



New species of *Anacanthorus* (Dactylogyridae: Anacanthorinae) from the gills of *Hoplerythrinus unitaeniatus* and *Erythrinus erythrinus* (Characiformes: Erythrinidae) of the coastal drainage in the Eastern Amazon, Brazil

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Abstract

Species of *Anacanthorus* are described from the gills of *Hoplerythrinus unitaeniatus* and *Erythrinus erythrinus* of drainage systems in the Northeastern Pará State, Brazil. *Anacanthorus scyphophallus* **sp. n.** has a male copulatory organ (MCO) with two small flaps in the distal portion; hooks with proximal shank dilatation comprising $\frac{1}{2}$ of the shank length. *Anacanthorus ataidei* **sp. n.** has an elongated MCO, with ribbon-like ornaments; hooks without proximal shank dilatation. *Anacanthorus siphonocommus* **sp. n.** has an MCO with aculeiform ornaments in the distal portion; hooks with proximal dilatation in the shank comprising $\frac{1}{2}$ of the shank length. *Anacanthorus maratininguensis* **sp. n.** has an MCO with a small projection in the form of a hook in the distal region; hooks with proximal dilatation comprising $\frac{1}{2}$ of the shank length. *Anacanthorus lacinimentulatus* **sp. n.** has an MCO with extrovert flap skirting its distal region; shank of hooks with proximal dilatation comprising $\frac{1}{2}$ of the total shank length. *Anacanthorus cururutuiensis* **sp. n.** presents an MCO with flexed lateral flap in the distal region; hooks with proximal dilatation in the shank comprising $\frac{1}{4}$ of the shank length. *Anacanthorus circumspatulatus* **sp. n.** has an MCO with ornaments in the form of pointed and interleaved blades; hooks with proximal shank dilatation comprising approximately $\frac{1}{2}$ of the shank length. *Anacanthorus acrophallus* **sp. n.** has MCO with a small pointed sinistral flap; hooks with proximal dilatation in the shank comprising $\frac{1}{3}$ of the shank length. The host-parasite diversity scenario and specificity of *Anacanthorus* species regarding their characiform hosts are also discussed in this study.

Key words: *Anacanthorus*, Dactylogyridae, ectoparasite, Erythrinidae, new species, Taxonomy

Introduction

Within Monogenoidea, *Anacanthorus* Mizelle & Price, 1965 stands out for representing the genus with the highest number of species known among neotropical dactylogyrids. The genus comprises 73 described species, parasites of characiform fishes (Cohen *et al.* 2013; Leão *et al.* 2015; Monteiro *et al.* 2015). Of this total, 68 species occur in Brazilian waters, of which 57 are reported for fish of the Amazon River basin. The remaining species are known for the basins of the Paraná River (6 species), São Francisco River (4 species), and one species, *Anacanthorus penilabiatus* Boeger, Husak & Martins, 1995, was found in fish farms of the São Paulo State (Boeger *et al.* 1995). *Anacanthorus* species are found parasitizing species of the following characiform families: Serrasalminidae (35 described species), Triportheidae (18 described species), and Bryconidae (15 described species) (Cohen *et al.* 2012; Cohen *et al.* 2013; Leão *et al.* 2015; Monteiro *et al.* 2015). Other four non-described species of *Anacanthorus* are reported for fishes of the family Erythrinidae from the upper Paraná River and its tributaries, Brazil: *Hoplias malabaricus* (Bloch) (n= 1); *Hoplerythrinus unitaeniatus* (Spix & Agassiz) (n= 2); and *Erythrinus erythrinus* (Bloch & Schneider) (n= 1) (Graça *et al.* 2013a; Graça *et al.* 2013b; Graça *et al.* 2018).

During a study on the diversity of Monogenoidea parasites from the gills of *H. unitaeniatus* and *E. erythrinus* of coastal drainages in the Northeastern Pará, Eastern Amazon, eight new species of *Anacanthorus* were collected. They are described in this manuscript, which presents the first species of the genus formally described for erythrinid fishes of the Amazon region.

Material and methods

Thirteen specimens of *E. erythrinus* and twelve of *H. unitaeniatus* were collected using dip nets, trawls, and fishhooks. The hosts were collected in four localities of the Northeastern Pará: Igarapé Cururutuia—Caeté River (Atlantic Basin, North / Northeast stretch; Sub-basins of the Gurupi and Turiaçu rivers), municipality of Bragança (1°4'44.55"S 46°44'18.54"W); Igarapé Arinandeua—Guamá River (Atlantic Basin, North / Northeast stretch; Sub-basins of the Meruu, Acará, and Guamá rivers), municipality of São Miguel do Guamá (1°37'42.50"S 47°29'45.06"W); Igarapé Maratininga—Moju River (Atlantic Basin, North / Northeast stretch; Sub-basins of the Meruu, Acará, and Guamá rivers) municipality of Tailândia (02°27'55.7"S 048°53'27.6"W); and Pratinha Community—Caeté River (Atlantic Basin, North / Northeast stretch; Sub-basins of the Gurupi and Turiaçu rivers) municipality of Bragança (1°5'2.49"S 46°49'44.67"W). The nomenclature of basins follows Brazil's National Water Agency, Ministry of the Environment, Brazil (<http://hidroweb.ana.gov.br/>).

Gill arches of hosts were removed and put into labeled vials containing warm water (~65°C). Each vial was vigorously shaken and, subsequently, formalin was added until reaching a 5% final solution. In the laboratory, the gill arches and wash sediment were analyzed using a Leica S6E stereomicroscope, and the helminths were removed, counted, and identified. For the morphological analysis, some specimens were stained with Gomori trichrome (Humason 1979; Boeger & Vianna 2006) and mounted on Dammar gum for studies on internal morphology; or mounted in Hoyer's or Gray & Wess mediums (Humason 1979; Boeger & Vianna 2006) to study the sclerotized structures. The illustrations were prepared using a light chamber coupled to a Leica DM 2500 optical microscope. Calculations of prevalence and mean intensity followed Bush *et al.* (1997). All measurements were obtained according to the procedures of Mizelle & Klucka (1953) and are presented in micrometers. The size of internal organs and other structures represents the largest measure in the dorso-ventral view and were measured using a micrometer eye-piece. The classification of hooks followed Mizelle & Price (1963). Morphological terminology is that of Kritsky & Mizelle (1968), Mizelle *et al.* (1968) and Boeger & Vianna (2006). The measurements are represented by the mean from the maximum and minimum lengths and the number of specimens measured (n). Type specimens of each new species were deposited in following Brazil's national collections: Helminthological Collection, Instituto Oswaldo Cruz (CHIOC), Rio de Janeiro, Rio de Janeiro State; Invertebrate Collection, Instituto Nacional de Pesquisas da Amazonia (INPA), Manaus, Amazonas State; and the Invertebrate Collection, Museu Paraense Emilio Goeldi (MPEG), Belém, Pará State.

Results

Class Monogenoidea Bychowsky, 1937

Subclass Polyonchoinea Bychowsky, 1937

Order Dactylogyridea Bychowsky, 1937

Dactylogyridae Bychowsky, 1933

Anacanthorus Mizelle & Price, 1965

Anacanthorus scyphophallus sp. n.

(Figs. 1–3)

Type-host: *Erythrinus erythrinus* (Bloch & Schneider), Erythrinidae.

Site of infection: Gills.

Type-locality: Igarapé Cururutuaia—Caeté River, municipality of Bragança, State of Pará, Brazil (1°4'44.55"S 46°44'18.54"W).

Prevalence: 50% of two hosts examined.

Mean intensity: 5 parasites per host infected.

Specimens deposited: Holotype: CHIOC no. 40037 a. 3 paratypes: CHIOC nos. 40037 b–d.

ZooBank registration: The Life Science Identifier (LSID) urn: lsid:zoobank.org:act:F168AB80-F090-46FA-BE3A-E1D45A7F5AA0.

Etymology: The specific epithet derives from the Greek (*scypho* = cup + *phallus* = penis) and refers to the MCO morphology, small and cup-shaped.

