

Revision of *Parancylodiscoides* Caballero y C. & Bravo-Hollis, 1961 (Monogenoidea: Dactylogyridae), with a redescription of *P. longiphallus* (MacCallum, 1915) from the Atlantic spadefish *Chaetodipterus faber* (Broussonet) (Acanthuroidei: Ehippidae) in the Gulf of Mexico

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Received: 19 July 2011 / Accepted: 18 August 2011
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Abstract The generic diagnosis of *Parancylodiscoides* Caballero y C. & Bravo-Hollis, 1961 (Monogenoidea: Dactylogyridae), with three valid species, was amended to include dactylogyrids having: a haptor with dorsal and ventral anchor/bar complexes, 14 hooks (seven pairs) and four reservoirs (two pairs); a dorsal bar with bifurcate ends; hooks with protruding, blunt and slightly depressed thumbs and undilated shanks; a dextroventral vaginal aperture leading to an elongate and oblique vaginal vestibule; a germarium dextral to the testis; a vas deferens looping the left intestinal caecum; a copulatory complex lacking an accessory piece; and two intestinal caeca lacking diverticula and united posterior to the gonads. *Parancylodiscoides* is most similar to *Sundatrema* Lim & Gibson, 2009, from which it differs only by the position of the vaginal aperture (sinistroventral in *Sundatrema* spp.) and by lacking a sucker-like genital pore. New information concerning the number and distribution of haptoral hooks, the relative positions of the gonads and the course of the vas deferens was provided for the type-species, *P. chaetodipteri* Caballero y C. & Bravo-Hollis, 1961. *Parancylodiscoides longiphallus* (MacCallum, 1915) Lim & Gibson, 2009

was redescribed based on specimens collected from the Atlantic spadefish *Chaetodipterus faber* from the Gulf of Mexico off Mississippi and Guaratuba Bay, Paraná, Brazil; its occurrence on the Atlantic spadefish from the Gulf of Mexico, Guaratuba Bay and off Puerto Rico represented new geographical records for this helminth. *Parancylodiscoides caballerobravorum* Cezar, Luque & Amato, 1999 was considered a junior subjective synonym of *P. longiphallus*. The monotypic *Isohaliotrema* Young, 1968 was placed in synonymy with *Parancylodiscoides* and its type-species, *I. platacis* Young, 1968, transferred to *Parancylodiscoides* as *Parancylodiscoides platacis* (Young, 1968) n. comb.

Introduction

Perciform fishes assigned to the Ehippidae of the suborder Acanthuroidei and known as spadefishes, batfishes and orbfishes are laterally compressed, marine (rarely brackish water), omnivorous fishes occurring in near-shore tropical to temperate waters of the Atlantic and Indo-Pacific Oceans (Froese & Pauly, 2011). The Ehippidae includes eight genera and 15 valid species.

Only six dactylogyrid species (Monogenoidea) are currently known to parasitise ehippids worldwide. The first dactylogyrid from an ehippid was described under the name *Diplectanum longiphallus* MacCallum, 1915 by MacCallum (1915), who collected it

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from the gills of Atlantic spadefish *Chaetodipterus faber* (Broussonet) held in the New York Aquarium. This helminth has undergone subsequent reassignments to *Ancyrocephalus* Creplin, 1839 by Johnston & Tiegs (1922), to *Tetrancistrum* Goto & Kikuchi, 1917 by Price (1937), to *Pseudohaliotrema* Yamaguti, 1953 by Young (1967) and to *Parancylodiscoides* Caballero y C. & Bravo-Hollis, 1961 by Lim & Gibson (2009). It remained the only dactylogyrid species described from an ephippid host until Pearse (1949) described *Ancyrocephalus chaetodipteri* Pearse, 1949 from *C. faber* off Beaufort, North Carolina, USA. Hargis (1955) considered *A. chaetodipteri* a junior synonym of MacCallum's species, which Price (1937) had earlier transferred to *Tetrancistrum*. Subsequently, Caballero y C. & Bravo-Hollis (1961) proposed *Parancylodiscoides*, with *P. chaetodipteri* Caballero y C. & Bravo-Hollis, 1961 from the Pacific spadefish *C. zonatus* (Girard) off Oaxaca, Mexico, as its type-species; and Young (1968) proposed *Isohaliotrema* Young, 1968 with *I. platacis* Young, 1968 from the gills of the dusky batfish *Platax pinnatus* (Linnaeus) off Australia as its type-species. Raju & Rao (1978) described *Ancyrocephalus rarus* Raju & Rao, 1978 from a single specimen collected from an orbfish *Ephippus orbis* (Bloch) in the Bay of Bengal, India. Cezar et al. (1999), who described *P. caballerobravorum* Cezar, Luque & Amato, 1999 from the Atlantic spadefish off Brazil, were apparently unaware of MacCallum's (1915) and Pearse's (1949) descriptions of dactylogyrids from this host, as neither of these nominal species were mentioned in their paper. Finally, *Sundatrema* Lim & Gibson, 2009, with *S. langkawiense* Lim & Gibson, 2009 as its type-species, was proposed for a dactylogyrid from the gills of orbfish off Malaysia (Lim & Gibson, 2009). Although *A. rarus* was considered a *species inquirenda* and *incertae sedis* by Lim & Gibson (2009), because of an inadequate original description by Raju & Rao (1978), the species is the only other nominal species described from orbfish and may represent the senior synonym of *S. langkawiense*. New collections of orbfish from the Bay of Bengal will be necessary to determine the status of the two species.

