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NEW AND PREVIOUSLY DESCRIBED SPECIES OF DACTYLOGYRIDAE (MONOGENOIDEA) FROM THE GILLS OF PANAMANIAN FRESHWATER FISHES (TELEOSTEI)

Edgar F. Mendoza-Franco*, M. Leopoldina Aguirre-Macedo, and Víctor M. Vidal-Martínez

Laboratory of Parasitology, Centro de Investigación y de Estudios Avanzados (CINVESTAV, Unidad Mérida), Carretera Antigua a Progreso Km. 6, Apartado Postal 73 "Cordemex," C.P. 97310 Mérida, Yucatán, Mexico. e-*mail: mfranco@mda.cinvestav.mx*

ABSTRACT: During an investigation of the diversity of metazoan parasites of 7 freshwater fish species from 3 localities in central Panama, the following gill dactylogyrid (Monogenoidea) species were found: *Aphanoblastella chagresii* n. sp. from *Pimelodella chagresi* (Heptapteridae); *Aphanoblastella travassosi* (Price, 1938) Kritsky, Mendoza-Franco, and Scholz, 2000 from *Rhamdia quelen* (Heptapteridae); *Diaphorocleidus petrosusi* n. sp. from *Brycon petrosus* (Characidae); *Gussevia asota* Kritsky, Thatcher, and Boeger, 1989, from *Astronotus ocellatus* (Cichlidae); *Sciadicleithrum panamensis* n. sp. from *Aequidens coeruleopunctatus* (Cichlidae); *Urocleidoides flegomai* n. sp. from *Piabucina panamensis* (Lebiasinidae); and *Urocleidoides similuncus* n. sp. from *Poecilia gillii* (Poeciliidae). Consideration of the comparative morphology and distribution of these parasites along with the evolutionary history of the host fishes suggests that diversification may be associated with geotectonic events that provided isolation of the Central American fauna with the uplift of the Panamanian Isthmus during early Pliocene (3 mya).

Central America comprises a tectonically dynamic part of the world that has interested biogeographers for many years (Rosen, 1976; Gayet et al., 1992; Iturralde and MacPhee, 1999). This diverse region has served as a corridor for organismic dispersal from South America upwards (and vice versa), and much attention has been focused on the Isthmus of Panama as a barrier to dispersal of marine organisms (Bermingham and Martin, 1998; Perdices et al., 2002). Within this scenario, knowledge of the diversity of the parasite fauna of fishes is still limited, as is the case for the monogenoidean parasites (Scholz et al., 1999; Aguirre-Macedo et al., 2001; Vidal-Martinez et al., 2001; Choudhury et al., 2002; Mendoza-Franco et al., 2003; Aguirre-Macedo and Scholz, 2005). Although species in this group of flatworms have already been extensively studied in fish from South America (Kritsky et al., 1986; Boeger and Kritsky, 1988; Kritsky et al., 1989, 1992; Boeger et al., 1994; Kritsky et al., 1996, 1997; Agarwal and Kritsky, 1998; Kohn and Cohen, 1998; Kritsky and Gutiérrez, 1998; Boeger and Kritsky, 2003), these same species are largely unstudied in Central America. Monogenoidean species were found during a study on metazoan parasites carried out in April 2006 in freshwater environments from several localities in the surroundings of Soberanía National Park in central Panama. In the present study, 7 dactylogyrid species (5 new) are described and/or reported from the gills of 7 fish species, and a possible explanation of the origin and speciation of these parasites in Central America based on their geographical distribution is provided.

MATERIALS AND METHODS

Fish were collected using beach seines, hook and line, and trammel nets from Rio Frijolito (09°09′53″N, 79°45′16″W), Lago Gatun (09°06′871″N, 79°41′721″W), and Lago Alajuela (09°15′00″N, 79°34′59.88″W) in the Chagres River Basin in central Panama. Live fish were brought to the laboratory, killed by pithing the brain, and examined for monogenoids. Worms were removed from gills, examined, and measured as temporary or permanent mounts fixed with ammonium picrate (Ergens, 1969). Additional specimens were mounted unstained in glycerin jelly for study of the sclerotized structures. All other measurements were obtained from unflattened specimens fixed in hot (≈90 C) or ambient temperature (≈30 C) formalin (4%), stained in Gomori trichrome and mounted in Canada balsam. Drawings were made with the aid of a drawing tube using an Olympus microscope with Nomarski interference contrast. Measurements, all in micrometers, 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 that of the haptor. Numbering of hook pairs follows the scheme illustrated in Mendoza-Franco, Violante-González, and Vidal-Martínez (2006). Type and voucher specimens are deposited in the United States National Parasite Collection, Beltsville, Maryland (USNPC); National Helminthological Collection of Mexico (CNHE), Institute of Biology, National Autonomous University of Mexico, Mexico; and the helminthological collection of the Institute of Parasitology, České Budějovice, Czech Republic (IPCAS), as indicated in the respective descriptions. Host names follow those in the Food and Agriculture Organization Fish Base (http://www.fishbase.org).

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* Current address: Smithsonian Tropical Research Institute, Naos Island Laboratories, Apartado Postal 0843-03092 Balboa, Ancon, Panama City, Republic of Panama.

DESCRIPTION

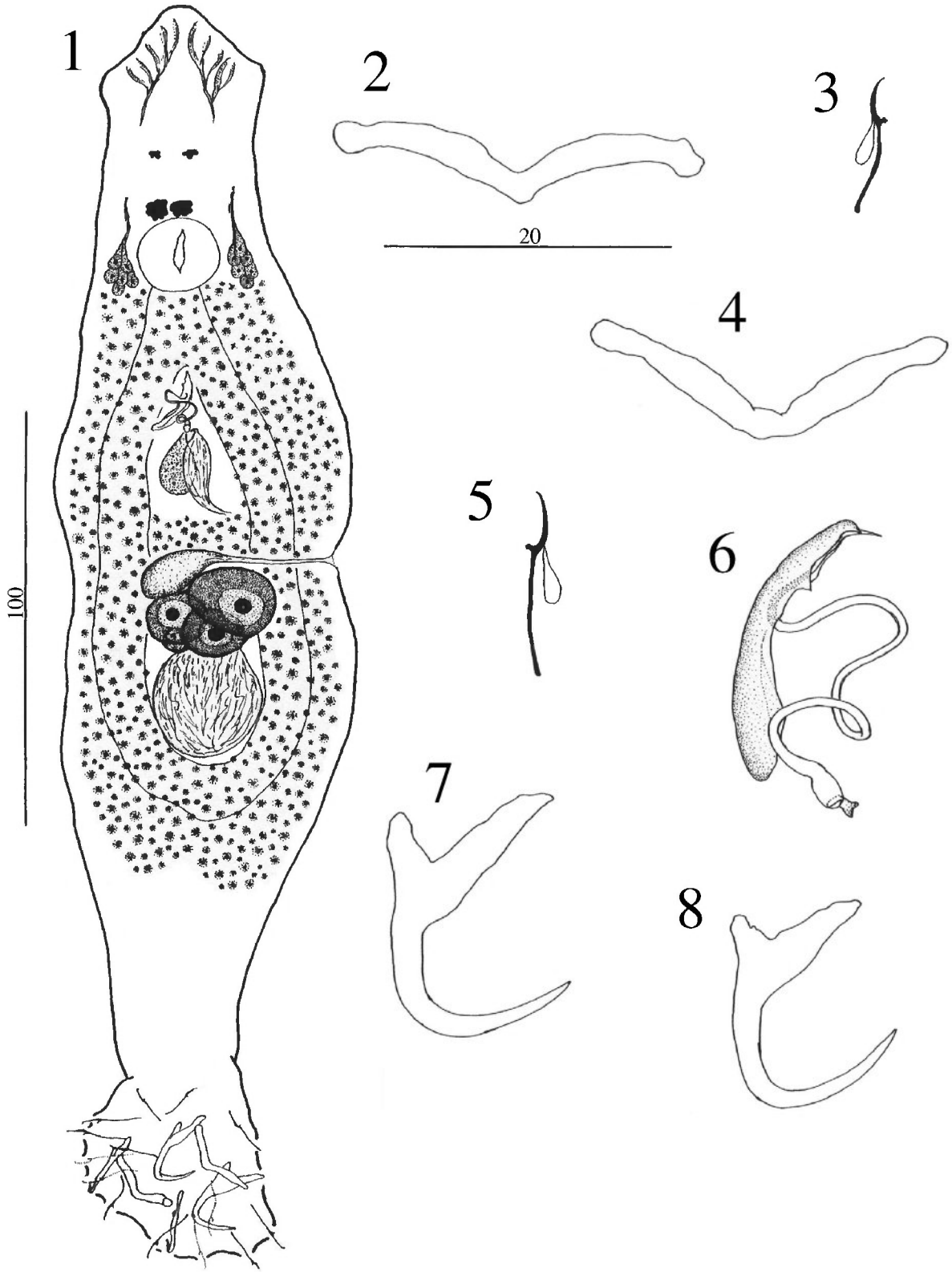
Aphanoblastella chagresii n. sp.