Description: (Based on four specimens, two mounted in Gomori trichrome, two mounted in Hoyer's). Elongated and fusiform body 378 (235–566; n=4) long, excluding the haptor, 88 (65–117; n=4) wide at the height of germarium (Fig. 1). Four cephalic lobes poorly developed; four groups of head organs; cephalic glands not observed. Two pairs of ocelli, anterior pair smaller than the posterior pair; accessory granules present or absent, oval-shaped, scattered in the cephalic area (Fig. 1). Pharynx subspherical 30 (24–36; n=4) long, 27 (21–37; n=4) wide; short esophagus (Fig. 1). Two intestinal caeca, confluent, posterior to the gonads (Fig. 1). Male copulatory organ (MCO) 27 (21–32; n=4) long, 11 (9–15; n=4) wide, sclerotized, tubular, short, cup-shaped with two small flaps in the distal portion (Fig. 2); accessory piece absent (Fig. 2). Seminal vesicle sigmoid. Gonads overlapping; germarium fusiform 57 (40–78; n=4) long, 21 (14–28; n=4) wide; testis oval 27 (n=1) long, 16 (n=1) wide, dorsal to germarium (Fig. 1). Prostatic reservoir, uterus, genital pore, and egg not observed. Peduncle elongated (Fig. 1). Haptor subtriangular 54 (31–73; n=4) long, 45 (30–56; n=4) wide (Fig. 1). 4A hooks not observed. Seven pairs of similar hooks 35 (34–37; n=3) long, blade moderately elongated, point short and slightly curved, thumb rounded and poorly developed and shank 17 (16–18; n=3) long, with proximal dilatation comprising ½ of the shank length (Fig. 3). Hook filament delicate, extending until near the shank dilatation (Fig. 3).

Remarks: *Anacanthorus scyphophallus* sp. n. is similar to *Anacanthorus brevicirrus* Monteiro, Kritsky & Brasil-Sato, 2010 based on the MCO morphology. *Anacanthorus scyphophallus* sp. n. has a hook with rounded thumb and shank with proximal dilatation comprising ½ of the shank length, whereas *A. brevicirrus* has reduced thumb and shank with a small dilatation in the proximal region in the form of a bulb, containing a translucent spot. Moreover, the new species is characterized by overlapping gonads (tandem in *A. brevicirrus*).

Anacanthorus ataidei sp. n.

(Figs. 4–7)

Type-host: *Erythrinus erythrinus* (Bloch & Schneider), Erythrinidae.

Site of infection: Gills.

Type-locality: Igarapé Cururutuaia—Caeté River, municipality of Bragança, State of Pará, Brazil (1°4'44.55"S 46°44'18.54"W).

Other localities: *Erythrinus erythrinus* (Prevalence: 20% of five hosts examined; Mean intensity: five parasites per host infected), Pratinha Community—Caeté River, municipality of Bragança, Pará State (1°5'2.49"S 46°49'44.67"W); *E. erythrinus* (Prevalence: 25% of the four hosts examined; Mean intensity: six parasites per host infected), Igarapé Maratinga—Moju River, municipality of Tailândia, Pará State (02°27'55.7"S 048°53'27.6"W).

Prevalence: 50% of two hosts examined.

Mean intensity: 10, 5 parasites per host infected.

Specimens deposited: Holotype: CHIOC no. 40026 a. 19 paratypes: CHIOC nos. 40026 b–k; INPA no. 801; MPEG nos. 151–155. 8 vouchers: CHIOC nos. 40027 a–c; INPA nos. 802–803; MPEG no. 156.

ZooBank registration: The Life Science Identifier (LSID) urn: lsid:zoobank.org:act:57058C57-7341-4762-B5E7-E6EEA4033EDB.

Etymology: The specific epithet of the species is named after a local legend from the Northeast Pará, Brazil. Ataíde is a man-like being who inhabits the floodplains and mangroves of Pará State and is known for having a prominent genital organ.

Comparative measurements: Table 1.

Description: (Based on twenty specimens, nine mounted in Gomori trichrome, eight mounted in Grey & Wess, and three mounted in Hoyer's). Body fusiform 301 (213–424; n=17) long, excluding the haptor, 81 (37–122; n=18) wide at the height of germarium (Fig. 7). Four cephalic lobes poorly developed; three groups of head organs; cephalic glands not observed (Fig. 7). Two pairs of ocelli, similar in size; accessory granules present, oval-shaped, little scattered in the cephalic area (Fig. 7). Pharynx spheric 20 (16–29; n=14) long, 20 (15–26; n=15) wide; oesophagus elongated (Fig. 7). Two intestinal caeca, confluent, posterior to the gonads (Fig. 7). Genital pore not observed. MCO 179 (112–239; n=11) long, sclerotized, tubular, elongated, extending proximally from the esophagus to close the peduncle region, comprising approximately 60% of the body length, with ribbon-like ornaments around the MCO (Fig. 4); accessory piece absent (Fig. 4). Seminal vesicle long, ascendant branch of the vas deferens looping the right intestinal caecum and posteriorly with a descendant branch, forming the seminal vesicle dorsal to germarium (Fig. 4). Gonads not overlapping; germarium pyriform 45 (33–62; n=12) long, 27 (19–35; n=12) wide; testis oval 26 (17–31; n=4) long, 22 (19–25; n=4) wide, posterior to germarium (Fig. 7). Uterus, muscular and with thick walls. Prostatic reservoir elongated, located near to the germarium with descendant duct directed to the of the MCO (Fig. 7). Peduncle short (Fig. 7). Haptor sub-hexagonal 34 (18–47; n=15) long, 34 (18–47; n=14) wide (Fig. 7). Similar 4A hooks 10 (9–11; n=7) long (Fig. 6). Seven pairs of similar hooks 16 (14–17; n=6) long; blade relatively elongated and slightly curved, point short and curved, delicate shank without proximal dilatation, thumb erect and slightly depressed (Fig. 5). Hook filament delicate, extending more than the half of the shank (Fig. 5).

Remarks: *Anacanthorus ataidei* sp. n. is similar to *Anacanthorus franciscanus* Monteiro, Kritsky & Brasil-Sato, 2010 parasite of *Brycon orthotaenia* Günther (Characiformes: Bryconidae) for having an elongated and tubular MCO. The new species differs from *A. franciscanus* by an elongated MCO, comprising approximately 60% of the body length with ornaments in the form of twisted slides around the MCO (in *A. franciscanus*, the MCO has no ornaments). Besides, *A. franciscanus* is characterized by the presence of the shank of hooks with proximal portion dilated in the form of a bulb with two translucent spots (in *Anacanthorus ataidei* sp. n., the hook has uniform shank).

TABLE 1. Comparative measurements (μm) of specimens of *Anacanthorus ataidei* sp. n. from the gills of *Erythrinus erythrinus* of three localities in Pará State, Brazil. MCO = male copulatory organ.

	Cururutua*	N	Tailândia	N	Pratinha	N
Body						
Length	301 (213–424)	27	390 (322–517)	5	338 (300–437)	3
Width	81 (37–122)	18	94 (70–142)	5	100 (75–137)	4
Haptor						
Length	34 (18–47)	15	55 (47–60)	5	68 (57–85)	3
Width	34 (18–47)	14	88 (67–115)	5	102 (95–112)	3
Pharynx						
Length	20 (16–29)	14	26 (25–30)	4	27 (22–31)	3
Width	20 (15–26)	15	27 (23–31)	4	30 (27–33)	3
MCO	179 (112–239)	11	207 (128–272)	5	209 (194–233)	3
Germarium						
Length	45 (33–62)	12	–	–	–	–
Width	27 (19–35)	12	–	–	–	–
Testis						
Length	26 (17–31)	4	–	–	–	–
Width	22 (19–25)	4	–	–	–	–
Hook pair 1–7	16 (14–17)	6	17 (16–18)	5	17 (17–18)	4
4A hooks	10 (9–11)	7	11	1	11 (10–11)	3

*Type locality

Anacanthorus siphonocommus sp. n.

(Figs. 8–11)

Type-host: *Hoplerythrinus unitaeniatus* (Spix & Agassiz), Erythrinidae.

Site of infection: Gills.

Type-locality: Igarapé Cururutuia—Caeté River, municipality of Bragança, State of Pará, Brazil (1°4'44.55"S 46°44'18.54"W).

Other localities: *Hoplerythrinus unitaeniatus* (Prevalence: 100% of four hosts examined; Mean intensity: 1,5 parasites per host infected), Igarapé Arinandeua—Guamá River, municipality of São Miguel do Guamá, Pará State (1°37'42.50"S 47°29'45.06"W).

Prevalence: 100% of one host examined.

