

DACTYLOGYRIDS (MONOGENOIDEA) PARASITIZING THE GILLS OF *ASTYANAX* SPP. (CHARACIDAE) FROM PANAMA AND SOUTHEAST MEXICO, A NEW SPECIES OF *DIAPHOROCLEIDUS* AND A PROPOSAL FOR *CHARACITHECIUM* N. GEN.

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ABSTRACT: *Diaphorocleidus orthodus* n. sp. and *Diaphorocleidus kabatai* (Molnar, Hanek and Fernando, 1974) Jogunoori, Kritsky, and Venkatanarasaiah, 2004 are detailed from *Astyanax orthodus* and *Astyanax aeneus*, respectively. *Palombitrema heteroancistrum* (Price and Bussing, 1968) is described from specimens collected from *A. aeneus*, and *Urocleidoides strombicirrus* (Price and Bussing, 1967) is reported for the first time from *A. aeneus* and *Astyanax fasciatus* in Panama. *Characithecium costaricensis* (Price and Bussing, 1967) n. comb. is detailed based on specimens from *A. aeneus*. *Characithecium costaricensis* is characterized by having overlapping gonads, a medioventral vaginal aperture, a copulatory complex consisting of single counterclockwise coil of the copulatory organ that is articulated to the accessory piece, and a haptor having 2 pairs of anchors, dorsal and ventral bars, and 14 hooks. Measurements of body size varied substantially among individual worms, both within and across different host species and locations. However, the morphological differences were insufficient to separate species of *Characithecium*. This result suggests limited parasite speciation across sympatric species of *Astyanax* in Mexico and Panama.

Urocleidoides Mizelle and Price, 1964, was erected for a species that infected *Poecilia reticulata* (Poeciliidae) in a California aquarium. Mizelle et al. (1968) emended it by adding gonads overlapping or tandem, male copulatory organ coiled with a single or multiple rings, 1 or 2 prostatic reservoirs, and vaginal pore on the left side of the body or absent. *Urocleidoides* included species from fishes in 5 orders (Atheriniformes, Characiformes, Gymnotiformes, Perciformes, and Siluriformes) until Kritsky et al. (1986) emended *Urocleidoides* and restricted it to species having a sinistral vaginal sclerite. Kritsky et al. (1986) transferred several species to *Gussevia* Kohn and Paperna, 1964, and designated 22 species as incertae sedis, including the 5 dactylogyrids: *Urocleidoides costaricensis* Price and Bussing, 1967; *Urocleidoides heteroancistrum* Price and Bussing, 1968; *Urocleidoides kabatai* Molnar, Hanek, and Fernando, 1974; *Urocleidoides strombicirrus* Price and Bussing, 1967; and *Urocleidoides trinidadensis* Molnar, Hanek, and Fernando, 1974, all of which infect species of *Astyanax* (Characiformes). Since the emendation by Kritsky et al. (1986), 10 of those 22 species incertae sedis in *Urocleidoides* have been reassigned. We detail 5 monogenoideans from *A. aeneus* (Günther, 1860), *A. fasciatus* (Cuvier, 1819), *A. orthodus* Eigenmann, 1907, and *Astyanax ruberrimus* Eigenmann, 1913 from Panama and southeastern Mexico.

Herein, we provide some supplemental observations of *P. heteroancistrum* (Price and Bussing, 1968) Suriano, 1997 and *U. strombicirrus* and describe a new species of *Diaphorocleidus*. We propose a new genus to accommodate a previously named dactylogyrid.

MATERIALS AND METHODS

Fish were collected by electrofishing and cast netting during August 2006 through May 2007 from 2 cenotes (Chaamac [20°51'53"N, 90°09'18"W] and Dzonot Cervera [21°22'36"N, 88°49'59"W]) in southeastern Mexico and 7 rivers (Aguas Claras at its confluence with the Bayano Lake [09°15'05.1"N, 78°41'11.2"W], Caldera [08°38'18"N, 82°23'36"W], Cardenas [09°60'17.5"N, 71°34'11.5"W], Chiriquicito

[08°41'14"N, 82°17'27"W], Nigua [09°16'44" N, 82°24'55"W], Piriati [09°03'36"N, 78°39'57"W], and Quebrada Traicionera [09°08'20.1"N, 82°18'25.0"W]) from the Republic of Panama. The collection, preparation, and descriptions of helminths follow Mendoza-Franco et al. (2007). Additional specimens were mounted unstained in Gray and Wess's medium to examine the sclerotized structures. Measurements, all in micrometers (μm), represent straight-line distances between extreme points and are expressed as the mean followed by the range and number (n) of structures measured in parentheses; body length includes the haptor. Numbering of hook pairs follows Mizelle (1936) and Mizelle and Price (1963). Type and voucher specimens have been deposited in the United States National Parasite Collection, Beltsville, Maryland (USNPC) and the National Helminthological Collection of Mexico (CNHE), Institute of Biology, National Autonomous University of Mexico, Mexico. Host names are from FishBase (Froese and Pauly, 2008) and the Smithsonian Tropical Research Institute Freshwater Fish Collection (Birmingham et al., 1997).

DESCRIPTION

Characithecium n. gen.

Diagnosis: Dactylogyridae Bychowsky, 1933. Body comprising cephalic region, trunk, peduncle, and haptor. Tegument smooth. Two terminal and 2 bilateral cephalic lobes present; 3 pairs of bilateral head organs present; cephalic glands unicellular, lateral, or posterolateral to pharynx. Four eyes. Mouth subterminal, midventral; pharynx comprising muscular or glandular bulb; esophagus short; 2 intestinal ceca, confluent posterior to gonads, lacking diverticula. Common genital pore medioventral, near level of intestinal bifurcation. Gonads intercecal, overlapping (testis dorsal to germarium); ovary ventral or anteroventral to testis. Vas deferens apparently looping left intestinal cecum; seminal vesicle a simple dilation of vas deferens; single prostatic reservoir. Copulatory complex comprising proximally articulated male copulatory organ (MCO) and accessory piece. MCO tubular, sclerotized, comprising a base from which a coiled shaft in counterclockwise direction arises; accessory piece with complex distal region associated with terminal portion of MCO. Seminal receptacle pregerminal; vaginal aperture midventral. Vitellaria coextensive with intestine. Haptor globose, with 7 pairs of hooks with Dactylogyridae distribution and 2 anchor-bar complexes. Ventral anchor larger than dorsal anchor. Ventral bar with posteromedial projection. Hooks similar, each with depressed thumb, delicate point, and shank comprising 2 subunits (proximal subunit expanded). Infecting gill of neotropical characiforms.

Taxonomic summary

Type species: *Characithecium costaricensis* (Price and Bussing, 1967) n. comb. from *A. aeneus* (Günther, 1860) in southeast Mexico.