(Figs. 1–8)

Diagnosis: Body fusiform, greatest width near posterior trunk. Cephalic margin narrow; cephalic lobes poorly to moderately developed; 3 bilateral pairs of head organs; cephalic glands indistinct. Eyes 4, posterior pair larger, closer together than anterior pair; accessory granules usually uncommon in cephalic region. Pharynx subspherical; esophagus moderately long. Peduncle broad; haptor subhexagonal. Ventral anchor with well-developed roots, straight shaft, elongated curved point. Dorsal anchor with short deep root, protruding superficial root, straight shaft moderately elongated, elongate curved point. Ventral bar, delicate, broadly V-shaped, with a poorly developed posteromedial protuberance; dorsal bar broadly V-shaped, bulbous ends directed laterally. Hooks similar, each with, protruding thumb, delicate shaft and point, fine shank; hook pair 1, reduced in size; FH loop about 40% shank length (pairs 2–7), 50% shank length (pair 1). Male copulatory organ (MCO) a coil of ~2.5 counterclockwise rings, base of male copulatory organ with small sclerotized plate. Accessory piece, comprising variable sheath along distal shaft of copulatory organ. Testis subspherical; seminal vesicle as dilation of vas deferens, indistinct, fusiform; one prostatic reservoir. Germarium subspherical to ovate, comprising comparatively few cells, slightly overlapping gonads; oviduct, ootype not observed; uterus delicate. Vaginal aperture sinistroventral, simple; vaginal canal tubular, straight to slightly slanted posteriorly into pyriform seminal receptacle. Measurements of 21 specimens studied from this host provided in Table I.

Taxonomic summary

Type host: Catfish *Pimelodella chagresi* (Steindachner, 1877) (Siluriformes: Heptapteridae).



FIGURES 1–8. *Aphanoblastella chagresii* n. sp. (**1**) Whole mount (composite, ventral view). (**2**) Ventral bar. (**3**) Hook (pair 1). (**4**) Dorsal bar. (**5**) Hook (pairs 2–7). (**6**) Copulatory complex (dorsal view). (**7**) Ventral anchor. (**8**) Dorsal anchor. All figures are drawn to the 20-μm scale, except 1 (100-μm).

TABLE I. Measurements of species of *Aphanoblastella* from species of *Pimelodella* and *Rhamdia* (Siluriformes) in the tropics.*

	A. chagresii†	*A. travassosi*‡	*A. travassosi*§	*A. travassosi*‖	*A. travassosi*†
	P. chagresi	*P. laticeps*	*R. guatemalensis*	*R. quelen*	*R. quelen*
Body length	236 (175–350; n = 16)	295 (180–375)	282 (204–364; n = 34)	390 (321–472)	364 (295–432; n = 11)
Greatest width	63 (42–82; n = 12)	85 (65–100)	104 (77–127; n = 32)	85 (75–91)	95 (80–112; n = 11)
Pharynx width	19 (14–22; n = 15)	20 (15–25)	28 (21–33; n = 23)	26 (24–28)	24 (21–29; n =10)
Haptor width	50 (40–60; n = 8)	—	55 (45–63; n = 31)	55 (42–61)	56 (51–74; n = 9)
Ventral anchor length	20 (19–20; n = 28)	18 (15–20)	22 (21–24; n = 13)	20 (19–21)	26 (24–29; n = 27)
Ventral anchor width	10 (9–15; n = 11)	—	16 (14–17; n = 11)	14 (13–14)	15 (14–17; n = 8)
Dorsal anchor length	16 (16–17; n = 21)	15 (14–20)	24 (21–27; n = 11)	17 (16–17)	27 (25–30; n = 20)
Dorsal anchor width	8 (8–10; n = 13)	—	16 (14–18; n = 12)	13 (12–14)	16 (14–18; n = 7)
Ventral bar length	23 (20–28; n = 18)	29 (23–40)	32 (29–37; n = 10)	30 (29–31)	30 (26–33; n = 17)
Dorsal bar length	24 (20–28; n = 11)	30 (25–42)	37 (31–44; n = 9)	23 (22–25)	35 (31–39; n = 9)
Hooks pairs 1, 3–7	14 (13–14; n = 21)	15 (10–17)	13 (12–14; n = 23)	9 (8–10)	12 (11–13; n = 20)
Hooks pair 2	10 (10–11; n = 7)	—	—	—	—
MCO# length	16 (15–17; n = 5)	85 (70–110)	41 (38–45; n = 5)		—
Accessory piece	18 (15–22; n = 14)	30 (25–35)	31 (28–36; n = 4)	29 (24–32)	32 (32–33; n = 3)
Germarium length	24 (19–28; n = 8)	—	28 (20–44; n = 23)	390 (321–472)	30 (22–37; n = 8)
Germarium width	25 (20–44; n = 9)	—	22 (18–25; n = 23)	—	21 (11–30; n = 8)
Testis length	29 (28–31; n = 7)	—	51 (40–59; n = 19)	—	58 (50–66; n = 6)
Testis width	27 (20–40; n = 7)	—	35 (25–46; n = 18)	—	28 (24–37; n = 5)

* Measurements (in μm) are mean, with range in parentheses; n = number of measurements.
† Present study.
‡ Measurements of *A. travassosi* from Argentina (Suriano, 1986).
§ Measurements of *A. travassosi* from southeast Mexico (Kritsky et al., 2000).
‖ Measurements of *A. travassosi* from Trinidad (Molnar et al., 1974).
Male copulatory organ.

Site of infection: Gills.