During surveys of marine fishes from the south-eastern United States for monogenoidean parasites, specimens of a species of *Parancylodiscoides* were collected from the gills of the Atlantic spadefish in the Gulf of Mexico. Examinations of these and available

museum specimens, material of *Parancylodiscoides* sp. collected earlier in Brazilian waters by Dr W.A. Boeger, Universidade Federal do Paraná, Curitiba, Paraná, Brazil, and the published literature revealed that *Parancylodiscoides* required review. The present study includes a revision of the genus and a redescription of MacCallum's (1915) species.

Materials and methods

About 10 Atlantic spadefishes were collected by hook-and-line from the Gulf of Mexico off Mississippi during August, 2007. These fishes were immediately killed and the gill baskets removed and placed in a Nasco WHIRL-PAK[®] plastic specimen bag containing hot (60°C) water. The bag was shaken vigorously for about 30 sec, after which sufficient concentrated formalin was added to achieve a 5% solution; the bag was labeled and along with its contents shipped to Idaho State University for study. Some helminths, picked from the sediments with a fine probe, were mounted unstained on microscope slides in Gray & Wess medium for the study of the sclerotised structures; other specimens were stained with Gomori's trichrome or Van Cleave's haematoxylin and mounted in Canada balsam for the study of their soft anatomy (Kritsky et al., 1978; Humason, 1979; Bullard et al., 2004). Illustrations were prepared with the aid of a camera lucida or microprojector. Measurements, all in micrometres, were obtained using a calibrated filar micrometer mounted on a phase-contrast microscope, were represented by straight-line distances between extreme points and were expressed as the mean followed by the range and number (n) of structures measured in parentheses; body length included that of the haptor. Scientific and common names of fishes were those listed in FishBase (Froese & Pauly, 2011) and verified in Eschmeyer & Fricke (2011). Specimens of *Parancylodiscoides longiphallus* collected for the present study were deposited in United States National Parasite Collection (USNPC), Beltsville, Maryland; the University of Nebraska State Museum, Harold W. Manter Laboratory (HWML), Lincoln, Nebraska; the Colección Nacional de Helminths, Universidad Nacional Autónoma de México (CNHE), Mexico City, Mexico; the Natural History Museum (NHMUK), London, United Kingdom; and the Meguro Parasitological Museum (MPM), Tokyo, Japan, as

indicated in the redescription of *P. longiphallus*. For comparison, the following specimens were examined: 9 syntypes, *Diplectanum longiphallus* MacCallum, 1915 (USNPC 35702); 14 vouchers (collection of W.A. Boeger), *Parancylo-discoides longiphallus* (MacCallum, 1915) Lim & Gibson, 2009 (USNPC 104780); 3 vouchers, *P. longiphallus* (USNPC 97043); holotype, 3 paratypes, *Sundatrema langkawiense* Lim & Gibson, 2009 (NHMUK 2008.8.12.1; 2008.8.12.2-3); holotype, 2 paratypes, *Isohaliotrema platacis* Young, 1968 (USNPC 61293, 61294); 2 paratypes, *P. caballerobravorum* Cezar, Luque & Amato, 1999 (CNHE 3432); 5 paratypes, *P. chaetodipteri* Caballero y C. & Bravo-Hollis, 1961 (CNHE 093); holotype, 14 paratypes (on two slides), *Ancyrocephalus bilobatus* Yamaguti, 1953 (MPM 23648); holotype, 3 paratypes (on two slides), *A. spinicirrus* Yamaguti, 1953 (MPM 23649); voucher, *Haliotrema neobilobatus* Bychowsky & Nagibina, 1970 (on MPM slide 23648 with holotype of *A. bilobatus*); and voucher, undetermined dactylogyrid species (on MPM slide 23648 with holotype of *A. bilobatus*).

Order Dactylogyridea Bychowsky, 1937

Family Dactylogyridae Bychowsky, 1933

Parancylo-discoides Caballero y C. & Bravo-Hollis, 1961

Syn. *Isohaliotrema* Young, 1968

Diagnosis

Body fusiform, slightly flattened dorsoventrally, comprising body proper (cephalic region, trunk and peduncle) and haptor. Tegument smooth. Two terminal and two bilateral subterminal cephalic lobes; three bilateral pairs of head organs; cephalic glands lateral, posterolateral and/or anterolateral to pharynx. Eyespots usually absent (granules generally dispersed), but one or two pairs rarely present; chromatic granules minute, subovate, scattered throughout cephalic and into anterior trunk regions. Mouth midventral, subterminal at level of head organs, opens into buccal tube; buccal tube extends posteriorly along mid-line of cephalic region to pharynx to form buccal cavity; pharynx a muscular, glandular bulb, with anterior end protruded into buccal cavity; oesophagus present; intestinal caeca two, lacking diverticula, confluent posterior to gonads. Common genital pore midventral, just posterior to intestinal bifurcation. Gonads intercaecal, juxtaposed, with germarium dextral to testis, or