Etymology: The genus name is for the host family Characidae and *thecium*, meaning a "little box" or "small case," and is in reference to

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the close host-parasite relationship of this taxon to Neotropical characiforms.

Remarks

Characithecium n. gen. is primarily characterized by having: (1) eyes; (2) overlapping gonads (testis dorsal to germarium); (3) a seminal vesicle formed by a simple dilation of the vas deferens; (4) an articulated MCO and accessory piece; (5) MCO with a coiled shaft in counter-clockwise direction; (6) vaginal aperture in midventral position; (7) ventral anchor larger than dorsal anchor; (8) ventral bar with posteromedial projection; and (9) hook shanks, each composed of 2 subunits (proximal subunit expanded). *Characithecium* is most similar to *Ancistrohaptor* Agarwal and Kritsky, 1998, a genus including species that infect *Triportheus* spp. by having eyespots, overlapping gonads, an accessory piece articulated to base of MCO, ventral anchor larger than dorsal anchor, and hook shanks composed of 2 subunits. However, *Characithecium* differs from *Ancistrohaptor* at least by having a medioventral vaginal aperture and a posteromedial projection on the ventral bar and by lacking an anteromedial groove on the ventral bar (present in *Ancistrohaptor* spp.).

Characithecium costaricensis (Price and Bussing, 1967) n. comb. (Figs. 1–10)

Supplemental observations (measurements based on 16 specimens from Chaamac and on 2 from Dzonot Cervera [brackets]): Body 280 (215–370; n = 11) [330] long, fusiform; greatest width 80 (54–100; n = 11) [88–95], usually at level of testis. Cephalic margin broad; cephalic lobes moderately developed; each head organ (see HO in Fig. 1) made up of groupings of terminations of cephalic gland (see Fig. CG in Fig. 1) ducts. Eyes subequal. Pharynx spherical, 16 (13–18; n = 9) [20] in diameter. Peduncle broad, relatively short; haptor 62 (55–72; n = 10) [70–72] wide. Ventral anchor 34 (33–35; n = 19) [38 (36–40; n = 3)] long, with elongate superficial root, short deep root, slightly straight shaft, moderately elongate point; base 17 (17–18; n = 8) wide. Dorsal anchor 28 (28–29; n = 10) [27] long, with tapered elongate superficial root, slightly straight shaft, moderately elongate point; base 14 (14–15; n = 5) wide. Ventral bar 21 (19–24; n = 10) [22] long, slightly arched posteriorly with expanded distal tips, bearing acute posteromedial projection. Dorsal bar 24 (23–25; n = 8) [22] long, slender, slightly arched posteriorly, with rounded tips. Hooks similar; each with protruding thumb, delicate shaft having a point and dilated shank; hook pairs 1 and 5 reduced in size; filamentous hooklet (FH) loop $\frac{1}{2}$ shank length (pairs 1 and 5); $\frac{1}{2}$ shank length (pairs 2, 3, 4, 6, and 7); hook pairs 2, 3, 4, 6, and 7: 19 (19–20; n = 20) [21] long; hook pair 5: 10 (10–11; n = 10) long. MCO a poorly defined counterclockwise coil, base poorly differentiated, apparently fused to short articulation piece connecting to accessory piece (see MCO, BA, and SA, respectively, in Fig. 6); coil 26 (24–22; n = 8) in diameter. Accessory piece 19 (18–21; n = 5) long, comprising 2 subunits. Vagina slightly sclerotized; seminal receptacle anterior to germarium (see SR in Fig. 1). Gonads overlapping, germarium 53 (35–70; n = 9) [55–40] long, 19 (15–24; n = 9) [17–19] wide; testis 18–25 long, dorsal, slightly visible at end of germarium; seminal vesicle a distal enlargement (expansion) of vas deferens; 1 prostatic reservoir; oviduct, ootype, uterus not observed. Vitellarium dense.

Taxonomic summary

Host and locality: *Astyanax aeneus* (Günther, 1860) (Characiformes: Characidae), Chaamac cenote (20°51'53"N, 90°09'18"W) in southeast Mexico.

Site of infection: Gills.

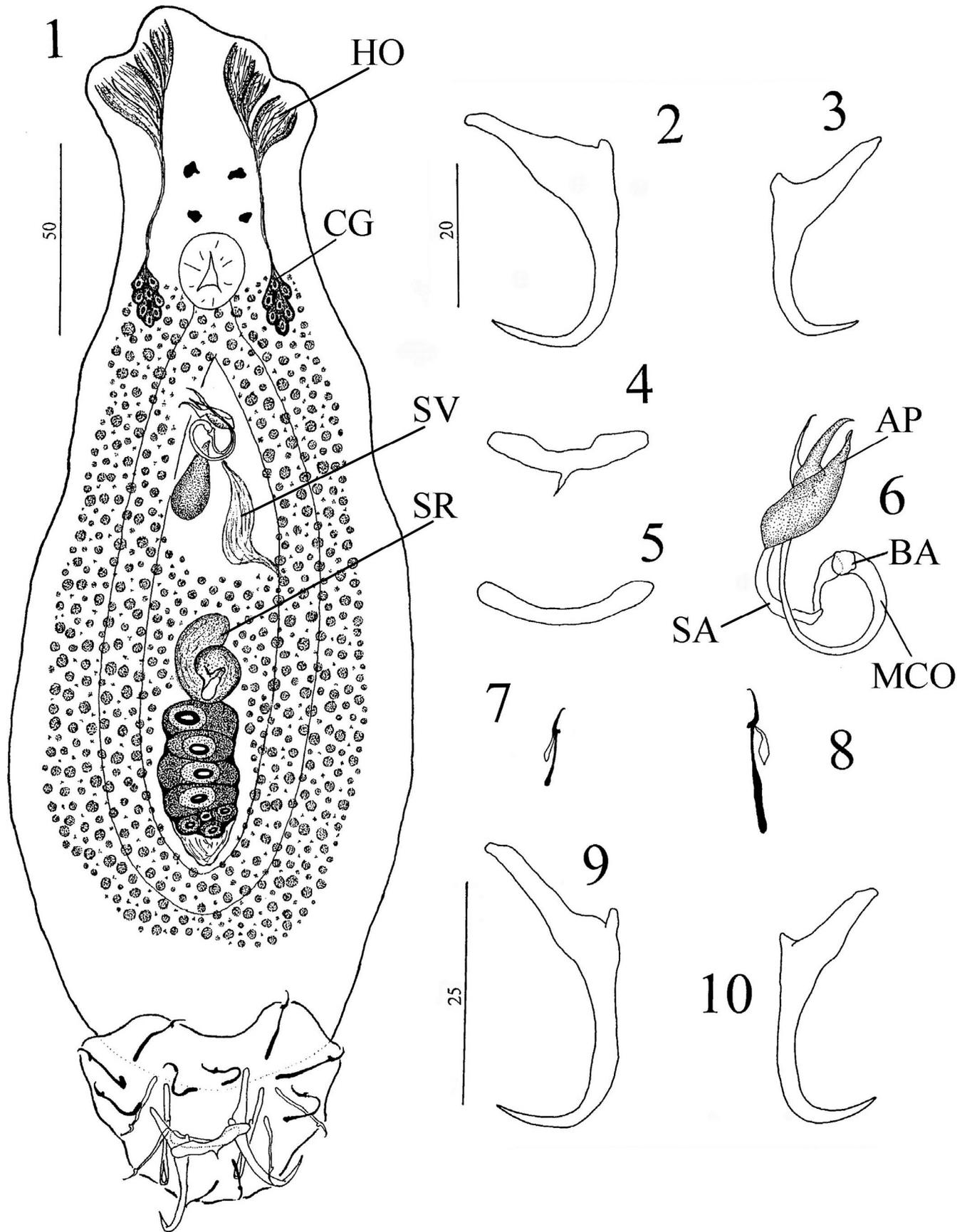
Other localities: Dzonot Cervera cenote in Mexico and Nigua River in Panama.