Type locality/collection date: Rio Frijolito (09°09′53″N, 79°45′16″W), Republic of Panama, April 2006.

Specimens deposited: Holotype (CNHE 5784); 10 paratypes (CNHE 5786), 5 paratypes (IPCAS M-431), and 5 paratypes (USNPC 99625).

Etymology: The specific name is derived from its host.

Remarks

Aphanoblastella was erected by Kritsky et al. (2000) to accommodate dactylogyrid species possessing tandem gonads, a coiled MCO with counterclockwise rings, unmodified anchors, a ventral bar with posteromedial projection, a nonarticulated MCO, and accessory piece simple and similar hooks with undilated shanks. Since then, 3 species of *Aphanoblastella* have been recognized from the gills of neotropical catfish species of *Rhamdia* (Siluriformes). These include: *Aphanoblastella travassosi* (Price, 1938) Kritsky, Mendoza-Franco, and Scholz, 2000 (type species) from *Rhamdia rogersi* (Regan, 1907), *R. sebae* (Valenciennes, 1840), and *R. quelen* (Quoy and Gaimard, 1824) (= *R. guatemalensis* in Perdices et al., 2002) in Costa Rica and Trinidad, respectively, and from *R. guatemalensis* (Günther, 1864) in Mexico; from *Pimelodella laticeps* Eigenmann, 1917 in Argentina; *A. robustus* (Mizelle and Kritsky, 1969) Kritsky, Mendoza-Franco and Scholz, 2000 from *Rhamdia* sp. in the Amazon River of Brazil, and *A. mastigatus* (Suriano, 1986) Kritsky, Mendoza-Franco and Scholz, 2000 from *R. sapo* (Valenciennes, 1840) in Argentina (see Molnár et al., 1974; Suriano, 1986; Kritsky et al., 2000). Based on comparative haptor morphology, *A. chagresii* n. sp. most closely resembles the type species, *A. travassosi* (as redescribed on the basis of specimens found in *R. guatemalensis* [Kritsky et al., 2000]). *Aphanoblastella chagresii* n. sp. differs from *A. travassosi* by having hooks of different size and an expanded accessory piece (rod-shaped in *A. travassosi*) and by lacking a posteromedial process on the ventral bar. Additionally, it differs in its shorter ventral (length 19–20 vs. 21–24 in *A. travassosi*) and dorsal (length 16–17 vs. 21–27) anchors and accessory piece (length 15–22 vs. 28–36) (see Table I). It is noteworthy that *A. chagresii* n. sp. from *P. chagresi* appears to be morphometrically similar to *A. travassosi* reported from *P. laticeps* in Argentina (Suriano, 1986; Kritsky et al., 2000). *Aphanoblastella chagresii* n. sp. and *A. travassosi* occur on the same geographic range of their hosts, *Pimelodella* spp., and both are relatively similar in the size of their ventral (length 19–20 vs. 15–20 in *A. travassosi* from *P. laticeps*) and dorsal (length 16–17 vs. 14–20) anchors (see Table I) and in the morphology of the accessory piece (compare figures 6 [present study] and 15 from the original redescription of *A. travassosi* in Suriano, 1986). Further, the hook measurements (length 10–17) provided by Suriano for *A. travassosi* fit into the ranges (length 10–14) of *A. chagresii* n. sp. All above mentioned suggests that *A. travassosi* from *P. laticeps* may be a synonym of *A. chagresii* n. sp., in other words, the same parasite species (*A. chagresii* n. sp.) on *Pimelodella* spp. If so, then a split between *Pimelodella* and *Rhamdia* resulted in speciation of *A. chagresii* n. sp. and *A. travassosi*, respectively (see phylogeny of *Rhamdia* in Perdices et al., 2002). Confirmation of the synonymy of *A. travassosi* from *P. laticeps* in Argentina with respect to *A. chagresii* n. sp. from *P. chagresi* in Panama will require further study of new specimens collected from *P. laticeps* and/or molecular research.

Aphanoblastella travassosi (Price, 1938) Kritsky, Mendoza-Franco and Scholz, 2000

Diagnosis: Comparative measurements by host presented in Table I.

Taxonomic summary

Host: Silver catfish, *Rhamdia quelen* (Quoy and Gaimard, 1824) (Siluriformes: Heptapteridae).

Site of infection: Gills.

Locality/collection date: Lago Alajuela (09°15′00″N, 79°34′59.88″W), Republic of Panama, April 2006.

Specimens deposited: 3 reference specimens (CNHE 5786), 5 in IPCAS (M-353), and 5 in USNPC (99626).

Remarks

The specimens fit the diagnosis of *A. travassosi*, the type species of the genus, which was redescribed by Kritsky et al. (2000) on the basis of specimens found in *R. guatemalensis* from cenotes (= sinkholes) in southeastern Mexico. Comparison of the present material with a voucher of *A. travassosi* from *R. guatemalensis* from the Parasitology Labo-

ratory, CINVESTAV, Merida, Mexico (CHCM 314), did not reveal any differences. The present finding of *A. travassosi* on *R. quelen* in Panama is a new geographical record.

Diaphorocleidus petrosusi n. sp.
(Figs. 9–15)

Diagnosis: Body 298 (242–337; n = 8) long, fusiform; greatest width 68 (57–75; n = 8) near midlength. Cephalic margin broad; cephalic lobes moderately developed; 3 bilateral pairs of head organs; cephalic glands indistinct. Eyes 4; members of posterior pair with conspicuous lens, larger, closer together than members of anterior pair; eye granule variable in size, usually elongate ovate; accessory granules in cephalic, anterior trunk regions. Pharynx spherical 17 (15–18; n = 7) diameter; esophagus short. Peduncle broad; haptor subhexagonal 66 (58–73; n = 7) wide. Anchors similar; each with poorly defined deep root, elongate superficial root, straight shaft, point short; ventral anchor 32 (30–34; n = 26) long, base 18 (16–20; n = 17) wide; dorsal anchor 22 (21–23; n = 15) long, base 12 (11–13; n = 11) wide. Ventral bar 24 (22–26; n = 15) long, straight to broadly U-shaped, ends enlarged, usually with anteromedial indentation; dorsal bar 20 (22–26; n = 15) long, broadly U-shaped. Hook 17 (15–18; n = 32) long, with 2 subunits; FH loop about 30% shank length. Copulatory organ a coil with about one and half counterclockwise rings, coil diameter of the first ring 16 (13–20; n = 12). Accessory piece 18 (16–20; n = 3) long, comprising a pincer shape distally that appears as 2 supporting processes. Gonads overlapping; testis elongate, fusiform, dorsoposterior to germarium, 12 (10–15; n = 3) long, 6 (5–8; n = 3) wide, ovate; seminal receptacle as expansion of vas deferens, sigmoid, pyriform; one prostatic reservoir. Germarium slightly oval, elongated, 44 (32–67; n = 6) long, 16 (13–20; n = 7) wide; oviduct, ootype not observed; submarginal sinistral vaginal aperture, a nondilated sclerotized tube into large medial seminal receptacle lying anterior to germarium; vitellaria limited in trunk, absent in regions of reproductive organs.

Taxonomic summary

Type host: Sábalo pipon *Brycon petrosus* Meek and Hildebrand, 1913 (Characiformes, Characidae).

Site of infection: Gills.

