they both share the presence of a pad surrounding the copulatory complex.

**Constrictoanchoratus n. gen.**

Diagnosis

Body divisible into cephalic region, trunk, haptor. Ventral cephalic lobe poorly developed or absent. Bilateral pairs of head organs opening laterally to cephalic region; cephalic glands lateral or posterolateral to pharynx. Eyes present (2 pairs); granules elongate. Mouth subterminal, midventral; pharynx muscular, glandular; oesophagus short. Two intestinal caeca, confluent posteriorly to gonads, lacking diverticula. Genital pore midventral near level of caecal bifurcation. Genital atrium muscular. Gonads tandem or testis post-germarial; testis dorsal to germinarium. Vas deferens looping left intestinal caecum; seminal vesicle a dilatation of vas deferens, sigmoid, looping dorso-ventrally before entering into the MCO. Copulatory complex comprising MCO, accessory piece; MCO sclerotized, coiled, clockwise, with conical base surrounded by sclerotized cap; circular sclerotized tandem brim associated with the base of the MCO present or absent; accessory piece sclerotized, non-articulated with the MCO. MCO length 26 (17–29; n = 5) (13–15; n = 2), Vaginal sclerite 28 (26–30; n = 5) 24 (23–27; n = 4). MCO, Male copulatory organ.

Table 5. Comparative measurements (in μm) of specimens of *Urolepides malabaricus* Rosim, Mendoza-Franco & Luque, 2011 from two localities.

<table>
<thead>
<tr>
<th>stripslashes From coastal rivers of north-east Pará</th>
<th>Paraná River</th>
</tr>
</thead>
<tbody>
<tr>
<td>Body length 312 (270–377; n = 6)</td>
<td>294 (260–352; n = 3)</td>
</tr>
<tr>
<td>Greatest width 88 (66–110; n = 7)</td>
<td>51 (47–58; n = 3)</td>
</tr>
<tr>
<td>Haptor length 74 (60–85; n = 6)</td>
<td>58 (55–60; n = 3)</td>
</tr>
<tr>
<td>Dorsal anchor length 34 (33–35; n = 3)</td>
<td>30 (26–35; n = 4)</td>
</tr>
<tr>
<td>Base width 18 (16–20; n = 3)</td>
<td>14 (15–15; n = 2)</td>
</tr>
<tr>
<td>Ventral anchor length 27 (26–28; n = 3)</td>
<td>33 (31–37; n = 4)</td>
</tr>
<tr>
<td>Base width 15 (14–16; n = 3)</td>
<td>15 (17–17; n = 2)</td>
</tr>
<tr>
<td>Ventral bar length 36 (34–37; n = 6)</td>
<td>24 (22–26; n = 3)</td>
</tr>
<tr>
<td>Dorsal bar length 30 (30–31; n = 2)</td>
<td>33 (32–35; n = 3)</td>
</tr>
<tr>
<td>Hook pair 1 15 (12–14; n = 3)</td>
<td>18 (n = 1)</td>
</tr>
<tr>
<td>Hook pairs 2–4, 6–7 22 (21–23; n = 3)</td>
<td>22 (20–25; n = 7)</td>
</tr>
<tr>
<td>MCO length 26 (17–29; n = 5)</td>
<td>13 (15–15; n = 2)</td>
</tr>
<tr>
<td>Vaginal sclerite 28 (26–30; n = 5)</td>
<td>24 (23–27; n = 4)</td>
</tr>
</tbody>
</table>
with caeca. Haptor armed with, 14 hooks (7 pairs) with ancyrocephaline distribution; hook comprising shank of two subunits. Pair of ventral, dorsal anchors; anchors with elongate superficial root, inconspicuous deep root; constriction present at the intersection between shaft and point. Ventral, dorsal bar present. Parasites of gills of Erythrinidae (Characiformes).