germarium lying to right of body mid-line and anterior region of testis. Testis entire, lobulate; vas deferens loops left intestinal caecum dorsoventrally (see following Remarks); one or two seminal vesicles simple dilations of vas deferens; one or two prostatic reservoirs. Copulatory complex comprises tubular male copulatory organ (MCO) lacking accessory piece. Oviduct short; oötype receives ducts of vitellarium and seminal receptacle; Mehlis' gland present; seminal receptacle anterior to gonads; uterus extends anteriorly along body mid-line to common genital pore. Vaginal aperture dextroventral in anterior trunk; vaginal vestibule elongate, oblique, unsclerotised or lightly sclerotised; narrow meandering vaginal canal arises from proximal end of vestibule, extends to seminal receptacle. Vitellarium coextensive with intestinal caeca. Two pairs of bilateral claviform reservoirs; anterior pair peduncular or located in anterior portion of haptor, emptying in haptor lateral to dorsal anchor pair; posterior reservoirs lie in lateral lobes of haptor, empty via broad duct between ventral anchors. Haptor with dorsal and ventral anchor/bar complexes, seven pairs of similar hooks with dactylogyrid distribution (Mizelle, 1936; Mizelle & Price, 1963). Anchors similar. Ventral bar simple; dorsal bar with bifurcate ends. Hook with slender shank of one subunit, with protruding blunt, slightly depressed thumb. Parasitic on gills of marine perciform fishes (currently restricted to Ephippidae).

Type-species: *P. chaetodipteri* Caballero y C. & Bravo-Hollis, 1961 from the Pacific spadefish *Chaetodipterus zonatus* (Girard), Ephippidae.

Other species: *P. longiphallus* (MacCallum, 1915) Lim & Gibson, 2009 from the Atlantic spadefish *Chaetodipterus faber* (Broussonet), Ephippidae; *P. platacis* (Young, 1968) n. comb. (syn. *Isohaliotrema platacis* Young, 1968) from the dusky batfish *Platax pinnatus* (Linnaeus), Ephippidae.

Remarks

Caballero y C. & Bravo-Hollis (1961) used a combination of morphological features to define *Parancylo-discoides*, none of which alone would appear to justify the genus. Among the more significant of these that require comment are: (1) a haptor with two anchor/bar complexes, 10 hooks (five pairs; two pairs ventral and three pairs marginal) and two haptoral

claviform glands (claviform reservoirs); (2) an “accessory organ or vesicle” and a prostatic reservoir at the level of the genital pore; and (3) the testis located posterior to the germarium. Examination of the available type- and voucher specimens of the three species herein assigned to *Parancylodiscoides* revealed that: (1) 14 hooks with a normal dactylogyrid distribution (Mizelle, 1936) and two pairs of claviform reservoirs were present; (2) the “accessory organ or vesicle” represented the second of two prostatic reservoirs (only one prostatic reservoir was observed in the type-specimens of *P. platacis*); and (3) the originally stated position of the gonads was inexact. Although Caballero y C. & Bravo-Hollis (1961) implied in the English summary of their paper that the gonads were tandem (testis postgermarial), their figure of the whole-mount of *P. chaetodipteri* accurately depicted the germarium lying to the right of the anterior end of the testis. This configuration occurred in the available specimens of *P. chaetodipteri* and *P. longiphallus*, whereas the gonads of *P. platacis* n. comb. are juxtaposed (germarium dextral).

Caballero y C. & Bravo-Hollis (1961) showed an intercaecal vas deferens in their whole-mount drawing of *P. chaetodipteri*. However, one of the paratypes (CNHE 093) of this species, a dorsal mount, clearly shows the vas deferens looping the left intestinal caecum dorsoventrally, whereas the vas deferens could not be traced in available specimens of *P. longiphallus* and *P. platacis*. Nonetheless, the vas deferens looping the left intestinal caecum is included as a diagnostic character in the amended diagnosis of *Parancylodiscoides* presented above.

In the amended generic diagnosis, a putative synapomorphic feature was not identified to distinguish *Parancylodiscoides* from all other genera comprising the Dactylogyridae, so it remains necessary to base the genus on a combination of morphological features. In addition to those discussed above, important diagnostic characters of *Parancylodiscoides*, as amended, included: (1) the presence of a dextroventral vaginal aperture opening into an elongate, oblique, unsclerotised vaginal vestibule; (2) the absence of an accessory piece in the copulatory complex; (3) haptoral hooks with protruding, blunt, slightly depressed thumbs and shanks composed of a single undilated subunit; (4) a dorsal bar with bifurcate ends; and (5) two intestinal caeca lacking diverticula and united posteriorly to the gonads.

Parancylodiscoides is most similar to the monotypic *Sundatrema*, which was defined by its type-species *S. langkawiense* parasitic on the orbfish (Ehippidae). Lim & Gibson (2009) defined the latter genus in part by *S. langkawiense* having a sinistroventral vaginal aperture and a midventral sucker-like genital pore just posterior to the intestinal bifurcation. All other diagnostic features of the haptor and of the reproductive and digestive systems corresponded to those of species of *Parancylodiscoides*, except that Lim & Gibson (2009) indicated in the generic diagnosis and in their figure 1 of the whole-mount of the type species that the gonads were tandem (germarium pretesticular). Examination of the severely flattened and damaged holotype (NHMUK 2008.8.12.1) of *S. langkawiense* clearly showed the germarium lying to the right of the body mid-line, dextral to the anterior end of the testis, as it does in *P. chaetodipteri* and *P. longiphallus* (see Fig. 4). Thus, the only features that separated the two genera were the position of the vaginal aperture and the sucker-like development around the common genital pore.