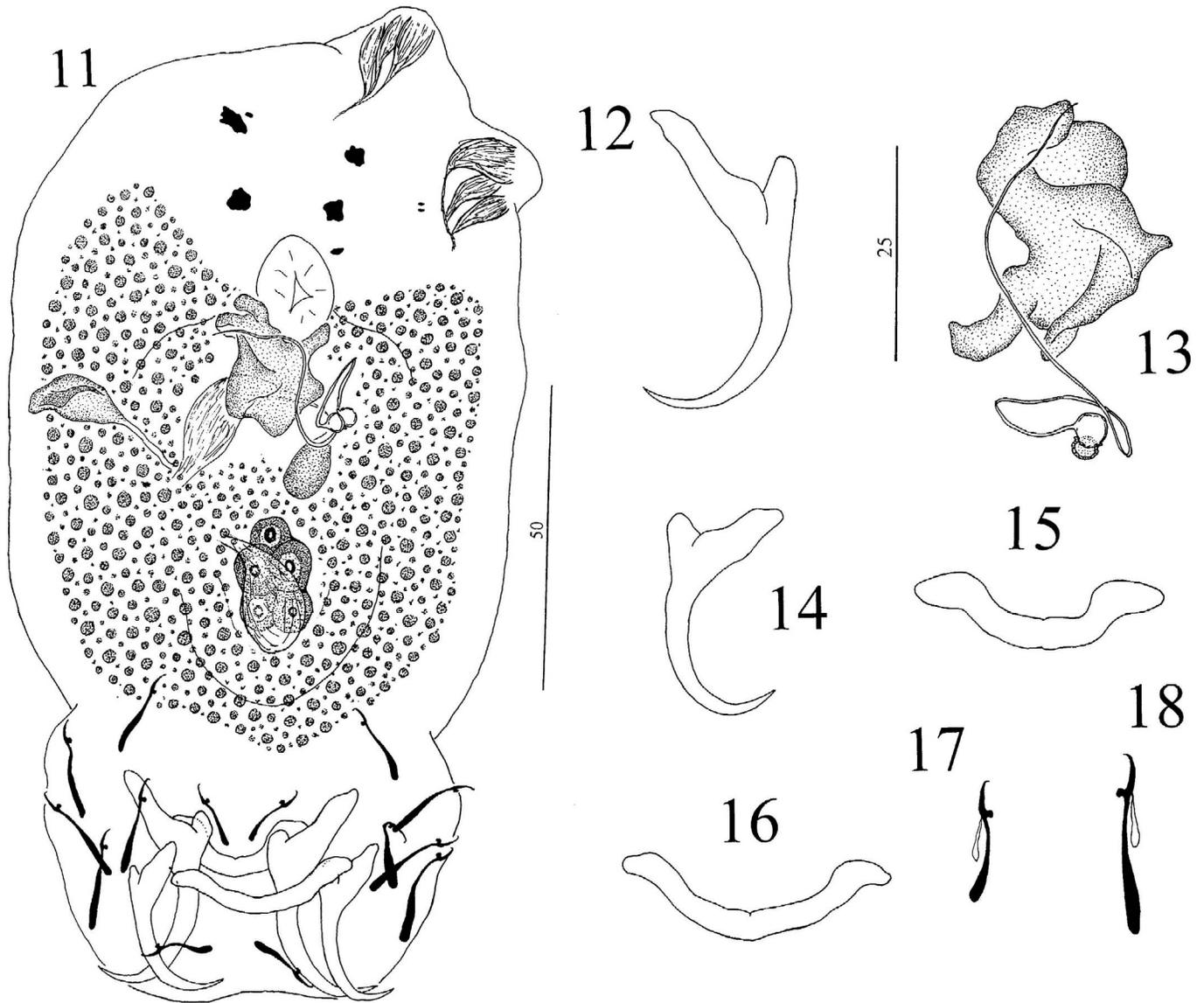
Other hosts and localities: *A. ruberrimus* from Cardenas and *A. fasciatus* from Aguas Claras and Piriati rivers in Panama (see Table I).

Synonyms: *Urocleidoidea costaricensis* (Price and Bussing, 1967) Kritsky and Leiby, 1972 from *A. fasciatus* (type host) in Colombia; *Urocleidoidea astyanacis* Gioia, Silva-Cordeiro and Toledo-Artigas, 1988 from *A. fasciatus* (Cuvier, 1819) and *Astyanax scabripinnis* (Jennyns, 1842) from Atibaia and Jaguari rivers, and tributaries near Campinas, São Paulo state, Brazil (Gioia et al., 1988).

TABLE I. Comparative measurements (in micrometers; mean with range in parentheses; n = number of structures measured) of *Characithecium costaricensis* (Price and Bussing, 1967) comb. n. (Monogeneoidea: Dactylogyridae) from 3 species of *Astyanax* (Characidae) from 6 rivers in Panama.