Type locality/collection date: Rio Frijolito (09°09′53″N, 79°45′16″W), Republic of Panama, April 2006.

Specimens deposited: Holotype (CNHE 5787); 3 paratypes (CNHE 5788), 4 paratypes (IPCAS M-432), and 3 paratypes (USNPC 99627).

Etymology: This species is derived from the specific name of its host.

Remarks

Placement of this new species in *Diaphorocleidus* is based on the generic diagnosis provided by Jogunoori et al. (2004), i.e., species with overlapping gonads, a coiled copulatory organ with counterclockwise rings, submarginal sinistral vaginal aperture, and hook shank with 2 subunits. The morphology of the features of the haptor and the copulatory complex distinguish *Diaphorocleidus petrosusi* n. sp. from the other 4 species of the genus that occur on fish of the Characidae (*Diaphorocleidus affinis* (Mizelle, Kritsky, and Crane, 1968) Jogunoori, Kritsky, and Venkatanarasaiah, 2004, from *Bryconops affinis* (Gunther, 1864); *Diaphorocleidus armillatus* Jogunoori, Kritsky, and Venkatanarasaiah, 2004, (type species) from *Gymnocorymbus ternetzi* (Boulenger, 1895); *Diaphorocleidus kabatai* (Molnár, Hanek, and Fernando, 1974), Jogunoori, Kritsky and Venkatanarasaiah, 2004, from *Astyanax bimaculatus* (Linnaeus, 1758), and *Diaphorocleidus microstomus* (Mizelle, Kritsky and Crane, 1968), Jogunoori, Kritsky and Venkatanarasaiah, 2004, from *Hemigrammus microstomus* Durbin, 1918) (Jogunoori et al., 2004). *Diaphorocleidus petrosusi* n. sp. most closely resembles *D. armillatus* from which it differs by having a distally pincer-shaped accessory piece (tortuous in *D. armillatus*), and by the comparative morphology of the dorsal anchors. Four dactylogyrid species have been described in South America: 3 from *Brycon melanopterus* (Cope, 1872) (*Jainus amazonensis* Kritsky, Thatcher, and Kayton, 1980; *Tereancistrium kerri* Kritsky, Thatcher, and Kayton, 1980, and *Trinibaculum braziliensis* Kritsky, Thatcher and Kayton, 1980) and 1 from *Brycon cephalus* (Günther, 1869) (*Annulotrematoides bryconi* Cuglianna, Silva Cordeiro, and Luque, 2003) (Kritsky et al., 1980; Cuglianna et al., 2003), but none of these parasite species show similarity with *Diaphorocleidus petrosusi* n. sp.

Gussevia asota Kritsky, Thatcher, and Boeger, 1989

Diagnosis: Ventral anchor 25–26 long. Dorsal anchor 26 (n = 2) long; base 10–11 wide. Ventral bar 30 long; dorsal bar 28 long. Hook 10–11 long. Proximal ring diameter of the MCO 16 long. Accessory piece 31 long.

Taxonomic summary

Host: Red oscar, *Astronotus ocellatus* (Agassiz, 1831) (Perciformes: Cichlidae).

Site of infection: Gills.

Locality/collection date: Lago Gatun (09°06′871″N, 79°41′721″W), Republic of Panama, April 2006.

Specimens deposited: 1 reference specimen (CNHE 5789).

Remarks

Measurements and the morphology of the sclerotized structures of the present specimen do not differ significantly from that figured in the original description. *Gussevia asota* is 1 of 3 originally described species (*G. astronoti* Kritsky, Thatcher, and Boeger, 1989 and *G. rogersi* Kritsky, Thatcher, and Boeger, 1989) on native *A. ocellatus* in South America (Brazil) and also reported from the same host species held in an aquarium in the United States (Kritsky et al., 1989). The finding of a single specimen of *G. asota* suggests that *A. ocellatus* has lost their original monogenoids since its colonization to Panama from South America. *Astronotus ocellatus* from Lago Gatun in Panama had only 2 specimens (one measured) on 6 fish. Thus, probably seasonality, i.e., low infection prevalences, could help to explain the absence of these South American monogenoids on *A. ocellatus* in Panama.

Sciadicleithrum panamensis n. sp.
(Figs. 16–22)

Diagnosis: Body fusiform; greatest width near midlength. Cephalic margin broad; cephalic lobes moderately developed; 3 bilateral pairs of head organs; cephalic glands indistinct. Eyes 4; members of posterior pair closer together than members of anterior pair; eye granule usually elongate ovate. Pharynx spherical; esophagus short to moderately long. Peduncle broad; haptor subhexagonal. Ventral anchor 25 (23–27; n = 15) long, with slightly appressed roots, evenly curved shaft, short point; base 11 (11–13; n = 11) wide. Dorsal anchor 23 (22–27; n = 13) long, with slightly depressed superficial root, poorly differentiated deep root, evenly curved shaft, short point; base 9 (8–9; n = 8) wide. Ventral bar 26 (23–28; n = 9) long, broadly V-shaped, with small enlarged ends; dorsal bar 23 (22–27; n = 8) long, yoke-shaped, with slightly enlarged ends, prominent anteromedial expansion. Hooks similar, each 12 (11–13; n = 34) long, with upright thumb, delicate point, shank; FH loop about 80% shank length. Gonads overlapping; testis ovate, dorsoposterior to germarium; seminal vesicle as expansion of vas deferens, fusiform; one prostatic reservoir, fusiform. MCO a coiled tube comprising 1.5 rings, base with slight flange. Accessory piece with broad basal portion terminating in diagonal opening, distal portion slightly pointed, lying within second shaft of the copulatory organ. Germarium with irregular margin; oviduct, ootype, uterus not observed. Vagina dextroventral, a slight sclerotized tube opening into small medial seminal receptacle; vitellaria dense throughout trunk, except absent in regions of reproductive organs.