**Taxonomic summary**

**Type species.** Constrictoanchoratus ptilonophallus n. gen. n. sp. from Hoplias malabaricus (Bloch).

**Site of infestation.** Gill filaments.

**Type locality.** Maracanã River, Municipality of Nova Timbóteua, Pará State, Brazil (1°7′46.32″S 47°21′11.64″W).

**Other species.** Constrictoanchoratus lemmyi n. gen. n. sp.

**Other records.** Constrictoanchoratus ptilonophallus n. gen. n. sp. from Hoplias malabaricus, Caeté River, Municipality of Bragança, Pará State, Brazil (1°3′54.82″S, 46°41′37.60″W); Itabocal River, Municipality of Iritiuia, Pará State, Brasil (1°51′59.82″S, 47°24′17.15″W); Piriá River, Municipality of Viseu, Pará State, Brasil (1°24′46.65″S, 46°17′36.72″W); Marapanim River, Municipality of Terra Alta, Pará State, Brazil (1°5′0.10″S, 47°55′43.98″W); and Gurupi River, Municipality of Viseu, Pará State, Brazil (1°17′37.6″S, 46°11′0.49″W). Constrictoanchoratus lemmyi n. gen. n. sp. from Hoplias malabaricus, Itabocal River, Municipality of Iritiuia, Pará State, Brasil (1°51′59.82″S, 47°24′17.15″W).

**Etymology.** The generic name is from the Latin (constrict = constriction) and refers to the morphology of anchors.

**Remarks**

Features that distinguish Constrictoanchoratus n. gen. from other dactylogyrid genera that occur in erythrinid hosts include the presence of a male copulatory organ coiled with clockwise rings; ventral and dorsal anchors with elongate superficial root and inconspicuous deep root, a constriction at the intersection between the shaft and the point; and hook with inflated shank.

The presence of a constriction at the intersection between the shaft and point in ventral and dorsal anchors in the haptor is an unusual feature in Neotropical dactylogyrids. The character also occurs in the monotypic, Rhinonastes pseudocapsaloideum Kritsky, Thatcher & Boeger, 1988. However, R. pseudocapsaloideum possesses a single ventral anchor–bar complex, and 1 ventral, 6 marginal pairs of hooks located in the disc-shaped haptor, whereas species of Constrictoanchoratus n. gen. have two pairs of anchor–bar complexes (1 ventral, 1 dorsal) and hooks with ancyrocephaline distribution (Mizelle, 1936). Also, R. pseudocapsaloideum was encountered in the nasal cavities of characiform fish from Prochilodontidae, while species of Constrictoanchoratus n. gen. were encountered on the gills of Erythrinidae.