Mean intensity: 7 parasites per host infected.

Specimens deposited: Holotype: CHIOC no. 40038 a. 3 paratypes: CHIOC nos. 40038 b–d. 9 vouchers: CHIOC nos. 40039 a–b; INPA no. 805; MPEG nos. 159–161.

ZooBank registration: The Life Science Identifier (LSID) urn: lsid:zoobank.org:act:F348B068-1E19-4729-94A3-18EFBAB15872.

Etymology: The specific epithet derives from the Greek (*siphono* = tube + *commus* = ornament) and refers to the MCO morphology, tubular with ornaments, observed in the new species.

Comparative measurements: Table 2.

TABLE 2. Comparative measurements (μm) of specimens of *Anacanthorus siphonocommus* sp. n. from the gills of *Hoplerythrinus unitaeniatus* of two localities in the Pará State, Brazil. MCO = male copulatory organ.

	Cururutuia*	N	S.M.G	N
Body				
Length	427 (301–597)	5	398 (397–477)	5
Width	125 (97–171)	6	104 (82–127)	5
Haptor				
Length	61 (51–93)	5	52 (47–57)	5
Width	88 (64–108)	4	51 (45–57)	5
Pharynx				
Length	34 (30–38)	3	36 (30–41)	5
Width	26 (20–33)	3	34 (30–41)	5
MCO	86 (67–98)	7	88 (77–99)	6
Germarium				
Length	67 (60–75)	2	32 (30–33)	3
Width	27 (22–32)	2	24 (20–28)	3
Testis				
Length	42 (33–59)	4	43 (42–44)	2
Width	28 (20–31)	4	32 (31–33)	2
Hook pair 1–7	41 (39–43)	2	40 (38–44)	4
4A hooks	14	1	11	1
Dilatation of the shank	20 (19–21)	2	21 (19–23)	4

*Type locality / S.M.G = São Miguel do Guamá

Description: (Based on seven specimens, four mounted in Gomori trichrome, three mounted in Hoyer's). Body fusiform 427 (301–597; n=5) long, elongated, excluding the haptor, 125 (97–171; n=6) wide at the height of germarium (Fig. 8). Four cephalic lobes moderately developed; four groups of head organs; cephalic glands not observed (Fig. 8). Two pairs of ocelli, anterior pair smaller than posterior pair; posterior pair of ocelli more distant than the anterior pair; accessory granules present, little scattered in the cephalic area (Fig. 8). Pharynx oval 34 (30–38; n=3) long, 26 (20–33; n=3) wide; short esophagus (Fig. 8). Two intestinal caeca confluent and posterior to the gonads (Fig. 8). Genital pore not observed. MCO 86 (67–98; n=7) long, sclerotized, tubular, elongated, having a dilatation in the medial portion with aculeiform ornaments in the distal region (Fig. 11); accessory piece absent (Fig. 11). Seminal vesicle sigmoid. Uterus with sclerotized distal region. Gonads overlapping, germarium fusiform 67 (60–75; n=2) long, 27 (22–32; n=2) wide; testis elongated 42 (33–59; n=4) long, 28 (20–31; n=4) wide, dorsal to germarium (Fig. 8). Prostatic reservoir not observed. Peduncle long. Haptor sub-hexagonal 61 (51–93; n=5) long,

88 (64–108; n=4) wide (Fig. 8). Similar 4A hooks 14 (n=1) long (Fig. 10). Seven pairs of similar hooks 41 (39–43; n=2) long; blade robust and slightly curved; shank elongated with proximal dilatation comprising more than ½ of the shank length; proximal shank dilatation 21 (20–22; n=2) long; short and softly curved point; thumb developed and rounded (Fig. 9). Hook filament delicate, extending until near the shank dilatation (Fig. 9).

Remarks: *Anacanthorus siphonocommus* **sp. n.** differs from the remaining congeneric species mainly based on the MCO morphology, due to the presence of dilatation in the medial portion and aculeiform ornaments in the distal region of the MCO; *Anacanthorus siphonocommus* **sp. n.** also has hooks with proximal dilatation in the shank, comprising more than ½ of the shank length.

Anacanthorus maratininguensis **sp. n.**

(Figs. 12–15)

Type-host: *Hoplerythrinus unitaeniatus* (Spix & Agassiz), Erythrinidae.

Site of infection: Gills.

Type-locality: Igarapé Maratininga—Moju River, municipality of Tailândia, Pará State, Brazil (02°27'55.7"S 048°53'27.6"W).

Other localities: *Hoplerythrinus unitaeniatus* (Prevalence: 100% of one host examined. Mean intensity: 5 parasites per host infected), Igarapé Cururutua—Caeté River, municipality of Bragança, Pará State (1°4'44.55"S 46°44'18.54"W); *H. unitaeniatus* (Prevalence: 100% of three hosts examined; Mean intensity: two parasites per host infected), Igarapé Arinandeua—Guamá River, municipality of São Miguel do Guamá, Pará State (1°37'42.50"S 47°29'45.06"W).

Prevalence: 42% of three hosts examined.

Mean intensity: 3,33 parasites per host infected.

Specimens deposited: Holotype: CHIOC no. 40033 a. 8 paratypes: CHIOC nos. 40033 b–c, 40034 a–b; INPA no. 807; MPEG nos. 164–165. 10 vouchers: CHIOC nos. 40035 a–b, 40036 a–b; INPA no. 806; MPEG nos. 162–163.

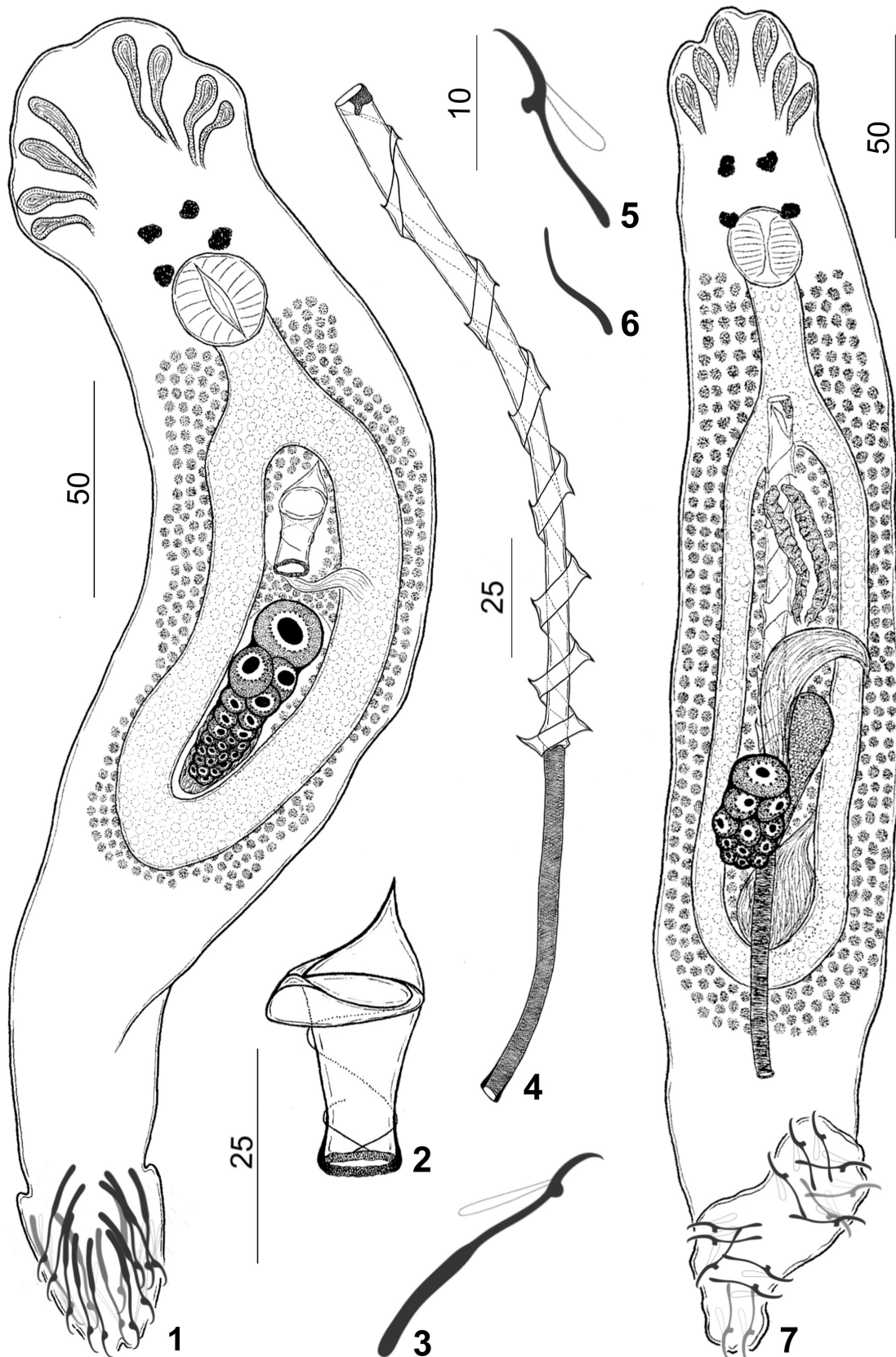
ZooBank registration: The Life Science Identifier (LSID) urn: lsid:zoobank.org:act:B94E19A2-2FAC-4C4A-84D4-04FE1EF2FF92.