Lim & Gibson (2009) argued that the relative position of the vaginal aperture may not be of generic importance and cited examples supporting this contention in species of *Thaparocleidus* Jain, 1952, *Bychowskyella* Akhmerov, 1952 and *Cornudiscoides* Kulkarni, 1969, where the apertures may be dextral or sinistral among respective congeners. To this list of dactylogyrid genera should be added *Sciadicleithrum* Kritsky, Thatcher & Boeger, 1989, *Urocleidoides* Mizelle & Price, 1964 (*sensu stricto*) and *Gussevia* Kohn & Paperna, 1964 (see Kritsky et al., 1986, 1989). Similarly, the sucker-like genital pore was likely a secondary development and, thus, an apparently weak character in support of *Sundatrema*. Sucker-like structures associated with the genital pore apparently developed secondarily in other dactylogyrid genera as well, including *Pseudohaliotrema* and *Euryhaliotrema* Kritsky & Boeger, 2002 (see Kritsky & Galli, 2007; Kritsky & Bakenhaster, 2011). Because *Sundatrema* appears to have little morphological support and may eventually be shown to be a junior subjective synonym of *Parancylodiscoides*, acceptance of the genus is herein considered provisional. Examination of additional ehippids and members of related families of fishes for dactylogyrids will be required to determine the validity of the genus and the value of a sinistroventral vaginal

aperture and a sucker-like genital pore as generic characters.

Thylacicleidus Wheeler & Klassen, 1988, *Pseudohaliotrema* and *Glyphidohaptor* Kritsky, Galli & Yang, 2007 resemble *Parancylodiscoides* by the inclusion of species having the germarium situated to the right of the testis. *Parancylodiscoides* was differentiated from *Thylacicleidus* by the dorsal bar having bifurcate ends (ends of dorsal bar rounded in *Thylacicleidus* spp.) and from *Pseudohaliotrema* and *Glyphidohaptor* by the absence of an accessory piece in the copulatory complex (present in *Pseudohaliotrema* and *Glyphidohaptor* spp.) (see Řehulková & Gelnar, 2005; Kritsky & Galli, 2007; Kritsky et al., 2007a). Whereas the host range may not be completely known for species of *Parancylodiscoides*, they are currently recorded only from ephippid fishes. Those of *Thylacicleidus*, *Pseudohaliotrema* and *Glyphidohaptor* are restricted to members of the Tetraodontidae (*Thylacicleidus*) and Siganidae (*Pseudohaliotrema* and *Glyphidohaptor*).

Young (1968) did not mention *Parancylodiscoides* nor the two previously described species (*P. chaetodipteri* and *P. longiphallus*) from ephippid hosts when he proposed the monotypic *Isohaliotrema* Young, 1968 and described its type-species, *Isohaliotrema platacis* Young, 1968, based on three specimens from *Platax pinnatus* off Australia. This was probably an intentional omission, however, because his new genus was primarily based upon the unique juxtaposed position of the gonads in *I. platacis* and previous investigators dealing with other dactylogyrids from ephippid hosts had failed to mention or stress the dextral position of the germarium relative to the testis. Comparison of the holotype and the two badly damaged paratypes of *I. platacis* (USNPC 61293, 61294) with available specimens of *P. chaetodipteri* and *P. longiphallus* revealed that the only feature distinguishing *I. platacis* was the juxtaposition of the gonads, with the germarium lying to the right of the testis. However, the degree of lateral overlap of the germarium with the testis exhibits some interspecific variation in *P. longiphallus* and depends, at least to some extent, upon the relative contraction of individual specimens. Finally, the three species from ephippid hosts share the basic morphology of the haptoral and copulatory sclerites and all other features of the reproductive and digestive systems. Thus, *Isohaliotrema* is considered a junior subjective synonym of

Parancylodiscoides and *I. platacis* transferred to the latter genus as *Parancylodiscoides platacis* (Young, 1968) n. comb.

***Parancylodiscoides chaetodipteri* Caballero y C. & Bravo-Hollis, 1961**

Syns *Pseudohaliotrematoides chaetodipteri* (Caballero y C. & Bravo-Hollis, 1961) Yamaguti, 1963 (lapsus); *P. chaetodipteri* (Caballero y C. & Bravo-Hollis, 1961) Yamaguti, 1963

Type-host and locality: Pacific spadefish *Chaetodipterus zonatus* (Girard), Ephippidae; off Salina Cruz, Oaxaca, Mexico.

Site of infection: Gills.

Specimens studied: 5 paratypes, CNHE 093.

Previous record: This species has not been recorded since its original description by Caballero y C. & Bravo-Hollis (1961).

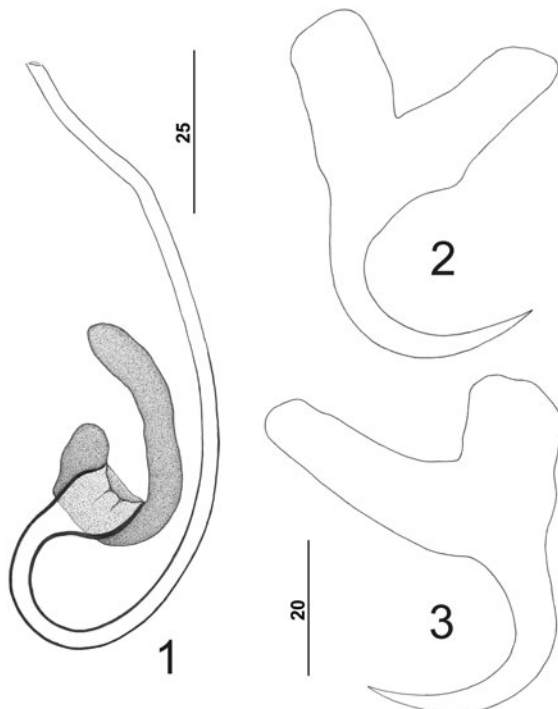
Remarks

Parancylodiscoides chaetodipteri (Figs. 1–3) is the type-species of the genus. It is nearly identical morphologically to *P. longiphallus*, from which it differs by having one long and one short arm associated with the base of the MCO (basal arms elongate and subequal in length in *P. longiphallus*) (compare Figs. 1 and 6). Furthermore, although the anchors of the two species are similar, those of *P. chaetodipteri* have comparatively shorter and stouter shafts and points (compare Figs. 2, 3 with 7, 9).