**Constrictoanchoratus ptilonophallus n. sp.**

**Description**

Based on 35 specimens (fig. 5); 13 mounted in Hoyer’s trichrome, 22 mounted in Hoyer’s medium. Body fusiform (fig. 5a), total length excluding haptor 386 (315–538; n = 20) long, 104 (81–160; n = 18) wide at level of germarium. Testament smooth. Cephalic margin tapered; poorly developed terminal lobes; three bilateral pairs of heads organs with rod-shaped secretion; cephalic glands unicellular, posteraloral to pharynx. Four eyes, posterior pair larger and slightly farther apart than anterior pair; accessory granules present in cephalic area, spherical. Mouth subterminal, midventral; pharynx sub-spherical, 28 (24–32; n = 11) long, 23 (20–27; n = 11) wide. Genital pore opening midventral; genital atrium muscular. Gonads overlapping; testis dorsal to germinarium. Testis saccate, 54 (48–58; n = 3) long, 18 (16–21; n = 4) wide. Prostatic reservoir not observed. MCO, with approximately 2½ rings, 171 (160–180; n = 11) long, base with a unilateral expanded sclerotized cap, distal aperture acute; circular sclerotized tandem brim associated with the base of the MCO with bilateral expanded sclerotized projections, wing shaped (fig. 5b). Accessory piece comprising an elongated sheath with a groove, which serves as a guide to MCO; proximal portion rounded, distal portion with one small elongate projection. Germinarium 54 (48–58; n = 3) long, 18 (16–21; n = 4) wide, elongated. Vagina comprising vaginal vestibule with soft tissue at proximal portion, heavily sclerotized at distal portion, cup-shape vaginal canal sclerotized, elongated, straight with spines at midpoint (fig. 5c). Seminal receptacle pyriform; Mehls’ glands, ootype not observed. Vitellaria dense throughout trunk, except in region of reproductive organs. Eggs not observed. Peduncle short. Haptor sub-hexagonal, 58 (55–75; n = 10) long, 86 (79–98; n = 11) wide. Anchors dissimilar. Ventral anchor (fig. 5i), base 38 (36–40; n = 8) long, with elongate superficial root 25 (24–28; n = 5) long, inconspicuous deep root, tip of superficial root covered with sclerotized cap; evenly curved shaft and point, forming angle of approximately 110°; distal portion of shaft, intersection shaft and point with longitudinal superficial groove; external shaft with expansion keel shaped; short point, robust; point extending at the level of tip of superficial root. Dorsal anchor (fig. 5j, k) 32 (30–34; n = 6) long, base 15 (14–15; n = 6) long, robust, with inconspicuous roots, evenly curved shaft, point; forming angle of approximately 110°; distal portion of shaft, intersection shaft and point with longitudinal superficial groove; short point, robust; point extending well past level of tip of inner base. Ventral bar (fig. 5b) 45 (41–50; n = 7) long, narrow, broadly V-shaped, with slightly enlarged ends. Dorsal bar (fig. 5g) 38 (38–45; n = 7) long, narrow, rod-shaped. Hooks similar in shape (fig. 5d–f), shank with inflation, erected thumb, lightly curved long shaft, delicate point, filamentous hook, loop of hook extending to union of shank subunits; hook pair 1, 18 (17–19; n = 7) long; pair 5, 15 (14–16; n = 3) long; pairs 2–4 and 6–7, 23 (22–23; n = 7) long.

**Taxonomic summary**

**Type host.** Hoplias malabaricus (Bloch).

**Site of infestation.** Gill filaments.
Type locality. Maracanã River, Municipality of Nova Timboteua, Pará State, Brazil (1°7′46.32″S, 47°21′11.64″W).

Other records. Hoplias malabaricus, Caeté River, Municipality of Bragança, Pará State, Brazil (1°3′54.82″S, 46°41′37.60″W); Itabocal River, Municipality of Irituia, Pará State, Brazil (1°51′59.82″S, 47°24′17.15″W); Maparanim River, Municipality of Terra Alta, Pará State, Brazil (1°5′0.10″S, 47°55′43.98″W); Piriá River, Municipality of Viseu, Pará State, Brazil (1°12′44.65″S, 46°17′36.72″W).

Specimens deposited. Holotype: CHIOC no. 38630a.
Fourteen paratypes: CHIOC nos 38630b, 38631a–e, 38653; INPA no. 709; MPEG nos 0086–0090. Nineteen vouchers: CHIOC nos 38632a–i, 38637; INPA no. 710; MPEG nos 0091–0095.

Etymology. The specific name (a noun) is from Greek (ptilon = wing + phallos = penis) and refers to the circular, sclerotized, tandem brim associated with the base of the male copulatory organ, with wing-shaped, bilateral, expanded, sclerotized projections.

Remarks
Constrictoanchoratus ptilonophilus n. gen. n. sp. is the type species of the genus. The new species is characterized
Constrictoanchoratus lemmyi n. sp.