Morphological structures	Locations and host species											
	Nigua		Quebrada		Caldera		Cardenas		Aguas Claras		Piriati	
	<i>A. aeneus</i>		<i>A. aeneus</i>		<i>A. aeneus</i>		<i>A. ruberrimus</i>		<i>A. fasciatus</i>		<i>A. fasciatus</i>	
Body length	246 (195–322; n = 5)	287	—	—	299 (222–388; n = 15)	—	—	—	—	254 (236–270; n = 3)	—	—
Greatest width	91 (80–105; n = 5)	102	—	—	86 (54–105; n = 16)	—	—	—	—	77 (59–100; n = 5)	—	—
Pharynx	13 (12–17; n = 4)	15	—	—	14 (11–15; n = 13)	—	—	—	—	17 (30–34; n = 6)	—	—
Haptor width	52 (43–60; n = 5)	64	—	—	54 (43–67; n = 12)	—	—	—	—	—	—	(56–63)
Ventral anchor length	33 (30–35; n = 30)	32 (28–34; n = 35)	32 (30–34; n = 11)	32 (30–34; n = 11)	32 (28–33; n = 22)	32 (28–33; n = 17)	32 (30–34; n = 6)	32 (30–34; n = 6)	32 (30–34; n = 6)	32 (28–35; n = 20)	—	—
Ventral anchor width	17 (16–19; n = 29)	17 (15–18; n = 30)	17 (16–18; n = 10)	17 (16–18; n = 10)	17 (16–18; n = 22)	17 (16–18; n = 17)	16 (15–17; n = 6)	16 (15–17; n = 6)	16 (15–17; n = 6)	16 (14–17; n = 12)	—	—
Dorsal anchor length	27 (26–28; n = 28)	26 (23–28; n = 33)	26 (24–27; n = 10)	26 (24–27; n = 10)	25 (24–27; n = 17)	25 (24–27; n = 17)	25 (23–27; n = 5)	25 (23–27; n = 5)	25 (23–27; n = 5)	25 (26–28; n = 12)	—	—
Dorsal anchor width	13 (11–14; n = 27)	12 (11–13; n = 28)	12 (11–13; n = 7)	12 (11–13; n = 7)	12 (11–13; n = 14)	12 (11–13; n = 14)	10 (9–11; n = 4)	10 (9–11; n = 4)	10 (9–11; n = 4)	10 (9–12; n = 10)	—	—
Ventral bar length	24 (19–27; n = 16)	24 (20–27; n = 17)	22 (20–26; n = 5)	22 (20–26; n = 5)	21 (19–23; n = 14)	21 (19–23; n = 14)	20 (20–21; n = 3)	20 (20–21; n = 3)	20 (20–21; n = 3)	20 (17–21; n = 12)	—	—
Dorsal bar length	25 (24–26; n = 12)	25 (22–28; n = 15)	23 (22–24; n = 5)	23 (22–24; n = 5)	23 (21–25; n = 11)	23 (21–25; n = 11)	22 (20–23; n = 3)	22 (20–23; n = 3)	22 (20–23; n = 3)	21 (18–24; n = 6)	—	—
Hook pair 2	20 (19–22; n = 52)	19 (18–21; n = 49)	19 (18–20; n = 11)	19 (18–20; n = 11)	20 (17–22; n = 33)	20 (17–22; n = 33)	18 (17–20; n = 8)	18 (17–20; n = 8)	18 (17–20; n = 8)	20 (19–21; n = 6)	—	—
Hook pairs 3, 4, 6, and 7	17 (16–18; n = 16)	16 (13–17; n = 17)	15 (15–16)	15 (15–16)	15 (14–16; n = 4)	15 (14–16; n = 4)	15 (14–15; n = 6)	15 (14–15; n = 6)	15 (14–15; n = 6)	16 (14–19; n = 20)	—	—
Hook pair 5	10 (n = 18)	11 (9–11; n = 16)	6 (n = 10)	6 (n = 10)	10 (n = 7)	10 (n = 7)	10 (10–11)	10 (10–11)	10 (10–11)	10 (10–11; n = 8)	—	—
Male copulatory organ length	33 (30–37; n = 16)	31 (25–37; n = 12)	—	—	25 (24–27; n = 7)	25 (24–27; n = 7)	(25–28)	(25–28)	(25–28)	28 (23–33; n = 7)	—	—
Accessory piece length	19 (16–21; n = 16)	20 (17–23; n = 12)	17 (16–18; n = 5)	17 (16–18; n = 5)	16 (15–18; n = 5)	16 (15–18; n = 5)	(17–18)	(17–18)	(17–18)	19 (17–23; n = 6)	—	—
Germarium length	18	—	—	—	50 (42–60; n = 8)	50 (42–60; n = 8)	—	—	—	—	—	—
Germarium width	19	—	—	—	18 (13–28; n = 8)	18 (13–28; n = 8)	—	—	—	—	—	—





FIGURES 11–18. *Diaphorocleidus orthodus*. (11) Whole mount (composite, dorsal view). (12) Ventral anchor. (13) Copulatory organ (ventral). (14) Dorsal anchor. (15) Ventral bar. (16) Dorsal bar. (17) Hook (pair 1). (18) Hook (pair 4). All figures are drawn to the 25- μ m scale, except 11 (50- μ m).

Specimens deposited: 11 voucher specimens in CNHE (6274, 6275, 6276); 9 in USNPC (100963, 100964, 100965).