Taxonomic summary

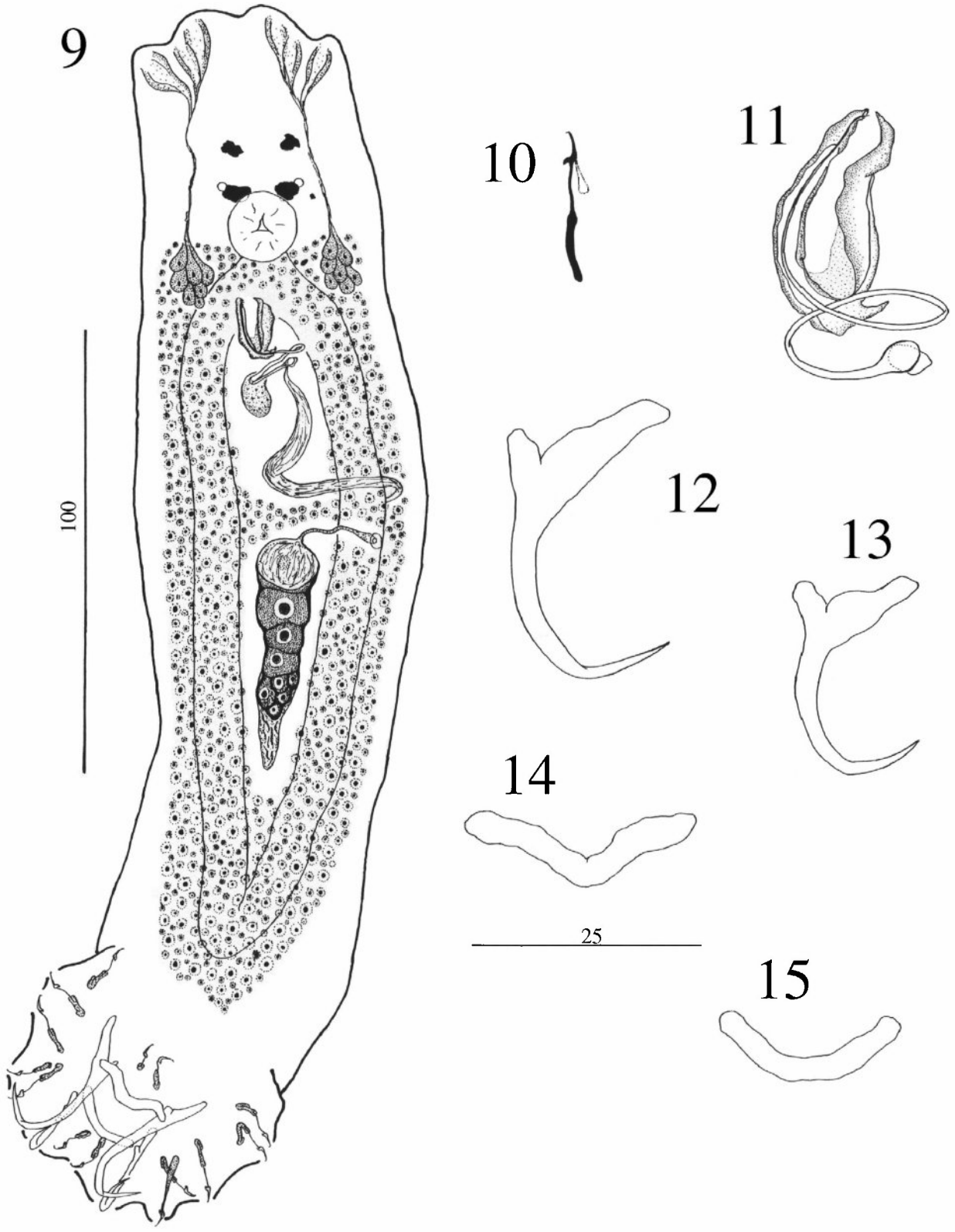
Type host: Chogorro *Aequidens coeruleopunctatus* (Kner, 1863) (Perciformes: Cichlidae).

Site of infection: Gills.

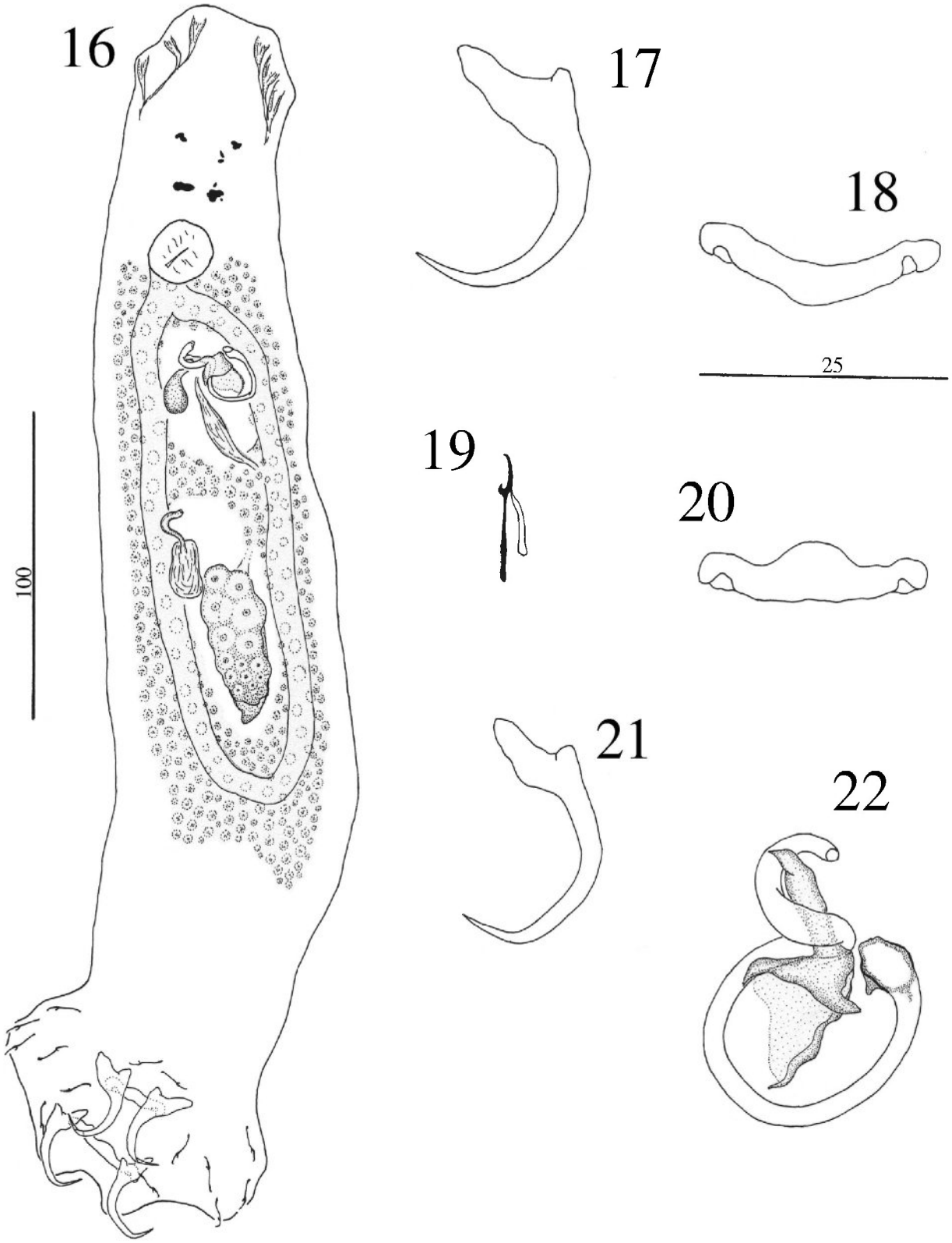
Type locality/collection date: Rio Frijolito (09°09′53″N, 79°45′16″W), Republic of Panama, April 2006.

Specimens deposited: Holotype (CNHE 5790); 2 paratypes (CNHE 5791) and 3 paratypes (USNPC 99628).

Etymology: This species is named for the country from which it was collected.



FIGURES 9–15. *Diaphorocleidus petrosusi* n. sp. (**9**) Whole mount (composite, ventral view). (**10**) Hook. (**11**) Copulatory complex (ventral view). (**12**) Ventral anchor. (**13**) Dorsal anchor. (**14**) Ventral bar. (**15**) Dorsal bar. All figures are drawn to the 25-µm scale, except 9 (100-µm).



FIGURES 16–22. *Sciadicleithrum panamensis* n. sp. (**16**) Whole mount (composite, ventral view). (**17**) Ventral anchor. (**18**) Ventral bar. (**19**) Hook. (**20**) Dorsal bar. (**21**) Dorsal anchor. (**22**) Copulatory complex (ventral view). All figures are drawn to the 25-μm scale, except 16 (100-μm).