Description
Based on six specimens (fig. 6); one mounted in Gomori’s trichrome, five mounted in Gray & Wess medium. Body fusiform, may be constricted near midlength, total length excluding haptor 415 (380–465; n = 4) long, 131(120–140; n = 4) wide at level of germarium. Tegument smooth. Cephalic margin tapered; poorly developed terminal lobes; three bilateral pairs of head organs with rod-shaped secretion; cephalic glands unicellular, posterolateral to pharynx. Four eyes, posterior pair larger than anterior pair; accessory granules present in cephalic area, elliptical. Mouth subterminal, midventral; pharynx spherical, 131 (120–140; n = 4) in diameter. Genital pore opening midventral; genital atrium muscular. Gonads overlapping; testis dorsal to germarium. Testis, prostatic reservoir not observed. MCO with approximately 1½ rings, 83 (80–85; n = 3) long base with sclerotized cap; distal aperture subterminal, hook shaped (fig. 6a). Accessory piece comprising an elongated sheath. Germarium 94 (87–100; n = 2) long, 40 (34–45; n = 2) wide, elongated. Vagina comprising vaginal vestibule, vaginal canal with soft tissue. Seminal receptacle pyriform; Mehlis’ glands, ootype not observed. Vitellaria dense throughout trunk, except in region of reproductive organs. Eggs not observed. Peduncle short. Haptor subhexagonal, 62 long, 103 wide. Anchors dissimilar. Ventral anchor (fig. 6e), base 16 (15–16; n = 3) long, with elongate superficial root, 38 (37–39; n = 3) long, inconspicuous deep root, anterior portion of superficial root covered with sclerotized cap; evenly curved shaft and point, forming angle of approximately 110°; short point, robust, extending at the level of tip of superficial root. Dorsal anchor (fig. 6f) base 18 (18; n = 2) long, robust, with elongate superficial root, subtriangular, 34 (33–35; n = 3) long, inconspicuous deep roots, evenly curved shaft, point; forming angle of approximately 100°, short point, robust; point extending well past level of tip of inner base. Ventral bar (fig. 6c) 54 (50–58; n = 2) long, slightly curved or straight rod with small terminal enlargements at ends, curved in anterior direction. Dorsal bar (fig. 6b) 40 (36–44; n = 2) long, narrow, rod-shaped, with bifurcated ends, slightly curved in posterior direction. Hooks similar in shape (fig. 6d), 18 (18–19; n = 4) long, shank with inflation, erected thumb, lightly curved long shaft, delicate point, filamentous hook, loop of hook extending to union of shank subunits.

Taxonomic summary
Type host. Hoplias malabaricus (Bloch).

Site of infestation. Gill filaments.

Type locality. Caeté River, Municipality of Bragança, Pará State, Brazil (1°3′54.82″S, 46°41′37.60″W).

Other records. Hoplias malabaricus, Itabocal River, Municipality of Irituia, Pará State, Brazil (1°51′59.82″S, 47°24′17.15″W).


Etymology. The specific name is in honor of ‘Lemmy’ Kilmister (1945–2015), leader of the heavy-metal band Motorhead, of whom the senior author is a big fan.

Remarks
This species differs from C. ptilonophallus n. gen. n. sp. mainly by having a male copulatory organ comprising a coil of about 1½ rings (2½ rings in C. ptilonophallus), distal aperture subterminal, hook-shaped (aperture terminal, acute in C. ptilonophallus); base with sclerotized margin, without sclerotized brims (present in C. ptilonophallus); vaginal vestibule and canal with soft tissue (heavily sclerotized in C. ptilonophallus); and dorsal bar with bifurcated ends (not bifurcated in C. ptilonophallus).

A key to the Dactylogyridae species from Erythrinidae is given below.
Key to Dactylogyridae species from Erythrinidae

1 Prostatic reservoir simple; male copulatory organ (MCO) a coiled tube; circular sclerotized tandem brim associated with the base of the MCO present or absent ................................................................. 2

- Prostatic reservoir separated into two/three zones; MCO a spiral tube (corkscrew like); circular sclerotized tandem brim associated with the base of the MCO present or absent .11 (Whittingtonocotyle)

2(1) Vaginal sclerite present; anchors with evenly curved shaft and point .............................. 3 (Urocleidoides)

- Vaginal sclerite absent; anchors with constriction at the intersection between shaft and point .......... 12 (Constrictioanchoratus)

3(2) MCO with two rings or fewer than two rings .......................................................................................................................... 4

- MCO with more than two rings ................................................................................................................................. 7

4(3) Anchors with superficial root at least three times larger than deep root; elongate shaft and point ... 5