Etymology: The specific epithet refers to the affluent river's name of the type locality of the species, Igarapé Maratininga.

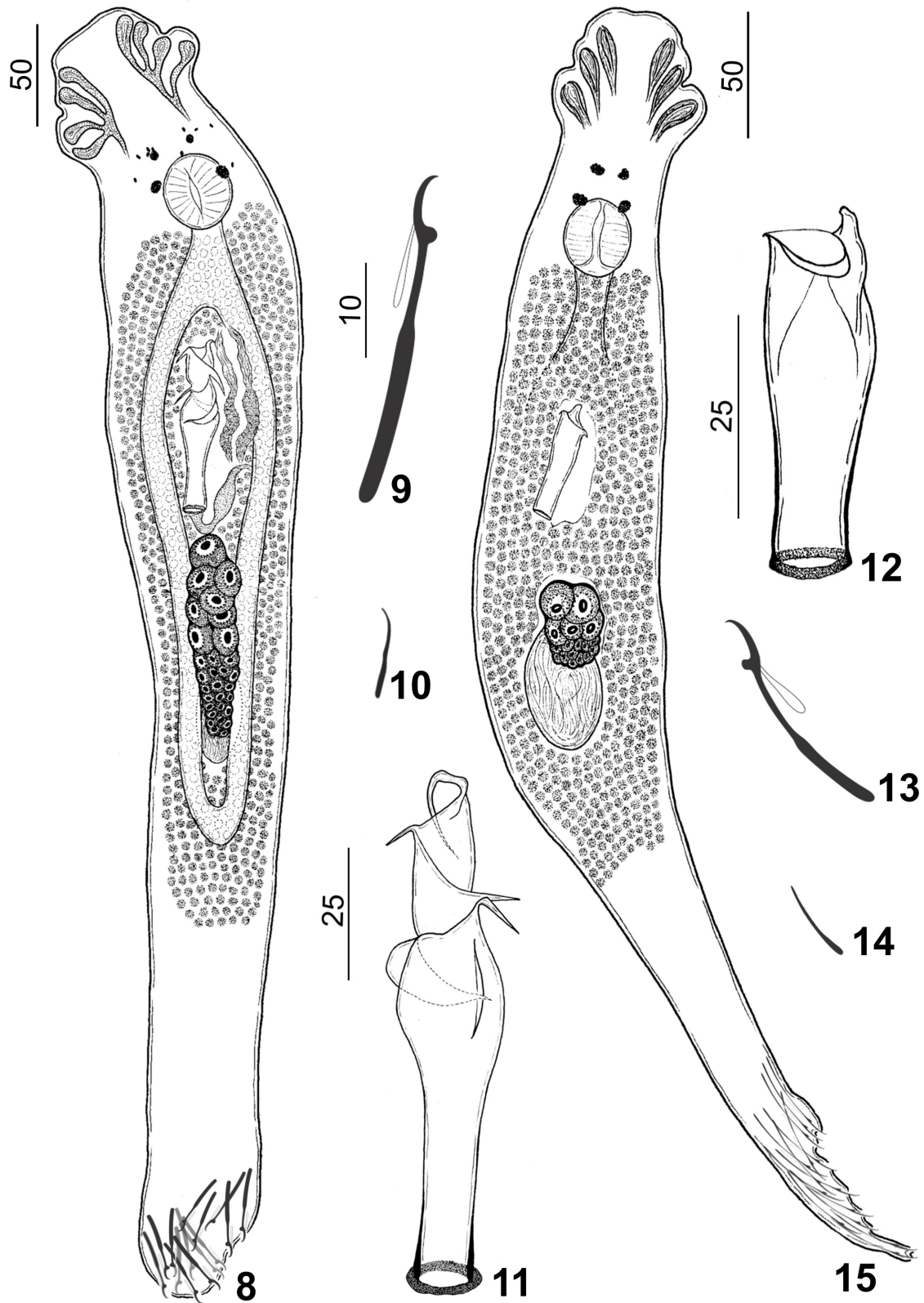
Comparative measurements: Table 3.

Description: (Based on nine specimens, six mounted in Hoyer's, two mounted in Gomori trichrome, one mounted in Grey & Wess). Body fusiform 424 (310–492; n=9) long, excluding the haptor, 97 (72–125; n=9) wide at the height of germarium (Fig. 15). Four cephalic lobes developed; three groups of head organs; cephalic glands not observed (Fig. 15). Two pairs of ocelli, posterior pair farther than the anterior pair; accessory granules absent (Fig. 15). Pharynx subspherical 33 (31–36; n=4) long, 32 (25–41; n=4) wide (Fig. 15). Two intestinal caeca, confluent, posterior to the gonads (Fig. 15). Genital pore not observed. MCO 45 (42–49; n=10) long, 13 (10–14; n=10) wide, sclerotized, tubular, with distal region more dilated than the proximal region, presenting a small projection in the form of a hook in the distal region (Fig. 12); accessory piece absent (Fig. 12). Seminal vesicle, uterus, and prostatic reservoir not observed. Gonads slightly overlapping (Fig. 15). Germarium pyriform 40 (35–46; n=2) long, 22 (19–25; n=2) wide; testis oval 50 (49–50; n=2) long, 27 (22–31; n=2) wide (Fig. 15). Peduncle elongated (Fig. 15). Haptor 40 (28–50; n=6) long, 54 (30–82; n=7) wide (Fig. 15). Similar 4A hooks 9 (9–10; n=3) long (Fig. 14). Seven pairs of similar hooks 26 (24–27; n=6) long, blade relatively long and slightly curved; shank with proximal dilatation comprising ½ of its length 10 (9–11; n=6) long; point short and slightly curved, thumb short and erect (Fig. 13). Hook filament delicate, extending until near the shank dilatation (Fig. 13).

Remarks: *Anacanthorus maratininguensis* **sp. n.** is similar to *Anacanthorus euryphallus* Kritsky, Boeger & Van-Every, 1992 based on the MCO morphology. However, *Anacanthorus maratininguensis* **sp. n.** differs from *A. euryphallus* by the presence of a small projection in the form of a hook in the distal region of the MCO, absence of an accessory piece, and by the hook morphology. *Anacanthorus euryphallus* has the shank of the hook without proximal dilatation, whereas *Anacanthorus maratininguensis* **sp. n.** has proximal shank dilatation comprising ½ of the shank length.



FIGURES 1–7. *Anacanthorus scyphophallus* sp. n. 1. Holotype whole-mount (ventral); 2. Male copulatory organ (MCO); 3. Hook. *Anacanthorus ataidei* sp. n. 4. MCO; 5. Hook; 6. 4A hooks; 7. Holotype whole-mount (ventral). Fig. 1 scale of 50 μ m; Figs. 2–3 scale of 25 μ m; Fig. 4 scale of 25 μ m; Figs. 5–6 scale of 10 μ m; Fig. 7 scale of 50 μ m.



FIGURES 8–15. *Anacanthorus siphonocommus* sp. n. **8.** Holotype whole-mount (ventral); **9.** Hook; **10.** Hook 4A; **11.** Male copulatory organ (MCO); *Anacanthorus maratinguensis* sp. n. **12.** MCO; **13.** Hook; **14.** 4A hooks; **15.** Holotype whole-mount (ventral). Fig. **8** scale of 50µm; Figs. **9–10** scale of 10µm; Fig. **11** scale of 25µm; Figs. **12–14** scale of 25µm; Fig. **15** scale of 50µm.