The two species, *P. chaetodipteri* and *P. longiphallus*, apparently represent another example of an amphiamerican “geminant” species pair within the Monogenoidea, with respective members occurring on the eastern and western sides of southern North America. Their phylogenetic histories are probably best explained by a vicariant co-evolutionary model in which the uprising of the Panamanian Isthmus during the Pliocene about 3.2 mya provided the disruption and subsequent isolation of historical populations of their common ancestor and ancestral host (Kritsky et al., 2009; Mendoza-Franco et al., 2009).

***Parancylodiscoides longiphallus* (MacCallum, 1915) Lim & Gibson, 2009**

Syns *Diplectanum longiphallus* MacCallum, 1915; *Ancyrocephalus longiphallus* (MacCallum, 1915) Johnston & Tiegs, 1922; *Tetrancistrum longiphallus*



Figs. 1–3 Male copulatory organ and anchors of *Parancylodiscooides chaetodipteri* Caballero y C. & Bravo-Hollis, 1961. 1. Male copulatory organ (ventral view). 2. Ventral anchor. 3. Dorsal anchor. Scale-bars: 1, 25 μm ; 2,3, 20 μm

(MacCallum, 1915) Price, 1937; *A. chaetodipteri* Pearse, 1949; *Pseudohaliotrema spirophallus* (MacCallum, 1915) of Young (1967) (lapsus); *P. longiphallus* (MacCallum, 1915) Young, 1967¹; *Tetrancistrum spirophallus* (MacCallum, 1915) of Young (1967) (lapsus); *Parancylodiscooides* sp. of Cezar & Luque (1999); *Parancylodiscooides caballerobravorum* Cezar, Luque & Amato, 1999

Type-host and locality: Atlantic spadefish *Chaetodipterus faber* (Broussonet), Ehippidae; New York Aquarium.

Site of infestation: Gills.

Source of current specimens: *Chaetodipterus faber*; off West Ship Island (Gulf of Mexico), Mississippi (30°12'45"N, 88°58'53"W), 2 August 2007; Guaratuba Bay, Paraná, Brazil, 4 November 1997; off Parguera, Puerto Rico, 20 September 1999.

Specimens studied: 9 syntypes (*Diplectanum longiphallus*), USNPC 35702; 34 voucher specimens (Gulf

of Mexico), USNPC 104799, HWML 49718, CNHE 7542, NHMUK 2011.7.28.1-4, MPM 20724; 14 voucher specimens (off Brazil), USNPC 104780; 3 voucher specimens (off Puerto Rico), USNPC 97043; 2 paratypes (*P. caballerobravorum*), CNHE 3432.