Remarks

Features of the haptor (ventral bar with cavities, hook with slender shank and upright thumb) and copulatory sclerites (MCO with clockwise rings) clearly indicate that present specimens comprise an undescribed species of *Sciadicleithrum*. This species resembles its 9 congeners from South America by sharing the following features: a sinistroventral vaginal aperture, overlapping gonads, absence of longitudinal lateral grooves on shaft and point of anchors, no disjunction between roots of ventral and dorsal anchors, and a copulatory organ comprising less than 2 rings (see Mendoza-Franco and Vidal-Martínez, 2005). While 2 other species of *Sciadicleithrum* (*S. aequidens* (Price and Schlueter, 1967) Kritsky, Thatcher and Boeger, 1989 and *S. cavanaughi* (Price, 1966) Kritsky, Thatcher, and Boeger, 1989) have apparently speciated from the South American species of *Aequidens maroni* (= *Cleithracara maroni*) (Steindachner, 1881) (Kritsky et al., 1989), speciation of *S. panamensis* n. sp. seems to have occurred through its host geographic range, *A. coeruleopunctatus* in Central America (the Atlantic slope of Panama and Pacific slope of Costa Rica [Food and Agriculture Organization Fish Base, http://www.fishbase.org]). Additionally, it has been demonstrated that *Aequidens* is a secondary fish (i.e., ability of the host to survive high salinities), with populations not genetically isolated from each other in Panama. Similarly, that ability in the common ancestor of *A. coeruleopunctatus* to cross short distances (e.g., to Panama from South America) through salt water could have allowed isolated populations of this host species with the consequent speciation of its monogenoid, *S. panamensis* n. sp.

Urocleidoides flegomai n. sp.

(Figs. 23–31)

Diagnosis: Body fusiform 256 (200–357; n = 15) long, with parallel lateral margins; greatest width 55 (45–72; n = 13) usually at level of testis. Cephalic margin broad; cephalic lobes well developed; 3 bilateral pairs of head organs; cephalic glands distinct. Eyes 4; subequal; eye granules frequently dissociated, small, usually ovate; accessory granules (granules not associated with the eyes) present in cephalic region and anterior trunk. Pharynx spherical 16 (11–20; n = 16) in diameter; esophagus moderately long. Peduncle broad; haptor hexagonal, 59 (51–74; n = 13). Ventral anchor 31 (28–36; n = 20) long, with elongate slightly depressed superficial root, short deep root, curved shaft, elongate point; base 16 (15–18; n = 13) wide. Dorsal anchor 25 (22–29; n = 18) long, with well-differentiated roots, curved shaft, elongate point; base 13 (12–15; n = 14) wide. Ventral bar 29 (24–36; n = 15) long, broadly V-shaped with enlarged terminations and a slight anteromedial indentation; dorsal bar 25 (21–32; n = 15) long, broadly U- or V-shaped, with terminations directed laterally. Hooks similar, each with protruding thumb, delicate shaft and point, dilated shank; hook pairs 1, 5 reduced in size; FH loop about 30% shank length (pairs 2, 3, 4, 6, 7), 50% shank length (pair 1); hook pairs 2, 3, 4, 7 — 23 (21–25; n = 14) long; hook pairs 1, 5 — 15 (14–15; n = 10) long; hook pair 6 — 19 (17–20; n = 19) long. Male copulatory organ a coil of ~4.5 rings, base with lateral flange, tube delicate, 13 (11–14; n = 9) diameter of the first ring. Accessory piece flabellate, 17 (15–20; n = 3) long. Vagina sinistral, a tortuous tube with distal coil connecting to a bulb prior to discharching into small medial seminal receptacle anterior to germarium. Gonads overlapping, germarium 13 (10–20; n = 10) long; testis dorsal, slightly visible at end of germarium; seminal vesicle a distal enlargement (expansion) of vas deferens; 1 prostatic reservoir; oviduct, ootype, uterus not observed. Vaginal sclerite 21 (20–25; n = 14) long, composed of grooved rod with distal hook, subterminal short projection. Vitellaria scattered throughout trunk, except absent in regions of reproductive organs.

Taxonomic summary

Type-host: Candela *Piabucina panamensis* Gill, 1877 (Characiformes: Lebiasinidae).

Site of infection: Gills.

Type locality/collection date: Rio Frijolito (09°09′53″N; 79°45′16″W), Republic of Panama, April 2006.

Specimens deposited: Holotype (CNHE 5792); 5 paratypes (CNHE 5793), 5 paratypes (IPCAS M-433), and 5 paratypes (USNPC 99629).

Etymology: The specific name is from Greek (*flegomai* = blaze, flame) and refers to the vernacular Spanish name of its host, candela.

Remarks

Based on the presence of sinistral vaginal sclerite, overlapping gonads, MCO with counterclockwise rings, and hooks with enlarged shanks (pairs 1, 5 usually reduced in size), this species is considered a new member of *Urocleidoides* (Mizelle and Price, 1964) Kritsky, Thatcher, and Boeger, 1986. *Urocleidoides* includes a group of 7 tropical species, which parasitize fishes of the Characidae (*Characidium caucanum* Eigenmann, 1912), Anostomidae (*Rhytiodus microlepis* Kner, 1858), Curimatidae (*Curimata argentea* [= *Steindachnerina argentea*] [Gill 1858]), and Erythrinidae (*Hoplias malabaricus* (Bloch, 1794)) within Characiformes and Poeciliidae (*Poecilia reticulata* (Peters, 1859) and *Xiphophorus helleri* (Heckel, 1848)) of the Cyprinodontiformes (Kritsky et al., 1986; Suriano, 1997; Jogunoori et al., 2004). *Urocleidoides flegomai* n. sp. found in *P. panamensis* represents the first record of *Urocleidoides* in another family (Lebiasinidae) within Characiformes. Based on the comparative morphology of the copulatory complexes and bars, the closest relatives of *U. flegomai* n. sp. are *U. vaginoclaustrum* Jogunoori, Kritsky, and Venkatanarasaiah, 2004 from *X. helleri*; *U. eremitus* Kritsky, Thatcher, and Boeger, 1986 from *H. malabaricus*; and *U. anops* Kritsky and Thatcher, 1974 from *C. caucanum* from the Neotropics (compare Figs. 24–28 [present study] and figs. 18, 22–25 for *U. vaginoclaustrum* in Jogunoori et al. [2004]; figs. 3, 6, and 7 for *U. eremitus* in Kritsky et al. [1986]; and 14, 16, and 17 for *U. anops* in Kritsky and Thatcher [1974]). Considering that the Characiformes (200 species in Africa and more than 1,200 species in the Neotropics in about 14–16 families) and Cyprinodontiformes (850 species in about 110 genera) comprise the most speciose assemblages of fishes in the tropics and North America (Costa, 1998), high diversification of *Urocleidoides* on these potential host species is to be expected.

Urocleidoides similuncus n. sp.