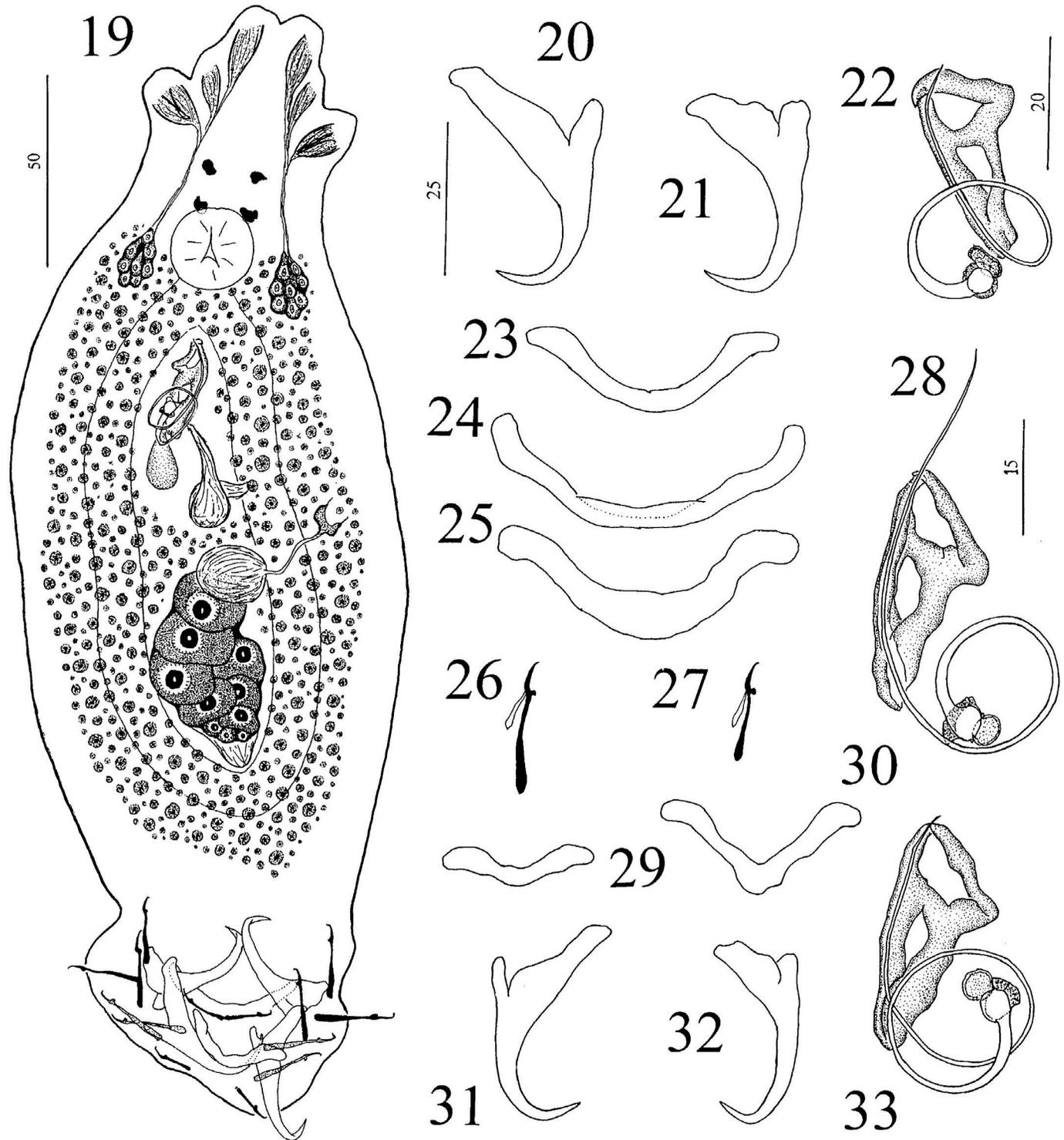
Remarks

Kritsky and Thatcher (1974) reported with additional morphometrical data for this species based on specimens collected from *A. fasciatus* in Colombia. Kritsky et al. (1986) emended *Urocleidoides* and considered *U. costaricensis* incertae sedis. *Characithecium costaricensis* is commonly reported from southern and central Mexico and Nicaragua as *U.*

costaricensis (Mendoza-Franco et al., 1999, 2003; Salgado-Maldonado et al., 2001). The description of *U. astyanacis* is identical to that of *Ch. costaricensis* and we consider *U. astyanacis* as a junior subjective synonym of *Ch. costaricensis*. Although *Ch. costaricensis* has been re-described (Kritsky and Leiby, 1972) and reported several times as *U. costaricensis* in the Neotropics, the description is based solely on the sclerotized structures from the copulatory complex and the haptor. Herein, a partial illustration of whole mounted specimens is provided (Fig. 1) to confirm the position of some of the internal organs. Most signif-

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FIGURES 1–10. *Characithecium costaricensis* (Price and Bussing, 1967) n. comb. from *A. aeneus* from southeast Mexico. (1) Whole mount (composite, ventral view; hooks not inked are in dorsal position). (2) Ventral anchor. (3) Dorsal anchor. (4) Ventral bar. (5) Dorsal bar. (6) Copulatory complex (dorsal). (7) Hook (pair 5). (8) Hook (pair 2). (9) Ventral anchor (these 2 latter structures are from *A. aeneus* from Panama). All figures are drawn to the 20- μ m scale, except 1 (50- μ m) and 9 and 10 (25- μ m). Abbreviations: AP, accessory piece; BA, base; CG, cephalic glands; HO, head organs; MCO, male copulatory organ; SA, short articulation; SR, seminal receptacle; SV, seminal vesicle.



FIGURES 19–33. *Diaphorocleidus kabatai*. (19) Whole mount (composite, ventral view). (20) Ventral anchor. (21) Dorsal anchor. (22) Copulatory complex (dorsal). (23) Ventral bar. (24, 25) Dorsal bars. (26) Hook (pair 2). (27) Hook (pair 1) (from *A. aeneus* from Dzonot Cervera in southeast Mexico). (28) Copulatory complex (dorsal). (29) Ventral bar. (30) Dorsal bar. (31) Ventral anchor. (32) Dorsal anchor. (33) Copulatory complex (dorsal) (from *A. fasciatus* from Piriati river in Panama). All figures are drawn to the 25- μm scale, except 19 (50- μm), 28 (15- μm), 22, 29–33 (20- μm).

TABLE II. Comparative measurements (in micrometers; mean with range in parentheses; n = number of structures measured) of *Diaphorocleidus kabatai* (Molnar, Hanek and Fernando, 1974) Jogunoori, Kritsky, and Venkatanarasaiah, 2004 (Monogeneidae: Dactylogyridae) from 3 species of *Astyanax* (Characidae) from 6 rivers in Panama.

Morphological structures	Locations and host species					
	Nigua	Caldera	Chiriquicito	Cardenas	Aguas Claras	Piriati
	<i>A. aeneus</i>	<i>A. aeneus</i>	<i>A. aeneus</i>	<i>A. riberrimus</i>	<i>A. fasciatus</i>	<i>A. fasciatus</i>
Body length	282–310	—	—	—	—	247–295
Greatest width	59–130	—	—	—	—	67–124
Pharynx	19 (n = 2)	—	—	—	—	15–25
Haptor width	60	—	—	—	—	48–60
Ventral anchor length	29 (28–30; n = 3)	31 (30–33; n = 12)	32 (30–33; n = 6)	30 (29–31; n = 8)	29 (26–31; n = 16)	29 (28–30; n = 8)
Ventral anchor width	16 (n = 2)	18 (15–19; n = 11)	17 (15–18; n = 7)	17 (17–18; n = 6)	17 (15–20; n = 15)	18 (16–20; n = 8)
Dorsal anchor length	(25–26)	27 (25–28; n = 12)	26 (25–28; n = 7)	25 (24–26; n = 10)	26 (24–28; n = 18)	26 (26–27; n = 8)
Dorsal anchor width	(14–15)	14 (12–16; n = 11)	14 (13–15; n = 7)	14 (12–15; n = 3)	13 (12–14; n = 11)	13 (12–14; n = 8)
Ventral bar length	30	25 (23–27; n = 6)	25 (24–26; n = 4)	24 (23–26; n = 5)	23 (22–24; n = 7)	22 (19–25; n = 5)
Dorsal bar length	34	30 (29–31; n = 6)	33 (31–36; n = 4)	30 (29–30; n = 6)	19 (25–31; n = 8)	27 (25–30; n = 6)
Hook pair 5	13	13 (12–15; n = 8)	13 (12–14; n = 5)	14	13 (12–15; n = 14)	14 (12–15; n = 11)
Hook pairs 2, 3, 4, 6, and 7	20 (20–21; n = 8)	20 (18–21; n = 24)	19 (17–20; n = 14)	19 (17–20; n = 13)	18 (17–20; n = 32)	19 (18–21; n = 20)
Male copulatory organ length	22	23 (22–25; n = 5)	25 (22–29; n = 5)	20	22 (20–27; n = 10)	14 (19–23; n = 5)
Accessory piece length	28	34 (32–35; n = 6)	34 (29–37; n = 3)	31 (30–32; n = 5)	34 (30–36; n = 10)	20 (31–34; n = 5)