- Anchors with superficial root twice as large as the deep root; short shaft and point; vaginal vestibule slightly sclerotized, bulb-shaped .......................................................... U. aimarai

5(4) Accessory piece delicate sheath, uniform; vaginal vestibule muscular or slightly sclerotized ...... 6

- Accessory piece distally bifurcated; vaginal vestibule muscular; parasites of nasal cavities ...... U. naris

6(5) Vaginal vestibule slightly sclerotized; anchors similar in size; dorsal bar slightly U-shaped with rounded ends; muscular pad surrounding the copulatory complex present .................. U. malabaricus

- Vaginal vestibule muscular; ventral anchor twice as large as the dorsal anchor; dorsal bar slightly U-shaped with bifurcated ends; MCO with proximal bulb .................................................. U. bulbophallus sp. n.

7(3) Anchors with inconspicuous deep roots (at least ⅛ the size of superficial root) ....................... 8

- Anchors with developed deep roots (no more than ¼ the size of superficial root) ..................... 9

8(7) Dorsal bar slightly U-shaped with rounded ends; vaginal canal heavily sclerotized at proximal portion with a dilatation at middle portion, distal portion an elongate tube slightly sclerotized .. U. paranae sp. n.

- Dorsal bar slightly U-shaped with bifurcated ends; vaginal canal slightly sclerotized, expanded as a corrugated bag ........................................................................................................ U. cuiabai

9(7) Eyespots present; vaginal aperture marginal; vaginal sclerite with grooves ............................ 10

- Eyespots absent; vaginal aperture ventral; vaginal sclerite without grooves ...................... U. xinguensis

10(9) Vaginal canal, heavily sclerotized, an undulated tube with a proximal looping .................. U. eremitus

- Vaginal canal slightly sclerotized, a corrugated bag .......................................................... U. brasiliensis

11(1) Prostatic reservoir separated into two zones; vaginal canal convolute; dorsal bar with long anteromedial process .......................... W. caelaei

- Prostatic reservoir separated in three zones; vaginal canal sigmoid; dorsal bar with short anteromedial process .................................................. W. jeju

12(2) Vaginal vestibule and vaginal canal heavily sclerotized; MCO with 2½ rings; circular sclerotized tandem brim associated with the base of the MCO present ...................... C. philonophallus n. gen. n. sp.

- Vaginal vestibule and vaginal canal with soft tissue; MCO with 1½ rings ................... C. lenmyi n. gen. n. sp.

Discussion

From the eight valid species of Monogenoidea known to parasitize the gills of species of Hoplias in Brazil, Argentina and Peru, only five species were reported for H. malabaricus. Urocleidoides eremitus was the first species of monogenoid described from this host species, which was captured in the rivers of the Occidental Brazilian Amazon Basin by Kritsky et al. (1986). Later, four other species of this genus (U. brasiliensis Rosim, Mendoza-Franco & Luque, 2011, U. cuiabai Rosim, Mendoza-Franco & Luque, 2011, U. malabaricus Rosim, Mendoza-Franco & Luque, 2011 and Urocleidoides naris Rosim, Mendoza-Franco & Luque, 2011) were described and/or reported from other Brazilian regions (south, south-east and mid-west regions of Brazil) (Rosim et al., 2011).

Mizelle & Price (1964) proposed Urocleidoides Mizelle & Price 1964 for their new species, U. reticulatus Mizelle &
Price, 1964. The new species was found parasitizing the gills of Poecilia reticulata Peters (Poeciliidae) collected in the Capitol Aquarium, Sacramento, California, USA. After the revision of the genus proposed by Kritsky et al. (1986), Urocleidoides was restricted to species possessing a sinistral vaginal sclerite, overlapping or tandem gonads, a male copulatory organ with counterclockwise rings, and the morphology of haptoral structures. Actually, the genus contains 20 valid species (Kritsky et al., 1986; Mendoza-Franco et al., 1999, 2007; Jogunoori et al., 2004; Mendoza-Franco & Reina, 2008; Moreira et al., 2015) from fish hosts representing two ostariophysian teleost orders (Characiformes and Gymnotiformes) and Cyprinodontiformes from South America, Central America and Mexico (table 6).