TABLE 3. Comparative measurements (μm) of specimens of *Anacanthorus maratininguensis* sp. n. from the gills of *Hoplerythrinus unitaeniatus* of three localities in the Pará State, Brazil. MCO = male copulatory organ.

	Tailândia*	N	Cururutua	N	S.M.G	N
Body						
Length	424 (310–492)	9	344 (279–405)	3	402 (347–545)	6
Width	97 (72–125)	9	115 (97–150)	3	79 (65–105)	6
Haptor						
Length	40 (28–50)	6	50 (38–57)	3	35 (30–45)	6
Width	54 (30–82)	7	78 (58–97)	3	54 (47–60)	6
Pharynx						
Length	33 (31–36)	4	38 (36–42)	3	32 (28–35)	6
Width	32 (25–41)	4	28 (27–29)	3	31 (25–35)	6
MCO	45 (42–49)	10	41 (40–45)	4	44 (41–49)	5
Germarium						
Length	40 (35–46)	2	47 (41–54)	3	36 (30–44)	3
Width	22 (19–25)	2	32 (29–34)	3	25 (24–27)	3
Testis						
Length	50 (49–50)	2	32 (22–42)	2	46 (44–47)	2
Width	27 (22–31)	2	30 (31–32)	2	33 (31–35)	2
Hook pair 1–7	26 (24–27)	6	25 (23–26)	3	28 (27–29)	4
4A hooks	9 (9–10)	3	9	1	10 (10–11)	2
Dilatation of the shank	10 (9–11)	6	–	–	11 (10–1)	4

*Type locality / S.M.G = São Miguel do Guamá

Anacanthorus lacinimentulatus sp. n.

(Figs. 16–19)

Type-host: *Hoplerythrinus unitaeniatus* (Spix & Agassiz), Erythrinidae.

Site of infection. Gills.

Type-locality: Igarapé Arinandeua—Guamá River, municipality of São Miguel do Guamá, State of Pará, Brazil (1°37'42.50"S 47°29'45.06"W).

Other localities: *Hoplerythrinus unitaeniatus* (Prevalence: 16% of six hosts examined; Mean intensity: two parasites per host infected), Igarapé Maratininga—Moju River, municipality of Tailândia, Pará State (02°27'55.7"S 048°53'27.6"W).

Prevalence: 33% of three hosts examined.

Mean intensity: 1 parasite per host infected.

Specimens deposited: Holotype: CHIOC no. 40031 a. 2 paratypes: CHIOC nos. 40031 b–c. 2 vouchers: CHIOC nos. 40031 a–b.

ZooBank registration: The Life Science Identifier (LSID) urn: lsid:zoobank.org:act:CEE15CB2-A8F7-44E8-8743-BC2FBC98CF65.

Etymology: The specific epithet derives from the Latin (*lacini* = flap + *mentul* = penis), and refers to the flap morphology in the distal region of the MCO.

Comparative measurements: Table 4.

Description: (Based on three specimens, two mounted in Gomori trichrome and one mounted in Hoyer's). Body fusiform 380 (337–410; n=3) long, excluding the haptor, 66 (52–85; n=3) wide at the height of germarium (Fig. 16). Four cephalic lobes developed; three groups of head organs; cephalic glands not observed (Fig. 16). Two pairs of ocelli, anterior pair smaller than the posterior pair; accessory granules absent (Fig. 16). Pharynx oval or subspherical 29 (28–30; n=3) long, 24 (20–28; n=3) wide; oesophagus elongated (Fig. 16). Two intestinal caeca confluent, posterior to the gonads (Fig. 16). Genital pore not observed. MCO 32 (24–38; n=3) long, 8 (6–9; n=3) wide, sclerotized, simple and tubular, with extrovert flap skirting the distal region of the MCO (Fig. 17); accessory

piece absent (Fig. 17). Seminal vesicle long, ascending from the vas deferens and looping the intestinal caecum near the testis (Fig. 16). Gonads not overlapping; germarium 43 (36–49; n=2) long, 21 (15–26; n=2) wide; testis posterior to germarium, oval 45 (44–46; n=2) long, 24 (22–25; n=2) wide (Fig. 16). Prostatic reservoir not observed. Peduncle elongated (Fig. 16). Haptor bilobed 34 (27–42; n=3) long, 52 (45–60; n=3) wide (Fig. 16). Similar 4A hooks, with a proximal region, dilated, comprising $\frac{1}{4}$ of the hook length (Fig. 18). Seven pairs of similar hooks 27 (n=1) long; blade slightly curved, point short and curved, shank with proximal dilatation 12 (n=1) long, comprising approximately $\frac{1}{2}$ of the total shank length; thumb erect and short (Fig. 19). Hook filament delicate, extending until near the shank dilatation (Fig. 19).

Remarks: *Anacanthorus lacinimentulatus* sp. n. differs from the other *Anacanthorus* species for having MCO with extrovert flap skirting its distal region and the absence of accessory piece. The hooks have a shank with proximal dilatation comprising approximately $\frac{1}{2}$ of the total shank length.

TABLE 4. Comparative measurements (μm) of specimens of *Anacanthorus lacinimentulatus* sp. n. from the gills of *Hoplerythrinus unitaeniatus* of two localities in the Pará State, Brazil. MCO = male copulatory organ.

	S.M.G.*	N	Tailândia	N
Body				
Length	380(337–410)	3	413(291–535)	2
Width	66(52–85)	3	103(132–75)	2
Haptor				
Length	34(27–42)	3	52(45–60)	2
Width	52(45–60)	3	64(57–70)	2
Pharynx				
Length	29(28–30)	3	–	–
Width	24(20–28)	3	–	–
MCO	32(24–38)	3	42(41–43)	2
Germarium				
Length	43(36–49)	2	–	–
Width	21(15–26)	2	–	–
Testis				
Length	45(44–46)	2	–	–
Width	24(22–25)	2	–	–
Hook pair 1–7	27	1	30(29–31)	2
4A hooks	–	–	–	–
Dilatation of the shank	12	1	13	2

*Type locality / S.M.G = São Miguel do Guamá

Anacanthorus cururutuiensis sp. n.

(Figs. 20–22)

Type-host: *Hoplerythrinus unitaeniatus* (Spix & Agassiz), Erythrinidae.

Site of infection: Gills.

Type-locality: Igarapé Cururutuia—Caeté River, municipality of Bragança, State of Pará, Brazil (1°4'44.55"S 46°44'18.54"W).

Other localities: *Hoplerythrinus unitaeniatus* (Prevalence: 66% of three hosts examined; Mean intensity: three parasites per host infected), Igarapé Arinandeua—Guamá River, municipality of São Miguel do Guamá, Pará State (1°37'42.50"S 47°29'45.06"W).

Prevalence: 100% of one host examined.

Mean intensity: 3 parasites per host infected.

Specimens deposited: Holotype: CHIOC no. 40030 a. 2 paratypes: CHIOC nos. 40030 b–c. 4 vouchers: INPA no. 804; MPEG nos. 157–158.

ZooBank registration: The Life Science Identifier (LSID) urn: lsid:zoobank.org:act:3D204F37-2579-48CE-9BC0-3617F4ADD7E4.

Etymology: The specific epithet alludes to the affluent river's name of the type locality of the species, Igarapé Cururutuia.

Comparative measurements: Table 5.