icantly, we report a medioventral vaginal aperture rather than a sinistral vagina as reported by Kritsky and Leiby (1972). We also report several new host species and geographical records for this species in Table I.

***Diaphorocleidus orthodus* n. sp.**
(Figs. 11–18)

Description (based on 14 slightly contracted specimens): Body 180–145 long, foliiform; greatest width 58–63 near level of testis. Cephalic margin broad; cephalic lobes moderately developed; 3 bilateral pairs of head organs and cephalic glands indistinct. Four eyes, subequal; few eye granules present in cephalic region. Pharynx subovate 14–15 in diameter. Peduncle broad; haptor hexagonal, 83 (76–92; n = 5) wide. Anchors similar; each with elongate superficial root, well-developed deep root, curved shaft, and short point; ventral anchor 36 (34–37; n = 23) long, base 20 (18–21; n = 19) wide; dorsal anchor 27 (25–28; n = 28) long, base 14 (14–15; n = 20) wide. Ventral bar 28 (25–28; n = 13) long, broadly U-shaped with enlarged terminations and a slight anteromedial and posteromedial indentation; dorsal bar 30 (27–31; n = 15) long, slender, broadly U-shaped, with terminations directed laterally. Hooks similar; each with protruding thumb, delicate shaft and point, dilated shank; hook pairs 1 and 5 reduced in size; FH loop $\frac{1}{3}$ shank length (pairs 1 and 5), $\frac{1}{2}$ shank length (pairs 2, 3, 4, 6, and 7); hook pairs 2, 3, 4, 6 and 7: 19 (17–20; n = 64) long; hook pairs 1 and 5: 14 (13–15; n = 24) long. MCO tubular, delicate, comprising a sinistral loop, base with spherical flange, diameter of a poorly defined ring 31 (25–35; n = 5). Accessory piece 25 (22–27; n = 14) long, round. Vaginal aperture sinistral. Seminal receptacle not observed. Gonads overlapping; testis dorsal, slightly visible at end of germarium; seminal vesicle a distal expansion of vas deferens; prostatic reservoir single. Oviduct, ootype, and uterus not observed. Vitellaria scattered throughout trunk, except in regions of reproductive organs.

Taxonomic summary

Type host: *Astyanax orthodus* Eigenmann, 1907 (Characiformes: Characidae).

Site of infection: Gills.

Type locality and collection date: Nigua river in Panama (09°16'44"N, 82°24'55"W), September 2006.

Specimens deposited: Holotype in CNHE (6277); 6 paratypes in CNHE (6278); and 7 in USNPC (100962).

Etymology: The specific epithet is for the host species.

Remarks

Diaphorocleidus orthodus n. sp. most closely resembles *Diaphorocleidus armillatus* Jogunoori, Kritsky, and Venkatanarasaiah, 2004 (type species of the genus) from the Neotropical *Gymnocorymbus ternetzi* (Characidae) by having anchors with elongate superficial root, but differs from this species at least by possessing an MCO comprising a sinistral loop (a coil of 2 counterclockwise rings in *D. armillatus*) and a base with a spherical flange (proximal and distal flanges in *D. armillatus*). This is the sixth named species of *Diaphorocleidus*-parasitizing characids and the second species of this parasite genus reported from the Neotropics (Jogunoori et al., 2004; Mendoza-Franco et al., 2007).

***Diaphorocleidus kabatai* (Molnar, Hanek, and Fernando, 1974) Jogunoori, Kritsky, and Venkatanarasaiah, 2004**
(Figs. 19–33)

Supplemental observations (measurements based on 5 specimens from Chaamac and on 6 from Dzont Cervera [brackets]): Body 270–298 [290 (248–347; n = 4)] long, fusiform; greatest width 90–105 [98 (80–115; n = 4)], usually at level of testis. Cephalic margin broad; cephalic lobes moderately developed; 3 bilateral pairs of head organs; cephalic glands present. Four eyes, subequal. Pharynx spherical 19–22 [22 (18–27; n = 4)] in diameter; esophagus short. Peduncle broad; haptor subrectangular 68–70 [83 (68–90; n = 3)]. Ventral anchor 34 (30–34; n = 6) [36 (31–37; n = 11)] long, with elongate superficial root, deep root narrowing distally, short shaft and point; base 19 (19–20; n = 6) [24 (19–27; n = 10)] wide. Dorsal anchor 29 (27–30; n = 6) [31 (30–32; n = 8)] long, with well-developed base, moderately short shaft, short point; base 15 (n = 6) [19 (15–20; n = 8)] wide. Ventral bar 27 (25–29; n = 4) [37 (28–43; n = 7)] long, slender, broadly U-

shaped with enlarged terminations; dorsal bar 35 (34–36; n = 4) [44 (36–52; n = 6)] long, variable, U- to V-shaped, with terminations directed laterally. Hooks similar, each with protruding thumb, delicate shaft and point, dilated shank; hook pairs 1 and 5 reduced in size; FH loop $\frac{1}{2}$ – $\frac{1}{2}$ shank length; hook pairs 2, 3, 4, 6, and 7: 19 (19–20; n = 9) [23 (19–24; n = 19)] long; hook pair 1: 16 (n = 3) [18 (17–18; n = 6)] long; hook pair 5: 14 (n = 2) [13 (13–14; n = 6)] long. MCO comprising a delicate coil of 1– $1\frac{1}{2}$ counterclockwise rings, base with lateral flange, proximal ring diameter 13–17 [15–22]. Accessory piece 24 (20–26; n = 5) [29 (23–33; n = 6)] long, variable, distally pincer-shaped. Vaginal aperture sinistral, a delicate tube leading into small medial seminal receptacle anterior to germarium. Gonads overlapping, germarium 30–45 [47 (34–55; n = 3)] long, 21 [21 (19–24; n = 3)] wide; testis dorsal, slightly visible at end of germarium; seminal vesicle a distal enlargement (expansion) of vas deferens; prostatic reservoir single. Oviduct, ootype, and uterus not observed. Vitellaria scattered throughout trunk, except in regions of reproductive organs. Measurements of specimens of *D. kabatai* from *Astyanax* spp. in Panama are provided in Table II.