Mendoza-Franco & Reina (2008) described Urocleidoides advenai Mendoza-Franco & Reina. 2008 taken from the gills of Brachy hypomnus occidentalis (Regan) (Gymnotiformes) in Central America. This species shares the morphology of the copulatory complex with other species of the Urocleidoides; however, it is also characterized by the absence of the vaginal sclerite. Mendoza-Franco & Reina (2008) considered that the main limitation in determining the diagnostic limits of Urocleidoides was the lack of a cladistic analysis for this genus.

For taxonomy purposes, we opted to follow Kritsky et al. (1986) in their taxonomic diagnosis of Urocleidoides; therefore, we consider U. advenai as belonging to Urocleidoides sensu lato. Besides U. advenai, nine other species of Urocleidoides are currently considered as incertae sedis and remain to be re-assigned to appropriate genera in the Neotropics: U. astyanacis Gioia, da Silva Cordeiro & de Toledo Artigas 1988, U. strictus Mizelle, Kritsky & Crane 1968, U. trinidadensis Molnar, Hanek & Fernando 1974 from Characiformes; U. carapus Mizelle, Kritsky & Crane 1968, U. gymnatus Mizelle, Kritsky & Crane 1968 and U. virescens from Gymnotiformes; and U. amazonensis Mizelle & Kritsky 1969, U. catus Mizelle & Kritsky 1969 and U. megorchis Mizelle & Kritsky 1969 from Siluriformes. We believe that future phylogenetic studies using morphological and/or molecular characters with appropriate taxon sampling will help us to define the real taxonomic status of these ten species.

Urocleidoides brasiliensis Rosim, Mendoza-Franco & Luque, 2011, U. cuiabai Rosim, Mendoza-Franco and Luque, 2011, U. eremitus Kritsky, Thatcher & Boeger, 1986 and U. malabaricus Rosim, Mendoza-Franco & Luque, 2011 are reported here for the first time to be parasitizing the gills of H. malabaricus from streams located in the Oriental Amazon Basin. The analysis of specimens of U. eremitus from different localities revealed that they are morphologically similar (figs 3 and 4). The only exception was U. eremitus from the Upper Paraná River floodplain, which represents a new species of Urocleidoides, described here as U. paraeae sp. n. We detected that the specimens of U. brasiliensis, U. cuiabai and U. malabaricus reported in the present work, differ morphometrically from those presented by Rosim et al. (2011). These authors also detected variations in the shape and size of haptoral structures of U. brasiliensis, U. cuiabai and U. eremitus from H. malabaricus captured in different locations in Brazil and considered them to be intraspecific variations. This is probably due to the geographic distance or even due to the results of phenotypic plasticity of parasites or host-induced morphological change, as suggested by León-Regagnon et al. (2005).

Domíngues & Marques (2011) also considered that the morphometric differences observed in some species of monogenoids from the genus Potamotrygonocotyle (Monocotylidae), which parasitize the gills of freshwater stingrays (Potamotrygonidae), could not be considered as evidence of interspecific variation. These authors conducted a cladistic analysis based on morphological characters for the species of Potamotrygonocotyle. The results suggested that there was no autopomorphic character that would sustain the maintenance of some nominal species as valid. Fehrleu-Ale & Littlewood (2011) conducted a molecular cladistic analysis on some species of Potamotrygonocotyle and discovered the existence of cryptic lineages, suggesting that the diversity of the genus may be underestimated.