(Figs. 32–40)

Diagnosis: Body 177 (168–192; n = 4) long, robust; greatest width 85–110 usually at level of testis. Cephalic margin broad; cephalic lobes well developed; 4 bilateral pairs of head organs; cephalic glands indistinct. Four eyes poorly developed, subequal; members of posterior pair usually farther apart than those of anterior pair; eye granules usually ovate. Pharynx spherical 19 (17–22; n = 5); esophagus short (contracted specimens). Peduncle broad; haptor subhexagonal. Anchors similar; each with robust base, truncate superficial root, well-developed deep root, angular bends at junctions of base and shaft and shaft and point; short point; ventral anchor 21 (20–22; n = 5) long; base 14 (14–15; n = 4) wide; dorsal anchor 19 (18–20; n = 6) long; base 15 (14–15; n = 5) wide. Ventral bar 25 (23–26; n = 3) long, with bulbous terminations; dorsal bar 22 (20–25; n = 3) long, rod-shaped to slightly arced, with enlarged ends. Hooks similar, each 10 (9–10; n = 7) long, with delicate shaft and point, protruding thumb, slightly dilated shank; FH loop about 80% shank length. Male copulatory organ a coil of ~3.25 rings, 19 (18–20; n = 3) diameter of the first ring, base with lateral flange, tube delicate. Accessory piece 20–22 long, flabellate. Gonads overlapping, germarium ovate; testis dorsal, ovate (lateral margins indistinct); seminal vesicle a distal enlargement (expansion) of vas deferens; 1 prostatic reservoir; oviduct, ootype, uterus not observed. Vagina sinistral, an elongate narrow sclerotized tube coiled prior to opening into irregular medial seminal receptacle; vaginal sclerite 23 (22–26; n = 4) long, a robust rod with distal hook, subterminal short projection, proximal portion with longitudinal groove. Vitellaria dense throughout trunk, except absent in regions of reproductive organs.

Taxonomic summary

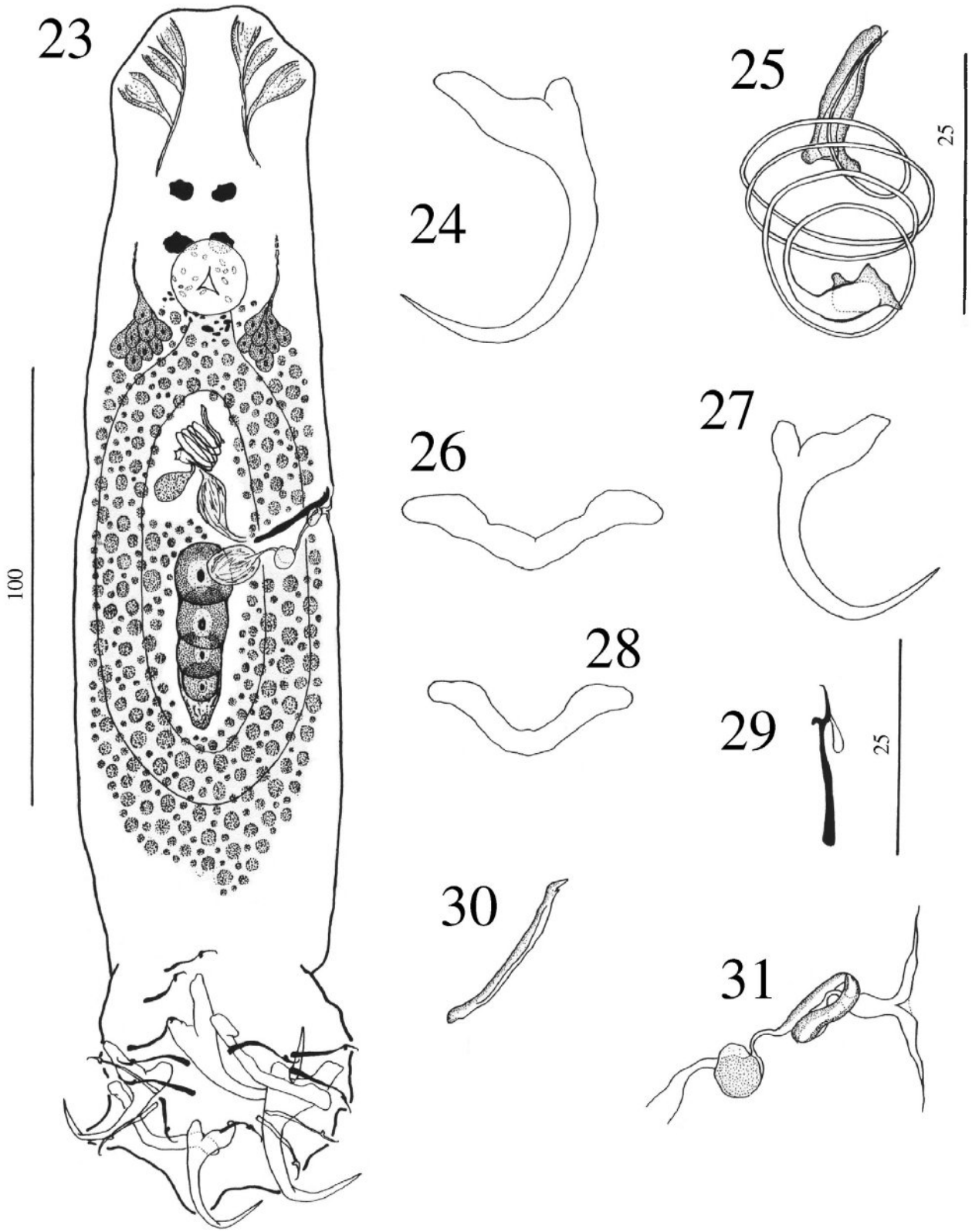
Type host: Molly *Poecilia gillii* (Kner, 1863) (Cyprinodontita, Poeciliidae).

Site of infection: Gills.