Taxonomic summary

Host and locality: *Astyanax aeneus* (Günther, 1860) (Characiformes: Characidae), Dzonot Cervera (21°22'36"N; 88°49'59"W) in southeast Mexico.

Site of infection: Gills.

Other localities: Chaamac cenote in Mexico, and Nigua, Caldera, and Chiriquito Rivers in Panama.

Other hosts and localities: *A. ruberrimus* from Cardenas and *A. fasciatus* from Aguas Claras and Piriati rivers in Panama (see Table II).

Specimens deposited: One voucher specimen in CNHE (6281).

Remarks

Kritsky et al. (1986) revised *Urocleidoides* and considered *U. kabatai* incertae sedis. Jogunoori et al. (2004) proposed *Diaphorocleidus* as a new species, *D. armillatus* from *G. ternetzi* (Characidae), and transferred several species in incertae sedis from *Urocleidoides* (s. l.) into *Diaphorocleidus* on the basis of those species having: (1) overlapping gonads; (2) an unarticulated copulatory organ and accessory piece; (3) a coiled MCO with counterclockwise rings; and (4) a sinistroventral vaginal aperture. Thus, Jogunoori et al. (2004) considered *U. kabatai* a species of *Diaphorocleidus*, based on the morphology of the copulatory complex described above. Based on comparisons of our current material with the original drawings of *Urocleidoides anops* (Figs. 19–23 in Mendoza-Franco et al., 1999) and *Ancyrocephalinae* gen. sp. (Figs. 11–18 in Mendoza-Franco et al., 2003), all specimens appear to be identical to *D. kabatai*, suggesting that *U. anops* and *Ancyrocephalinae* gen. sp. were previously misidentified (see Figs. 19–33 and Table II).

Palombitrema heteroancistrum (Price and Bussing, 1968)

Suriano 1997

(Figs. 34–45)

Supplemental observations (measurements based on 12 specimens from Chaamac and on 35 specimens from Dzonot Cervera [brackets]): Body 355 (285–480; n = 12) [327 (260–395; n = 35)] long, fusiform; greatest width 103 (94–110; n = 9) [98 (75–127; n = 34)], usually at the level of testis. Cephalic margin broad; cephalic lobes moderately developed; 3 bilateral pairs of head organs; cephalic glands present. Four eyes, subequal. Pharynx spherical, 19 (16–23; n = 12) [21 (17–23; n = 33)] in diameter; esophagus moderately long. Peduncle broad; haptor subrectangular, 69 (62–85; n = 8) [75 (65–88; n = 38)] wide. Ventral anchor 18 [18–19 (n = 10)] long, with well-differentiated roots, slightly depressed superficial root, short tapered deep root, curved shaft, short point; base 13 (12–15; n = 10) wide. Dorsal anchor 27–28 (n = 6) [27 (26–28; n = 14)] long, having poorly differentiated deep root and curved shaft bearing short point; base 12–15 [15 (14–16; n = 11)]

wide. Ventral bar 23 (21–26; n = 4) [22 (20–32; n = 16)] long, broadly V-shaped with expanded terminations and a slight posteromedial indentation; dorsal bar 30 (28–33; n = 5) long, variable, rod or slightly U-shaped, with terminations directed laterally. Hooks dissimilar; each with delicate shaft and point, dilated shank; FH loop $\frac{1}{2}$ – $\frac{1}{2}$ shank length; hook pairs 2, 3, and 4: 18 (n = 3) [16 (16–17; n = 14)] long; hook pair 6: 10–11 [11 (10–12; n = 11)] long; hook pair 7: 33 (31–34; n = 4) long; hook pairs 1 and 5: 11 (10–12; n = 8) long. MCO a delicate coiled tube of about $1\frac{1}{2}$ poorly defined counterclockwise rings, base with lateral flange, diameter of the proximal ring 17 (17–19; n = 4). Accessory piece 26 (23–29; n = 8) long, flabellate, comprising 2 subunits, proximal subunit connected to the base of MCO. Vagina sinistral, a well-sclerotized tortuous tube directed posteriorly, twisted before connecting to seminal receptacle; seminal receptacle small, medial, anterior to germarium. Gonads overlapping, germarium 52 (40–80; n = 8) [51 (38–67; n = 19)] long, 31 (27–35; n = 7) [30 (20–45; n = 27)] wide; testis dorsal, slightly visible at end of germarium 15 [12 (10–17; n = 6)] long, 14 [12 (10–14; n = 5)] wide; seminal vesicle a distal enlargement (expansion) of vas deferens; prostatic reservoir single; oviduct, ootype, uterus not observed. Vitellaria scattered throughout trunk, absent in regions of reproductive organs; large glandular mass posterior to vitellaria. Measurements of specimens of *P. heteroancistrum* from *Astyanax* spp. in Panama are provided in Table III.

Taxonomic summary

Host and locality: *Astyanax aeneus* Günther, 1860 (Characiformes: Characidae), Chaamac cenote (20°51'53"N, 90°09'18"W) in southeast Mexico.

Site of infection: Gills.

Other localities: Dzonot Cervera cenote in Mexico, and Nigua and Quebrada Rivers in Panama.

Another host and locality: *Astyanax fasciatus* from Piriati River in Panama (see Table III).

Specimens deposited: Two voucher specimens in CNHE (6279, 6280).

Remarks

Our supplemental observations are intended to complement Suriano's (1997) redescription of *P. heteroancistrum*, which includes highly diagrammatic figures of the haptor structures that do not accurately represent the morphology of anchors and hooks (Suriano's Figs. 2, 3, and 6). Further, Suriano (1997) indicates that *P. heteroancistrum* has an "ovary anterior to testis," while the drawing (Fig. 1 in that paper) depicts gonads in tandem. The gonads of *P. heteroancistrum* are clearly overlapping in specimens that we evaluated. Considering these discrepancies, we provide new illustrations, measurements, and morphological information for this species. For instance, the large glandular mass posterior to vitellaria observed in the present specimens of *P. heteroancistrum* (Fig. 34) may be associated with the haptor. This gland mass appears to be similar to that described for *Cichlidogyrus hallitipicus* Price and Kirk, 1967 and *Duplaccessorius andinus* Viozzi and Brugni, 2004 (see El-Naggar and Kearn, 1989; Viozzi and Brugni, 2004). To date, there are other 2 species of *Palombitrema* (*Palombitrema chascomusense* [Suriano, 1981] Suriano, 1997 and *Palombitrema triangulum* [Suriano, 1981] Suriano, 1997 from *Curimata gilberti* [Curimatidae] and *Oligosarcus jenynsi* [Characidae]) reported in Argentina. *Palombitrema heteroancistrum* has previously been reported in Costa Rica, Colombia, Nicaragua, and Mexico (Kritsky and Leiby, 1972; Kritsky and Thatcher, 1974; Mendoza-Franco et al., 1999, 2003); its occurrence in Panama represents a new geographical record.