Gasques et al. (2015) proposed the first molecular characterization of Urocleidoides cuiabai and U. malabaricus from Hoplias aff. malabaricus captured in the Upper Paraná River floodplain (Brazil) based on a fragment of the cytochrome c oxidase subunit 1 (COI) gene. These authors suggested that U. malabaricus could represent a cryptic lineage, based on the magnitude of genetic divergence. Although U. malabaricus is characterized mainly by the possession of a muscular pad surrounding the copulatory complex, this feature was also reported for U. eremitus from the East Atlantic Basin and Paraná River Basin (Rosim et al., 2011) (see also comments under the Remarks on U. eremitus), which challenges the taxonomy of the species when based on morphology or molecular data alone. Therefore, it raises the question: whether Gasques et al. (2015) were dealing with a cryptic species of ‘U. malabaricus complex’ or if there was a misidentification of a congenic species, such as U. eremitus. We suggest that a detailed taxonomic/morphological characterization be undertaken, and we also recommend that more than two species be included to propose an optimal phylogenetic tree for this group.

Parasitic organisms have been used as biological markers to discriminate fish stocks and to determine migration routes (Mackenzie, 1987, 2002), as well as to evaluate the phylogenetic relationships of their hosts (Brooks & Glen, 1982; Brooks et al., 1989; Brooks & McLennan, 1991, 1993; Hoberg, 1992; Klassen, 1992). Among the parasite groups in fish hosts, monogeneoid parasites represent an excellent biological marker (Tirard et al., 1992; Lambert & El Gharbi, 1995) and an excellent evolutionary model (Boeger & Kritsky, 1989, 1997, 2003; Domingues & Boeger, 2005), mainly because they possess a direct life cycle (monoxenic) and an exceptional host specificity (Bychowsky, 1957). In addition to morphological, genetic and molecular assessment, other features, such as parasite infestation, could be a valuable source of information and could potentially be used for host species recognition.

Morphological, cytogenetic and molecular evidence indicates that H. malabaricus is a species complex (Bartolino et al., 2000; Oyakawa, 2003; Santos et al., 2009). Santos et al. (2009) reported that some lineages of erythrinid fish recognized as H. malabaricus belong to a different species when comparing cytogenetic and molecular
The occurrence of monogenoidean parasites infesting H. malabaricus from different Brazilian river basins provides evidence that the diversity of monogeneoids from this host requires further study. Nadler & Pérez-Ponce de Léon (2011) suggested that parasitological studies should include broader aspects of comparative biology, such as systematics, evolution, ecology and biogeography/phylogeography.

Finally, it is an open question whether U. paranai n. sp. should be restricted only to the Paraná River, in the same way as U. bulbohullus n. sp. and species of Constrictoanchoratus are restricted only to the coastal drainage ecosystem of the Oriental Amazon rivers. The taxonomic status of species of Uroleidoides infecting H. malabaricus collected from other hydrographic basins should be studied for a more refined analysis, especially with the verification of molecular data and appropriate tax sampling.

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Table 6. List of species of Uroleidoides sensu stricto. Orders of fishes: Gym., Gymnotiformes; Char., Characiformes; Cyp., Cyprinodontiformes. Countries: ARG, Argentina; BRA, Brazil; COL, Colombia; ESA, El Salvador; GUA, Guatemala; IND, India; MEX, Mexico; PAN, Panama; TRI, Trinidad.