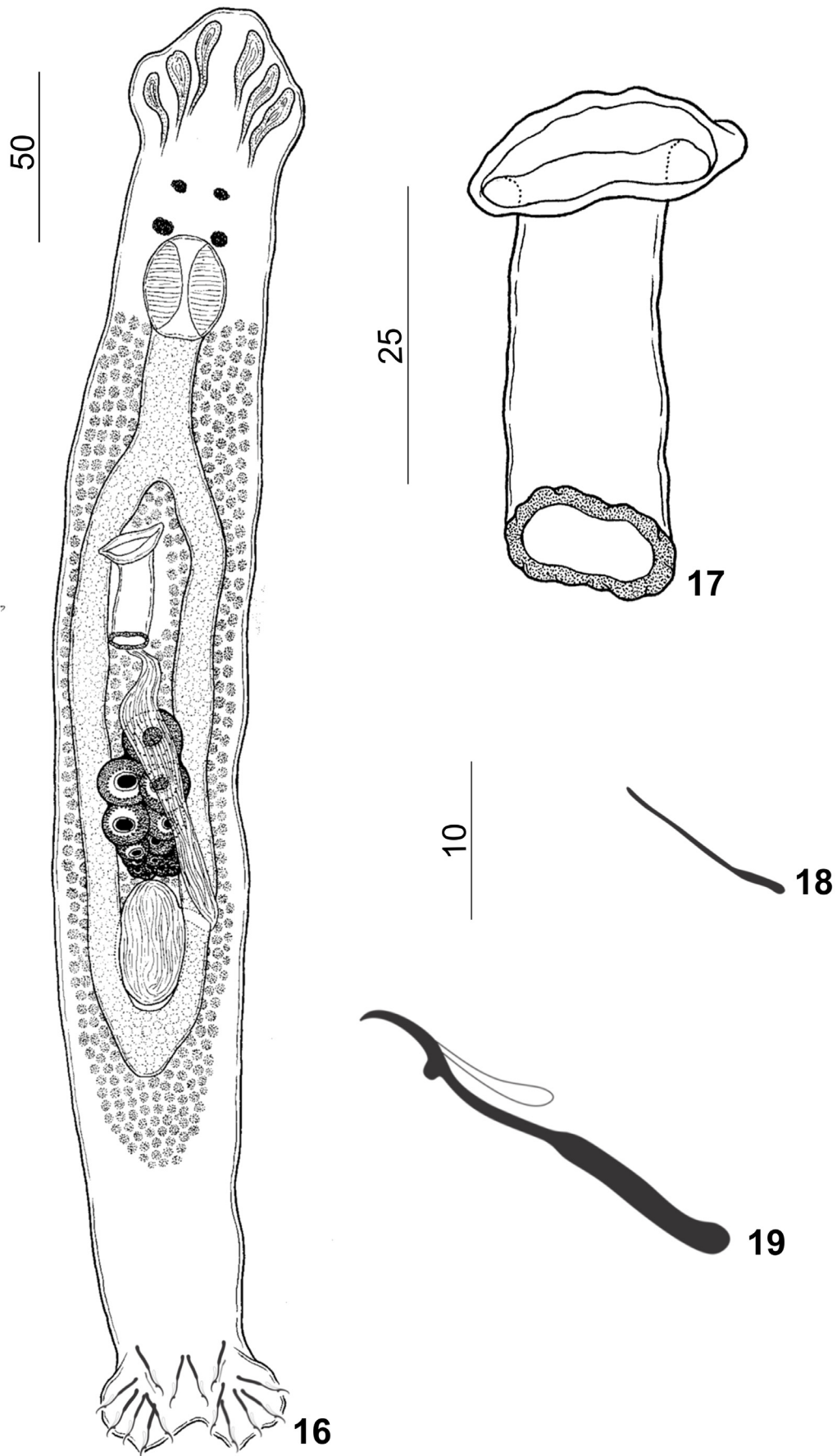
Description: (Based on four specimens, three mounted in Hoyer's, one mounted in Gomori trichrome). Body fusiform 450 (423–489; n=3) long, excluding the haptor, 124 (95–151; n=3) wide at the height of germarium. Four cephalic lobes developed; three groups of head organs; cephalic glands not observed. Two pairs of ocelli; anterior pair smaller than posterior pair; accessory granules absent. Pharynx spherical 41 (39–44; n=3) long, 40 (36–44; n=3) wide; short esophagus. Two intestinal caeca, confluent, posteriorly. Genital pore not observed. MCO 42 (36–49; n=3) long, sclerotized, tubular, with distal region wider than the proximal region, and flexed lateral flap in the distal region of the MCO (Fig. 20); accessory piece absent (Fig. 20). Seminal vesicle, prostatic reservoir, and gonads not observed. Peduncle elongated. Haptor sub-hexagonal 39 (30–42; n=3) long, 72 (54–87; n=3) wide. Similar 4A hooks, with proximal dilatation comprising ½ of the hook length 9 (9–10; n=9) long (Fig. 21). Seven pairs of similar hooks 17 (17–18; n=2) long, blade slightly curved; shank with proximal dilatation comprising approximately ¼ of the shank length, shank dilatation 4 (n=1) long; point short and curved, thumb erect and slightly truncated (Fig. 22). Hook filament delicate, extending more than the half of the shank length (Fig. 22).

TABLE 5. Comparative measurements (µm) of specimens of *Anacanthorus cururutuiensis* sp. n. from the gills of *Hoplerythrinus unitaeniatus* of two localities in the Pará State, Brazil. MCO = male copulatory organ.

	Cururutuia*	N	S.M.G	N
Body				
Length	450 (423–489)	3	421 (355–535)	6
Width	124 (95–151)	3	88 (50–137)	6
Haptor				
Length	39 (30–42)	3	41 (30–47)	6
Width	72 (54–87)	3	70 (47–87)	6
Pharynx				
Length	41 (39–44)	3	37 (33–47)	6
Width	40 (36–44)	3	40 (25–58)	6
MCO	42 (36–49)	3	41 (34–46)	6
Germarium				
Length	–	–	44 (39–49)	2
Width	–	–	23 (22–23)	2
Testis				
Length	–	–	62	1
Width	–	–	16	1
Hook pair 1–7	17 (17–18)	1	18 (18–19)	4
4A hooks	–	–	10	1
Dilatation of the shank	4	1	4 (3–4)	4

*Type locality / S.M.G = São Miguel do Guamá

Remarks: *Anacanthorus cururutuiensis* sp. n. differs from the remaining congeneric species based on the MCO morphology with distal region wider than the proximal region, and flexed lateral flap in the distal region, and for having hooks with proximal dilatation comprising ¼ of the shank length, and thumb erect and slightly truncated. Specimens of *Anacanthorus* were found parasitizing *H. unitaeniatus* of the Igarapé Arinandeua in São Miguel do Guamá, Pará State. The specimens are similar to *Anacanthorus cururutuiensis* sp. n. based on the MCO morphology, although with small morphological variation (*i.e.*, the shank of the hook without evident proximal dilatation was observed in some specimens, and MCO without flexed lateral flap). However, the specimens do not have morphometric variations in comparison to the specimens of the type-locality (See Table 5). Thus, these morphological variations are considered here as intraspecific.



FIGURES 16–19. *Anacanthorus lacinimentulatus* sp. n. **16.** Holotype whole-mount (ventral); **17.** Male copulatory organ (MCO); **18.** 4A hooks; **19.** Hook. Fig. **16** scale of 50µm; Fig. **17** scale of 25µm; Figs. **18–19** scale of 10µm.

***Anacanthorus acrophallus* sp. n.**

(Figs. 23–25)

Type-host: *Hoplerythrinus unitaeniatus* (Spix & Agassiz), Erythrinidae.

Site of infection: Gills.

Type-locality: Igarapé Arinandeua—Guamá River, municipality of São Miguel do Guamá, State of Pará, Brazil (1°37'42.50"S 47°29'45.06"W).

Prevalence: 66% of three hosts examined.

Mean intensity: 1,5 parasites per host examined.

Specimens deposited: Holotype: CHIOC no. 40024. 2 paratypes: CHIOC nos. 40025 a–b.

ZooBank registration: The Life Science Identifier (LSID) urn: lsid:zoobank.org:act:DFCCF79B-0944-4AC9-A9DB-4391828B8C1B.

Etymology: The specific epithet derives from the Greek (*acro* = point + *phallus* = penis) and refers to the MCO morphology, based on the presence of a pointed flap in its distal portion.

Description: (Based on three specimens mounted in Hoyer's). Body fusiform 468 (425–512; n=2) long, excluding the haptor, 117 (115–120; n=2) wide at the height of germarium. Four cephalic lobes developed; three groups of head organs; cephalic glands not observed. Two pairs of ocelli, posterior pair slightly bigger than the anterior pair; accessory granules not observed. Pharynx oval 45 (36–60; n=3) long; 34 (27–47; n=3) wide; oesophagus moderately elongated. Two intestinal caeca confluent and posterior to the gonads. Genital pore not observed. MCO 27 (26–29; n=3) long, 10 (9–11; n=3) wide, sclerotized and short, with a small pointed sinistral flap (ventral view) (Fig. 23); accessory piece absent (Fig. 23). Seminal vesicle, germarium, prostatic reservoir and testicles not observed. Uterus with anterior portion slightly sclerotized. Haptor 57 (50–65; n=3) long, 74 (47–95; n=3) wide. Peduncle short or elongated. Similar 4A hooks with portion posterior slightly dilated 14 (n=1) long (Fig. 24). Seven pairs of similar hooks 23 (22–24; n=3) long; blade relatively long and recurved, point short and curved, shank with proximal dilatation 6 (6–7; n=3) long, comprising 1/3 of the total shank length, thumb robust and depressed (Fig. 25). Hook filament delicate, extending until the half of the shank, proximal to the dilatation (Fig. 25).