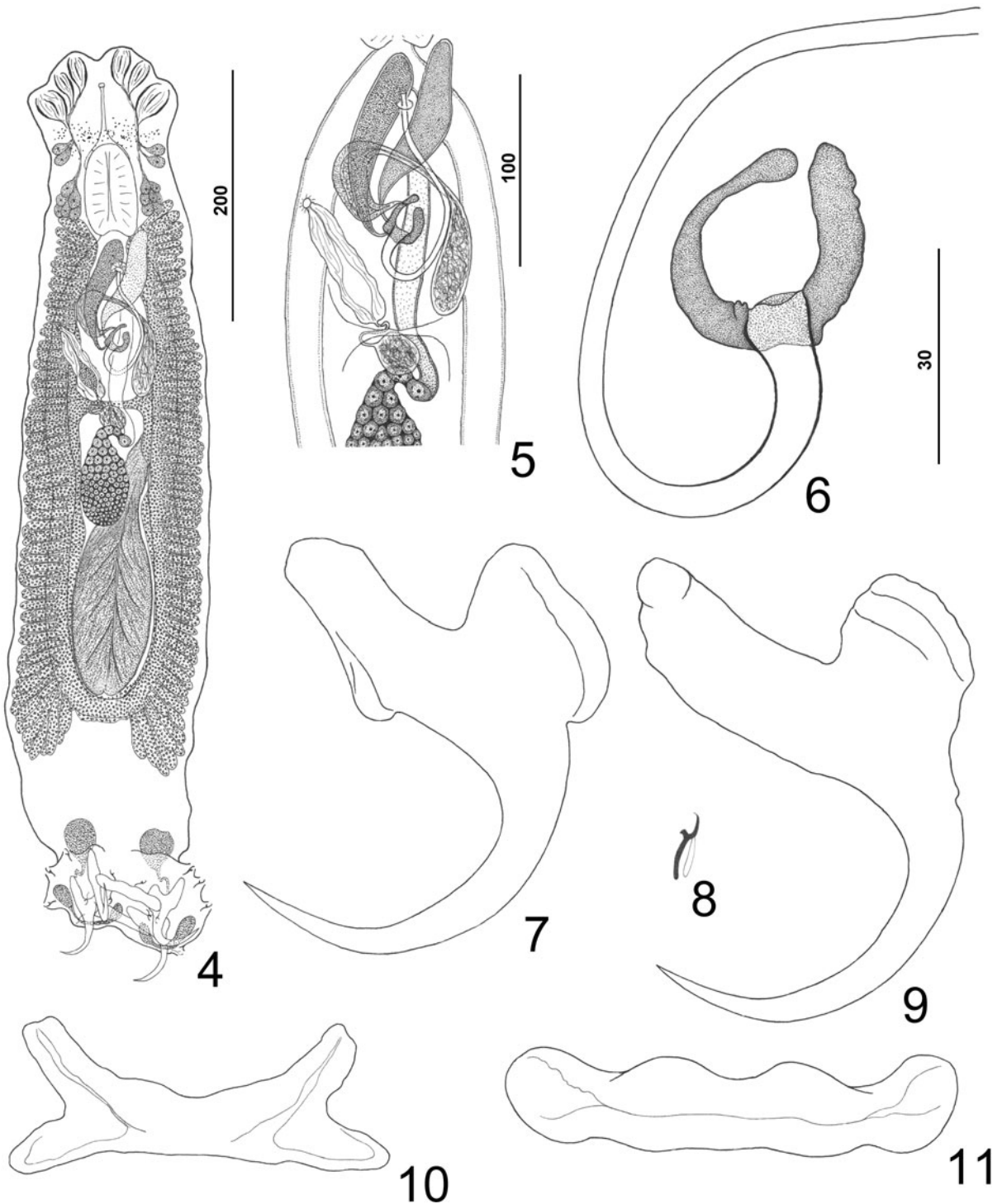
Previous records: *Chaetodipterus faber*: New York Aquarium (MacCallum, 1915, as *D. longiphallus*); off Beaufort, North Carolina (Pearse, 1949, as *Ancyrocephalus chaetodipteri*); off Alligator Harbor, Florida (Hargis, 1955, as *Tetrancistrum longiphallus*); Chesapeake Bay (Zwerner & Lawler, 1972, as *T. longiphallus*); Virginia Key (Biscayne Bay), Florida (Skinner, 1978, as *T. longiphallus*); coastal zone of the State of Rio de Janeiro, Brazil (Cezar & Luque, 1999, and Cezar et al., 1999, as *Parancylodiscooides* sp. and *P. caballerobravorum*, respectively).

Redescription (Figs. 4–11)

[Based on specimens from Gulf of Mexico, Mississippi, and Guaratuba Bay, Brazil. Measurements of specimens from Brazil follow those from Gulf of Mexico in brackets, respectively.] Body 850 (692–1,015; n = 22) [964 (745–1,213; n = 8)] long; greatest width 180 (139–245; n = 23) [184 (126–219; n = 8)] usually at testicular level. Cephalic region broad, with well-developed cephalic lobes and head organs; cephalic glands in 2 bilateral groups lateral and anterolateral to pharynx. Eyespots absent (granules generally dispersed); chromatic granules sparse to numerous, rarely randomly accumulated into clusters anterior to pharynx. Pharynx 76 (66–93; n = 23) [72 (63–79; n = 9)] long, 46 (38–53; n = 23) [49 (44–55; n = 9)] wide, elongate ovate, with 2 bilateral lobes on posterior end.

Testis ovate, 203 (144–279; n = 14) [257 (222–308; n = 4)] long, 79 (53–103; n = 14) [100 (65–153; n = 4)] wide, usually appearing lobulate, with narrowed anterior end lying sinistrodorsal to germarium. Seminal vesicle variable in size, fusiform, lying to left of MCO. Two large prostatic reservoirs elongate pyriform; right reservoir filled with dark-staining (Gomori's stain) granular material; left reservoir containing fine, lightly stained reticulate material. MCO 86 (75–101; n = 8) [90 (83–94; n = 4)] long, a J-shaped tubular shaft with 2 elongate subequal basal arms. Germarium 112 (84–147; n = 23) [101 (71–131; n = 5)] long, 52 (37–69; n = 14) [55 (40–69; n = 5)] wide, pyriform, with anterior end

¹ Lim & Gibson (2009) attributed the combination *Pseudohaliotrema longiphallus* (MacCallum, 1915) to Yamaguti (1963), but this is clearly an error.



Figs. 4–11 *Paracylloides longiphallus* (MacCallum, 1915) Lim & Gibson, 2009. 4. Whole-mount (ventral view, composite). 5. Terminal portion of reproductive system (ventral view, composite). 6. Male copulatory organ (dorsal view). 7. Ventral anchor. 8. Hook. 9. Dorsal anchor. 10. Dorsal bar. 11. Ventral bar. Scale-bars: 4, 200 μm ; 5, 100 μm ; 6–11, 30 μm

significantly tapered and recurved posteriorly, then bending anteriorly as oviduct; oötype and Mehlis' gland inconspicuous. Vaginal aperture at level of base of MCO; vaginal vestibule large, variable, elongate fusiform, lightly sclerotised, lying diagonally on right side of body anterior to germarium; vaginal duct narrow, arising from proximal end of vaginal vestibule, meandering towards, and with small dilation just before connecting with, seminal receptacle. Seminal receptacle subspherical, just anterior to recurvature of germarium in body mid-line. Vitellarium dense; vitelline ducts arising from near mid-length of each lateral vitelline field, uniting in body mid-line to form short, posteriorly directed, common vitelline duct. Egg not observed.