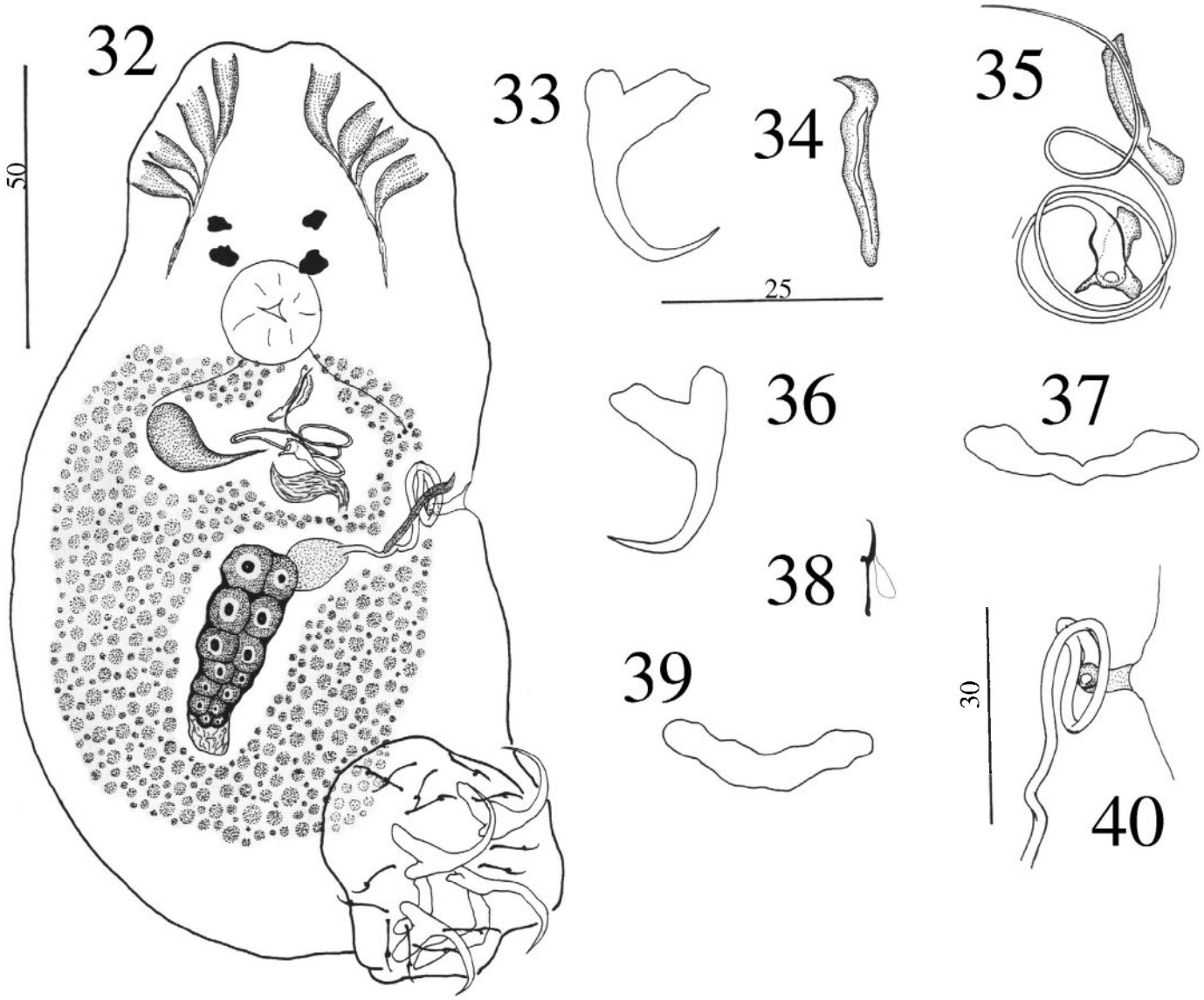
Type locality/collection date: Rio Frijolito (09°09′53″N, 79°45′16″W), Republic of Panama, April 2006.

Specimens deposited: Holotype (CNHE 5794); 4 paratypes (CNHE 5795) and 2 paratypes (USNPC 99631).

Etymology: The specific name is from Latin (*simil/is* = similar + *uncus* = hook) and refers to the similar size of hooks.



FIGURES 23–31. *Urocleidoides flegomai* n. sp. (**23**) Whole mount (composite, ventral view). (**24**) Ventral anchor. (**25**) Copulatory complex (dorsal view). (**26**) Ventral bar. (**27**) Dorsal anchor. (**28**) Dorsal bar. (**29**) Hook. (**30**) Vaginal sclerite. (**31**) Vagina. All figures are drawn to the 25-μm scale as Figure 29, except 23 (100-μm) and 25 (25-μm).



FIGURES 32–40. *Urocleidoides similuncus* n. sp. (**32**) Whole mount (composite, ventral view). (**33**) Ventral anchor. (**34**) Vaginal sclerite. (**35**) Copulatory complex (ventral view). (**36**) Dorsal anchor. (**37**) Ventral bar. (**38**) Hook. (**39**) Dorsal bar. (**40**) Vagina. All figures are drawn to the 25-μm scale, except 32 (50-μm) and 40 (30-μm).

Remarks

Urocleidoides similuncus n. sp. differs from congeneric species by possessing similar anchors, each with a robust base, superficial root with truncate tip, and by having hooks of similar size. It resembles *U. flegomai* n. sp., *U. eremitus*, and *U. anops* in the general morphology of the copulatory complex. Specimens of *U. similuncus* n. sp. from *P. gillii* were strongly contracted, apparently a result of premature fixation while the worms were still alive (see Fig. 32). That contraction is reflected in the comparatively shorter body lengths, measuring only 168–192 in specimens from *P. gillii* in the Frijolito River compared with those of *U. flegomai* n. sp. (length 200–357) from *P. panamensis* in the same locality. This is the only described species of *Urocleidoides* with hooks of similar size.

DISCUSSION

In the present study, 7 species (5 new) of monogenoids infesting the gills of fish species of 5 families within the Characiformes (Characidae and Lebiasinidae), Cyprinodontiformes (Poeciliidae), Perciformes (Cichlidae), and Siluriformes (Pimelodidae = Heptapteridae) were found. Molecular and morphological comparisons suggest that South American fish taxa are the most basal groups in characid, cichlid, and pimelodid phylogeny, followed by its Neotropical forms, creating putative monophyletic sister groups (Perdices et al., 2002). Based on this conclusion and considering the morphology and host range of the monogenoidean species found in this study (species of *Urocleidoides* on Characiformes, species of *Sciadicleithrum* and *Aphanoblastella* on Cichlidae and Pimelodidae) the hypothesis of a common evolutionary history with the South American clade is supported. The current zoogeographical distribution of monogenoidean species (except for *G. asota*) from different genera found in Panama may be initially explained by dispersal of a common ancestor of each genus to this region, i.e., by primary and/or secondary host species from parent

drainages in South America. This ability of hosts to invade new geographical areas could have allowed sufficient evolutionary time for them to overlap into different biogeographic regions to produce their own endemic lineages along with their parasites in Central America. For instance, based on molecular data, it has been suggested that *Rhamdia* sp. colonized Central America (late Pliocene, 5 mya), much later than *Rivulus* spp. (Cyprinodontiformes) (15.9–18.4 mya) and the heroine cichlids (11.3–13 mya) (Perdices et al., 2002; Chakrabarty, 2006). The 2 latter groups are secondary freshwater fishes, which may have dispersed through brackish or marine water before the uplift of the Isthmus of Panama (Perdices et al., 2002). This could result in loss of the monogenoids due to a lack of tolerance to high salinities experienced during colonization. Consistent with this hypothesis, only 1 of the 3 monogenoidean species (*G. asota*, *G. astronoti*, and *G. rogersi*) from the gills of *A. ocellatus* from native habitats in South America (Brazil) was found in Panama. Furthermore, *Cichla ocellaris* harbors 3 species of *Gussevia* in South America, but none of them was found on the 5 *C. ocellaris* individuals we examined. Although this also could be explained by sampling error, parasitological studies on Mexican cichlids conducted since 1987 have showed only 4 species of *Sciadicleithrum* compared to its 9 congeners from South America (Vidal-Martinez et al., 2001; Mendoza-Franco and Vidal-Martinez, 2005). Therefore, the possibility exists that the low number and/or absence of monogenoidean species in native cichlids from Central America and the Greater Antilles (e.g., Cuba) (Mendoza-Franco, Vidal-Martínez et al., 2006) by invasion of its secondary host species or its derivatives to these areas from South America (Chakrabarty, 2006) could be a result of loss of parasites (Mendoza-Franco and Vidal-Martinez, 2005). Historical factors such as geotectonic events within Central America would help to explain how these fish groups have radiated from basal lineages within Central America exhibiting their own distinct fauna and probably endemic species of monogenoids, e.g., *Brycon petrosus* as the probable original host for those monogenoidean species (e.g., *D. kabatai*) infesting *Astyanax* spp. in the Neotropics.

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