Remarks: *Anacanthorus acrophallus* sp. n. is similar to *Anacanthorus scyphophallus* sp. n. and *A. brevicirrus* due to the presence of a short and tubular MCO. However, *Anacanthorus acrophallus* sp. n. differs from *Anacanthorus scyphophallus* sp. n. mainly by the hook morphology since *Anacanthorus acrophallus* sp. n. has hooks with shank showing a proximal and robust dilatation, comprising 1/3 of the shank length, and a short, extended and slightly depressed thumb. On the other hand, *Anacanthorus scyphophallus* sp. n. has hooks shank with shank showing a proximal dilatation comprising 1/2 of the shank length, and a rounded and short thumb. *Anacanthorus brevicirrus* differs from *Anacanthorus acrophallus* sp. n. also by the hook morphology since it has a small bulb with a translucent spot in the proximal portion of the shank, which is not found in *Anacanthorus acrophallus* sp. n.

***Anacanthorus circumspatulatus* sp. n.**

(Figs. 26–28)

Type-host: *Erythrinus erythrinus* (Bloch & Schneider), Erythrinidae.

Site of infection: Gills.

Type-locality: Igarapé Cururutuaia—Caeté River, municipality of Bragança, Pará State, Brazil (1°4'44.55"S 46°44'18.54"W).

Prevalence: 100% of one host examined.

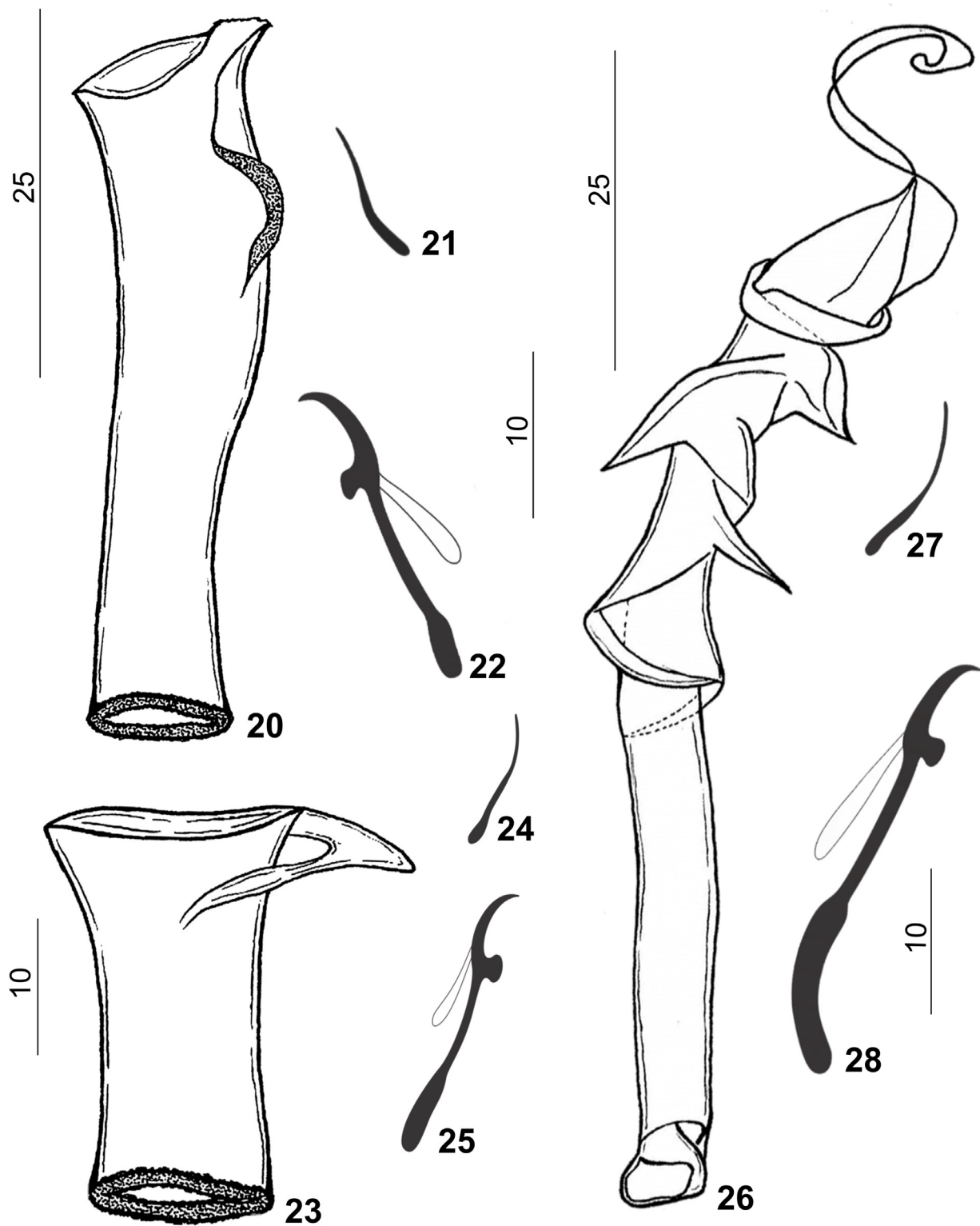
Mean intensity: 2 parasites per host infected.

Other localities: *Erythrinus erythrinus* (Prevalence: 14% of seven hosts examined; Mean intensity: two parasites per host infected), Igarapé Maratininga—Moju River, Tailândia, Pará State (02°27'55.7"S 048°53'27.6"W).

Specimens deposited: Holotype: CHIOC no. 40028 a. 1 paratype: CHIOC no. 40028 b. 2 vouchers: CHIOC nos. 40029 a–b.

ZooBank registration: The Life Science Identifier (LSID) urn: lsid:zoobank.org:act:37327D29-D790-4145-8086-35543E65EE71.

Etymology: The specific epithet derives from the Latin (*circum* = around + *spatula* = small blades), and refers to the ornament in the form of small blades distributed around the MCO.



FIGURES 20–28. *Anacanthorus cururutuiensis* sp. n. 20. Male copulatory organ (MCO); 21. 4A hooks; 22. Hook; *Anacanthorus acrophallus* sp. n. 23. MCO; 24. 4A hooks; 25. Hook; *Anacanthorus circumspatulatus* sp. n. 26. MCO; 27. 4A hooks; 28. Hook. Fig. 20 scale of 25µm; Figs. 21–22 scale of 10µm; Figs. 23–25 scale of 10µm; Fig. 26 scale of 25µm; Figs. 27–28 scale of 10µm.

Comparative measurements: Table 6.

Description: (Based on two specimens, mounted in Hoyer's). Body fusiform 314 (283–346; n=2) long, excluding the haptor, 108 (100–116; n=2) wide at the height of germarium. Cephalic lobes developed; three groups of developed head organs; cephalic glands not observed. Two pairs of ocelli; anterior pair smaller than posterior pair; accessory granules ellipsoids, present or absent. Pharynx spherical 30 (28–32; n=2) long, 34 (32–36; n=2) wide. Esophagus not observed. Two intestinal caeca, confluent, posteriorly. Genital pore not observed. MCO 104 (101–107; n=2) long, sclerotized, tubular, moderately long, with ornaments in the form of pointed and small interleaved blades distributed helically around the MCO, extending from the medial region to the distal region of the MCO (Fig. 26); accessory piece absent (Fig. 26). Seminal vesicle, prostatic reservoir, and gonads not observed. Peduncle short. Haptor sub-hexagonal 42 (30–54; n=2) long, 74 (56–93; n=2) wide. Similar 4A hooks 9 (n=1) long, with proximal portion dilated, comprising 1/3 of the hook length (Fig. 27). Seven pairs of similar hooks, blade slightly curved and robust 28 (n=1) long; shank with proximal dilatation comprising approximately 1/2 of its length; point short and curved; thumb slightly depressed and robust (Fig. 28). Hook filament delicate, extending proximally to the shank dilatation (Fig. 28).