Haptor 107 (85–124; n = 20) [102 (93–117; n = 8)] long, 144 (118–165; n = 20) [132 (115–144; n = 8)] wide, subrectangular. Ventral anchor 61 (51–68; n = 9) [59 (54–62; n = 5)] long, with hump on inner surface of base, elongate superficial root, massive deep root, curved shaft and long point extending to about level of tip of superficial root; dorsal anchor 67 (60–75; n = 9) [66 (63–68; n = 5)] long, similar in shape to that of ventral anchor except lacking hump on inner surface of base. Ventral bar 65 (58–72; n = 9) [58 (53–62; n = 3)] long, with undulating anterior and posterior margins and slightly enlarged, rounded ends; dorsal bar 51 (42–57; n = 6) [44 (37–50; n = 4)] long, flattened, with bifurcate ends; anterior arm of bifurcation slightly longer than posterior arm. Hook 11 (9–12; n = 14) [11 (10–12; n = 11)] long.

Remarks

This species was originally named *Diplectanum longiphallus* by MacCallum (1915), but Johnston & Tieg (1922) subsequently considered *Diplectanum* Diesing, 1858 a junior synonym of *Ancyrocephalus* Creplin, 1839 and transferred the species to the latter genus as *A. longiphallus* (MacCallum, 1915) Johnston & Tieg, 1922. Price (1937) resurrected *Diplectanum* from synonymy for a group of species having squamodiscs and transferred *A. longiphallus* to *Tetrancistrum* Goto & Kikuchi, 1917. The species remained assigned to this genus until the revision of *Tetrancistrum* by Young (1967), who transferred the species to *Pseudohaliotrema* Yamaguti, 1953 as *P. longiphallus* (MacCallum, 1915) and as *P. spirophallus* (MacCallum, 1915)

(a lapsus). Subsequent revisions of *Pseudohaliotrema* by Lim (2002) and Kritsky & Galli (2007) and *Tetrancistrum* by Kritsky et al. (2007b) excluded the species from both genera, with the respective authors considering it *incertae sedis*. Lim & Gibson (2009) transferred the species to *Parancylodiscoides* as *P. longiphallus* (MacCallum, 1915) based on their observations of five syntypes of *D. longiphallus* held in the USNPC (35702) and the species' morphological similarity to *P. chaetodipteri*.

Although *P. longiphallus* has frequently been collected and reported from Atlantic spadefishes off North America, existing descriptions of the species are generally inadequate. Those by MacCallum (1915) and Pearse (1949) were, for the most part, nonspecific, whereas the redescription by Price (1937) included erroneous observations that have subsequently been repeated in the literature. Price (1937) clearly switched the identities of the haptor bars when he stated that the ventral bar was narrow with bifid ends; this error was repeated by Lim & Gibson (2009). Descriptions of the condition of the eyespots (eyes) in *P. longiphallus* have varied among authors, with MacCallum (1915) and Pearse (1949) mentioning the presence of four (two pairs), while Price (1937), using MacCallum's specimens, indicated their absence. Hargis (1955) stated, "Eyespots are present, consisting of many small, melanistic granules scattered in the antero-dorsal region". It is obvious that various authors have defined the eyespot differently and differed in their understanding of how the melanistic granules might function during light detection. In the present paper, an eyespot is defined as one of the paired accumulations of granules that normally occur in the cephalic region immediately anterior to the pharynx. Although random accumulations of granules may occur in the cephalic and anterior trunk regions of *P. longiphallus*, eyespots are considered to be absent in this species.

Cezar et al. (1999) described *P. caballerobravorum* from the gill filaments of *Chaetodipterus faber* off Brazil; the species was differentiated from its only congener, *P. chaetodipteri*, by having a bilobed testis and an accessory (second) prostatic reservoir. Cezar et al. (1999) did not mention and apparently were unaware of MacCallum's (1915) species from the Atlantic spadefish, at that time known under Young's (1967) recombination *Pseudohaliotrema longiphallus*. Examination of all dactylogyrid specimens

from Atlantic spadefishes during the present study, including the two paratypes of *Parancylodiscoides caballerobravorum* (CNHE 3432), the syntypes of *Diplectanum longiphallus* (USNPC 35702) and all vouchers identified herein as *P. longiphallus*, revealed that all specimens were conspecific and that *P. caballerobravorum* represented a junior subjective synonym of *P. longiphallus*. The bilobed testis reported by Cezar et al. (1999) represented two anteroventral lobes of the testis that, depending on the quality of fixation and type of stain, varied in shape and size; additional smaller lobes that occur in the posterior portion of the testis were not depicted by Cezar et al. (1999). The haptor and copulatory sclerites of all Brazilian specimens were morphologically identical to those of specimens from the Gulf of Mexico; the comparatively larger soft organs of specimens from Brazil were apparently the result of differences in the condition of the specimens when fixed in formalin. No other morphological details were found to justify *P. caballerobravorum*.

During the search for geographical records, three specimens collected and identified as *Pseudohaliotrema longiphallus* from the Atlantic spadefish off La Parguera, Puerto Rico, and deposited in the USNPC (97043) by Dr E. H. Williams were examined and determined to represent *Parancylodiscoides longiphallus*. These specimens from off Puerto Rico, and those from the Gulf of Mexico off Mississippi and Guaratuba Bay, Paraná, Brazil, all represented new geographical records for *P. longiphallus*.

***Parancylodiscoides platacis* (Young, 1968) n. comb.**
Syn. *Isohaliotrema platacis* Young, 1968

Type-host and locality: Dusky batfish *Platax pinnatus* (Linnaeus), Ehippidae; Moreton Bay, Queensland, Australia.