<table>
<thead>
<tr>
<th>Parasite</th>
<th>Host species</th>
<th>Host order</th>
<th>Host family</th>
<th>Country</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>U. brasiliensis</td>
<td>Hoplias malabaricus</td>
<td>Char.</td>
<td>Erythrinidae</td>
<td>MEX</td>
<td>Mendoza-Franco et al. (1999)</td>
</tr>
<tr>
<td>U. cuibai</td>
<td>H. malabaricus</td>
<td>Char.</td>
<td>Erythrinidae</td>
<td>BRA</td>
<td>Rosim et al. (2011)</td>
</tr>
<tr>
<td>U. eremitus</td>
<td>H. malabaricus</td>
<td>Char.</td>
<td>Erythrinidae</td>
<td>BRA</td>
<td>Kritsky et al. (1986)</td>
</tr>
<tr>
<td>U. flegomai</td>
<td>Patubica panamensis</td>
<td>Char.</td>
<td>Lebiasinidae</td>
<td>PAN</td>
<td>Mendoza-Franco et al. (2007)</td>
</tr>
<tr>
<td>U. malabaricuisi</td>
<td>H. malabaricus</td>
<td>Char.</td>
<td>Erythrinidae</td>
<td>BRA</td>
<td>Rosim et al. (2011)</td>
</tr>
<tr>
<td>U. naris</td>
<td>H. malabaricus</td>
<td>Char.</td>
<td>Erythrinidae</td>
<td>BRA</td>
<td>Rosim et al. (2011)</td>
</tr>
<tr>
<td>U. paradoxus</td>
<td>Leporinus elongatus</td>
<td>Char.</td>
<td>Anostomidae</td>
<td>BRA</td>
<td>Kritsky et al. (1986)</td>
</tr>
<tr>
<td>U. reticulatus</td>
<td>Poecilia reticulata</td>
<td>Cyp.</td>
<td>Poeciliidae</td>
<td>TRIN</td>
<td>Mizele &amp; Price (1964)</td>
</tr>
<tr>
<td>U. similancus</td>
<td>Poecilia gliii</td>
<td>Cyp.</td>
<td>Poeciliidae</td>
<td>PAN</td>
<td>Mendoza-Franco et al. (2007)</td>
</tr>
<tr>
<td></td>
<td>Profundulus oaxacae</td>
<td>Cyp.</td>
<td>Profundulidae</td>
<td>MEX</td>
<td>Mendoza-Franco et al. (2015)</td>
</tr>
<tr>
<td></td>
<td>Profundulus sp. 1</td>
<td>Cyp.</td>
<td>Profundulidae</td>
<td>MEX</td>
<td>Mendoza-Franco et al. (2015)</td>
</tr>
<tr>
<td></td>
<td>Profundulus sp. 2</td>
<td>Cyp.</td>
<td>Profundulidae</td>
<td>MEX</td>
<td>Mendoza-Franco et al. (2015)</td>
</tr>
<tr>
<td></td>
<td>Profundulus labialis</td>
<td>Cyp.</td>
<td>Profundulidae</td>
<td>MEX</td>
<td>Mendoza-Franco et al. (2015)</td>
</tr>
<tr>
<td></td>
<td>Profundulus guatemalensis</td>
<td>Cyp.</td>
<td>Profundulidae</td>
<td>GUA</td>
<td>Mendoza-Franco et al. (2015)</td>
</tr>
<tr>
<td></td>
<td>Profundulus kreiseri</td>
<td>Cyp.</td>
<td>Profundulidae</td>
<td>ESA</td>
<td>Mendoza-Franco et al. (2015)</td>
</tr>
<tr>
<td></td>
<td>P. binaculata</td>
<td>Cyp.</td>
<td>Poeciliidae</td>
<td>PAN</td>
<td>Mendoza-Franco et al. (2015)</td>
</tr>
</tbody>
</table>

character, and at least some karyotypic strains are related to H. malabaricus. Recent studies indicate that a single karyomorph of H. malabaricus can harbour more than one species of Hoplias (Marques et al., 2013). Among parasites, Uroleidoides sensu stricto has the largest range, parasitizing nine families of three orders. On the host-parasite network proposed by Braga et al. (2014), Uroleidoides is indicated as a provincial hub with many interactions, and most of them are modular, being influenced by spatial structure and phylogenetic relatedness of species.

The occurrence of monogenoidean parasites infesting H. malabaricus from different Brazilian river basins provides evidence that the diversity of monogeneoids from this host requires further study. Nadler & Pérez-Ponce de Léon (2011) suggested that parasitological studies should include broader aspects of comparative biology, such as systematics, evolution, ecology and biogeography/phylogeography.

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Conflict of interest

None.

Ethical standards

Specimens were collected under the license for collection of biological material (43381–1) granted by the Instituto Chico Mendes de Conservação da Biodiversidade (ICMBio).

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India, the proposal of *Heterotylotus* n. g. and *Diaphorocotyleus* n. g., and the reassignment of some previously described species of *Urocletoides* Mizelle & Price, 1964 (Polyonchoinea: Dactylogyridae). *Systematic Parasitology* 58, 115–124.