Remarks: Based on the MCO morphology, *Anacanthorus circumspatulatus* sp. n. is similar to *Anacanthorus ataidei* sp. n., since both species share the presence of a tubular and elongated MCO, with ornaments around it. However, they differ from each other by the hook morphology. *Anacanthorus circumspatulatus* sp. n. has the shank of hooks with a proximal dilatation comprising approximately 1/2 of the total shank length, a characteristic that is not observed in *Anacanthorus ataidei* sp. n., which has the shank of the hook without a proximal dilatation.

TABLE 6. Comparative measurements (μm) of specimens of *Anacanthorus circumspatulatus* sp. n. from the gills of *Erythrinus erythrinus* of two localities in the Pará State, Brazil. MCO = male copulatory organ.

	Cururuíua*	N	Tailândia	N
Body				
Length	314 (283–346)	2	485(447–522)	2
Width	108 (100–116)	2	130 (127–132)	2
Haptor				
Length	42 (30–54)	2	50 (40–60)	2
Width	74 (56–93)	2	93 (85–102)	2
Pharynx				
Length	30 (28–32)	2	33 (30–36)	2
Width	34 (32–36)	2	53 (50–55)	2
MCO	104 (101–107)	2	106 (104–108)	2
Germarium				
Length	–	–	–	–
Width	–	–	–	–
Testis				
Length	–	–	–	–
Width	–	–	–	–
Hook pair 1–7	26	1	29	2
4A hooks	–	–	9	2
Dilatation of the shank	9	1	10	2

*Type locality

Discussion

Species of Monogenoidea belonging to *Urocleidoides* Mizelle & Price, 1964, *Protorhinoxenus* Domingues & Boeger, 2002, *Whittingtonocotyle* Santos-Neto, Rodrigues & Domingues, 2015, and *Constrictoanchoratus* Ferreira, Rodrigues, Cunha & Domingues, 2017 are reported parasitizing the gills of the fish species of Erythrinidae, with most of the species reported for *Hoplias malabaricus* (Cohen *et al.* 2013; Ferreira *et al.* 2017). Specimens of *Ana-*

canthorus were reported for the first time parasitizing members of Erythrinidae by Graça *et al.* (2013a), where one *Anacanthorus* species was recorded as gill parasite of *H. aff. malabaricus* of the upper Paraná River basin. Graça *et al.* (2018) reported four other likely new *Anacanthorus* species, parasites of *H. unitaeniatus* (n= 2), *E. erythrinus* (n= 1), and *H. malabaricus* (n= 1) of the upper Paraná River and its affluents, however, these species have not yet been formally described. In this study, eight new *Anacanthorus* species are described, representing the first species of the genus reported for species of Erythrinidae in the Amazon region.

Anacanthorus species are exclusive gill parasites of members of four families of Neotropical characiforms, the Serrasalminidae, Triportheidae, Erythrinidae, and Bryconidae (Cohen *et al.* 2012; Cohen *et al.* 2013; Leão *et al.* 2015; Monteiro *et al.* 2015). Braga *et al.* (2015) suggested that the sharing of neotropical monogenoid parasites within Characiformes is more intense when compared to other groups of freshwater fish, most probably due to the diversification of this fish lineage occurring in the neotropical continent. Thus, the phylogenetic contiguity observed in Characiformes probably allowed the parasite species to reach hosts belonging to phylogenetically distant lineages. In this context, we can infer that the phylogenetic contiguity observed among the neotropical characiforms could be the main factor contributing to a greater reach of host families parasitized by *Anacanthorus* species. However, Brooks & McLennan's (2002) concepts of false generalists and false specialists (*i.e.*, false specialists are generalists restricted to a few or a single resource due to ecological factors, and false generalists are specialized in a resource that is phylogenetically generalized) could also explain the wide range of hosts. In this case, neotropical Characiformes could share phylogenetically widespread resources among host families, which would be used by monogenoid species.

Most monogenoid lineages appear to be restricted to their hosts at higher taxonomic levels, at least at the family level, probably because of broad historical constraints (*e.g.*, immunological or morphological) acting on a large scale (Boeger & Kritsky 1997; Desdevises *et al.* 2002). Studies on the interaction between monogenoids and their hosts in the Neotropical region evidenced a restricted composition of the Monogenoidea fauna influenced by the phylogenetic relationship and geographic distribution of its hosts (Braga *et al.* 2015). Using molecular data, Graça *et al.* (2018) performed a study on the coevolutionary relationships between the *Anacanthorus* and their characiform host species of Bryconidae, Serrasalminidae, and Erythrinidae. These authors verified that, in both phylogenies, there was high topological congruence between the parasites and hosts lineages, suggesting a common evolutionary history between these organisms. The results of Graça *et al.* (2018) corroborate with the scenarios presented above since each fish species had an exclusive composition of *Anacanthorus* species.

In this study, comparative analysis of sclerotized structures (*i.e.*, copulatory complex and hooks) of *Anacanthorus* species and their occurrence in several characiform lineages appears to have a high specificity when considering the host family or subfamily levels. *Anacanthorus* species on erythrinids have a tubular MCO, with or without ornaments; lack an accessory piece; and have hooks with presence or absence of a proximal dilatation in the shank. These characteristics are not shared among the other species of the genus described for the families Serrasalminidae (J-shaped MCO and accessory piece not articulated to it; hooks with truncated thumb and shank with proximal dilatation); Triportheidae (tubular MCO, with accessory piece articulated to its base; hooks with an erect thumb, slightly truncated, and a bulb at the termination of the shank); Bryconidae (tubular MCO; accessory piece membranous; hooks with a poorly developed thumb; delicate shank of the hook, having a bulb with translucent spots in the proximal portion); and also, the subfamily Salmininae (tubular MCO, the accessory piece with articulated branches to its base; hooks with an expanded and depressed thumb; shank delicate and curved with a bulb lacking translucent spots at the termination of the shank) (See Boeger & Kritsky 1988; Kritsky *et al.* 1992; Van Every & Kritsky 1992; Monteiro *et al.* 2010; Cohen *et al.* 2012; Monteiro *et al.* 2015).

Monteiro *et al.* (2010) described *A. franciscanus* and *A. brevicirrus* from *Brycon orthotaenia* (Günther) (Bryconidae: Bryconinae) of São Francisco River basin, and observed that these species share morphological characteristics with some species collected in the Amazon basin (*i.e.*, *Anacanthorus kruidenieri* Kritsky, Thatcher & Kayton, 1979, *Anacanthorus brevis* Mizelle & Kritsky, 1969, and *Anacanthorus elegans* Kritsky, Thatcher & Kayton, 1979), all parasites of *Brycon melanopterus* (Cope). These similarities are based on the morphology of the copulatory complex (tubular MCO and membranous accessory piece are found in four of the five species) and hooks (poorly developed thumb and a bulb at the termination of the shank with translucent spots). Monteiro *et al.* (2010) suggest that the sharing of such characteristics among these *Anacanthorus* species could represent a monophyletic lineage within the genus and that possible vicariant and coevolutionary events could have been responsible for their emergence.

However, support for the monophyletic nature of these different parasite groups of different host families and

subfamilies will only be provided through a phylogenetic analysis addressing all *Anacanthorus* species found parasitizing members of Characiformes. This analysis will be critical to better understand the phylogenetic relationships between these lineages, and the biogeography and coevolution of *Anacanthorus* and its hosts.

Acknowledgments

We would like to thank the members of Laboratório de Sistemática e Coevolução—LASCO (Universidade Federal do Pará) for assistance during the collecting trips. This work was partially supported by Programa de Pós-Graduação em Biologia Ambiental da Universidade Federal do Pará for granting a M. Sc. Scholarship and collecting trip grant to J. F. S.-N.; research grants from the Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq) (PROTAX N° 001/2015—440526/2015-9), and Fundação Amazônia de Amparo a Estudos e Pesquisas do Pará (FAPESPA) (ICAAF 017-2018) to M.V.D. Specimens were collected under the license for collection of biological material (43381) granted by the Instituto Chico Mendes de Conservação da Biodiversidade (ICMBio).

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