Urocleidoides strombicirrus (Price and Bussing, 1967) Kritsky and Thatcher, 1974

Supplemental observations: (see Table IV).

←

FIGURES 34–45. *Palombitrema heteroancistrum*. (34) Whole mount (composite, ventral view; hooks not completely inked are in dorsal position). (35) Ventral anchor. (36) Copulatory complex (dorsal). (37) Dorsal anchor. (38) Ventral bar. (39–40) Dorsal bars. (41) Hook (pair 1). (42) Hook (pair 5). (43) Hook (pair 2). (44) Hook (pair 6). (45) Hook (pair 7). All figures are drawn to the 25- μ m scale, except 34 (50- μ m).

TABLE III. Comparative measurements (in micrometers; mean with range in parentheses; n = number of structures measured) of *Palombitrema heteroancistrum* (Price and Bussing, 1968) Suriano 1997 (Monogenoidea: Dactylogyridae) from 2 species of *Astyanax* (Characidae) from 3 rivers in Panama.

Morphological structures	Locations and host species		
	Nigua	Quebrada	Piriati
	<i>A. aeneus</i>	<i>A. aeneus</i>	<i>A. fasciatus</i>
Body length	270	299 (268–337; n = 7)	306 (270–355; n = 20)
Greatest width	75	91 (66–105; n = 7)	80 (40–100; n = 21)
Pharynx	15	15 (13–16; n = 7)	18 (14–21; n = 23)
Haptor width	63	64 (50–75; n = 7)	66 (45–79; n = 22)
Ventral anchor length	20 (19–20; n = 4)	20 (19–21; n = 15)	17 (16–18; n = 20)
Ventral anchor width	12 (12–13; n = 4)	13 (12–15; n = 15)	12 (10–13; n = 20)
Dorsal anchor length	28 (27–30; n = 4)	29 (28–30; n = 16)	26 (25–26; n = 19)
Dorsal anchor width	14 (13–15; n = 4)	15 (14–18; n = 16)	12 (10–14; n = 18)
Ventral bar length	(23–25)	22 (18–26; n = 12)	22 (18–24; n = 9)
Dorsal bar length	(31–32)	31 (28–34; n = 7)	24 (22–27; n = 8)
Hook pairs 2, 3, and 4	16 (n = 3)	15 (14–16; n = 31)	14 (13–15; n = 27)
Hook pair 6	11 (n = 5)	11 (10–12; n = 29)	11 (10–12; n = 22)
Hook pair 7	29 (29–30; n = 4)	30 (28–33; n = 8)	26 (23–30; n = 19)
Male copulatory organ length	(15–20)	18 (17–20; n = 7)	15 (13–17; n = 5)
Accessory piece length	(22–26)	27 (24–30; n = 10)	32 (27–35; n = 11)
Germary length	25	36 (32–42; n = 3)	28 (22–38; n = 3)
Germary width	35	22 (21–25; n = 3)	19

Remarks

The morphometrical data presented in Table IV allowed us to identify this species as *U. strombicirrus*. After revision of *Urocleidoides*, this species was considered in incertae sedis by Kritsky et al. (1986). Since then, no generic reassignment has been made for *U. strombicirrus*, yet, it has been reported from Colombia and Nicaragua (see Mendoza-Franco et al., 2003). This study represents the first report of *U. strombicirrus* from Panama.

DISCUSSION

The 3 monogenoidean genera, *Characithecium* n. gen., *Diaphorocleidus*, and *Palombitrema* (plus *U. strombicirrus*), are morphologically well separated. *Diaphorocleidus* includes 6 species infecting hosts in *Astyanax*, *Bryconops*, *Brycon*, *Gymnocorymbus*, and *Hemigrammus*. *Palombitrema* includes 3 species infecting species of *Curimata* (Curimatidae) and *Oligosar-*

cus (Characidae) in South America, as well as species of *Astyanax* in the Neotropics (Jogunoori et al., 2004; Mendoza-Franco et al., 2007; present study). *Characithecium* possesses only a single species, *Ch. costaricensis* (Price and Bussing, 1967) comb. n., which infects 3 host species of *Astyanax* across Central America, from southeastern Mexico to Panama. The body size of individual specimens of *Ch. costaricensis* varied substantially both within and across different host species and locations. However, the morphological differences were insufficient to designate or separate new species of *Characithecium* (see Table I). Similar morphometric differences, where morphologically identical specimens differ in size, have been found in other dactylogyrids (Kritsky et al., 1989, 2007). The continuous distribution of *Ch. costaricensis* on *Astyanax* spp. from South America to central Mexico (Salgado-Maldonado et al.,

TABLE IV. Comparative measurements (in micrometers; mean with range in parentheses; n = number of structures measured) of *Urocleidoides strombicirrus* (Price and Bussing, 1967) (Monogenoidea: Dactylogyridae) from 2 species of *Astyanax* (Characidae) from 3 rivers in Panama.

Morphological structures	Locations and host species		
	Quebrada <i>A. aeneus</i>	Chiriquicito <i>A. aeneus</i>	Piriati <i>A. fasciatus</i>
Body length	310–368	—	—
Greatest width	115–137	—	—
Pharynx	25–32	—	—
Haptor width	85–88	—	—
Ventral anchor length	42–43	41–42	39–40
Ventral anchor width	20	21–22	20–21
Dorsal anchor length	—	25–26	24–25
Dorsal anchor width	—	12–14	12–13
Ventral bar length	40–42	37	46
Dorsal bar length	31	30	31
Hook pairs 2, 3, 4, 6, and 7	—	20 (19–22; n = 3)	20 (19–21; n = 10)
Male copulatory organ length	—	—	15–17

2001, 2004) suggest that dispersal across Central America has resulted in limited speciation within this genus. Similarly, the apparently low level of host specificity of *Ch. costaricensis* could also reduce the potential for speciation. While *Ch. costaricensis* reportedly infects only *Astyanax* spp. (Mendoza-Franco et al., 1999, 2003), a thorough examination of other fish genera within Characidae could increase our knowledge of the host specificity and diversification patterns of this species and other dactylogyrids that infect species of *Astyanax*.

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