Site of infestation: Gills.

Specimens studied: Holotype and 2 paratypes, USNPC 61293, 61294.

Previous record: This species has not been recorded since its original description as *Isohaliotrema platacis* by Young (1968).

Remarks

Parancylodiscoides platacis (Fig. 12) closely resembles its two congeners, *P. chaetodipteri* and *P. longiphallus*, in the general morphology of the body,

haptor armament and reservoirs, and in the primary organisation of the reproductive and digestive systems. It differs from these species by having juxtaposed gonads with the germarium dextral to the testis (germarium lying to the right of the anterior end of the testis in congeners) and by possessing a single elongate arm arising from the base of the male copulatory organ (Fig. 12) [two arms unequal in length in *P. chaetodipteri* (Fig. 1); two elongate subequal arms in *P. longiphallus* (Fig. 6)].

In the generic diagnosis of *Isohaliotrema* and the description of its type-species, Young (1968) indicated that only two (one pair) reservoirs were associated with the haptor. However, examination of the type-specimens of *I. platacis* (USNPC 61293, 61294) revealed that two pairs of reservoirs occurred in locations consistent with those of its two congeners. The anterior pair was peduncular and possessed dilated ducts that extended into the lateral lobes of the haptor, where they emptied lateral to the dorsal anchors; the second pair of reservoirs was located in the lateral haptoral lobes ventral to and overlapping the ducts of the peduncular reservoirs and had ducts extending posterior to the anchor points, where they recurved anteriorly to empty between the ventral anchors. Young (1968) apparently missed the ventral

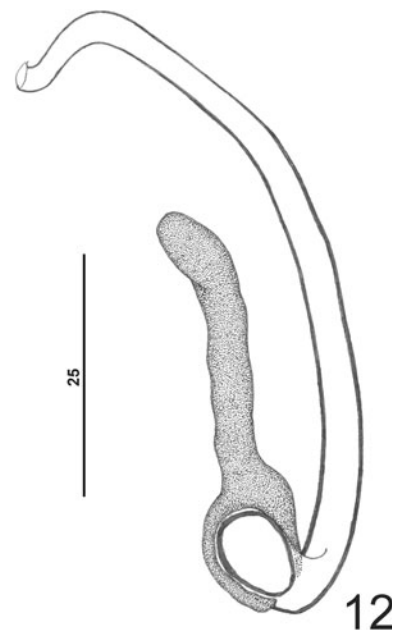


Fig. 12 Male copulatory organ of *Parancylodiscoides platacis* (Young, 1967) n. comb. (ventral view)

reservoirs because he did not observe that the ducts of the peduncular reservoirs were distinct from the ventral reservoirs, where they overlapped in the lateral haptor lobes.

Discussion

As knowledge on species diversity of dactylogyrids increases, it has become increasingly difficult to identify morphological features that specifically define generic boundaries within the Dactylogyridae. Over 40 years ago, John Mizelle postulated “that when a comprehensive number of monopisthocotylean (polychocotylean) species are described, genera and higher taxa may insensibly intergrade with one another as segments in a continuous succession of species that differ radically only at remotely separated points” (Mizelle & Kritsky, 1969; parentheses *nobis*). Mizelle’s forecast appears to be coming to fruition, especially among some dactylogyrids parasitising marine fishes. At the present time, comparatively few marine dactylogyrid genera are clearly defined by unambiguous synapomorphies, and frequently characters previously thought to be unambiguous have later been shown to be less salient as intermediate forms have been discovered and described and our knowledge of species diversity has increased. Once considered a clearly defined genus with comparatively few species, *Haliotrema* Johnston & Tiegs, 1922, for example, which now contains more than 100 species parasitising marine fishes representing 30 + teleost families, was considered an unnatural taxon by Klassen (1994) and Kritsky & Stephens (2001). As a result, new genera have been proposed to include species previously assigned to *Haliotrema* as putative monophyletic groups based on other morphological features (see Euzet & Suriano, 1977; Kritsky & Boeger, 2002; Plaisance & Kritsky, 2004; Lim & Justine, 2011).

Species of *Parancylodiscoides* lack an unambiguous feature that would distinguish the genus from all other marine dactylogyrid genera, including *Sundatrema*, the only other genus with species restricted to ephippid hosts. Unlike *Haliotrema*, where subdivision of the genus has occurred as information on species diversity has increased, the generic boundaries of *Parancylodiscoides* will probably expand with the addition of new members. Species assigned to *Sundatrema* are nearly identical to those of

Parancylodiscoides, with only two major characters distinguishing them: *Parancylodiscoides* spp. with a dextroventral vaginal aperture and a simple genital pore; *Sundatrema* spp. with a sinistroventral vaginal aperture and a sucker-like genital pore. However, these characters are probably secondary developments. Surveys for dactylogyrids occurring on the 11 (of 15) ephippid species remaining to be examined and on fishes of related teleost families will undoubtedly result in the discovery of new species of *Parancylodiscoides* that will likely require a conceptual expansion to the extent that *Sundatrema* may become its junior synonym. That a widened definition of *Parancylodiscoides* will be necessary is supported, in part, by the dactylogyrids presently known to occur on the gills of drepaneid fishes.

Once included as a subfamily of the Ephippidae (see Nelson, 1984), the monotypic Drepaneidae (suborder Percoidei) (with three species) (see Johnson, 1984; Nelson, 1994) has been inferred to be the sister group of the suborder Acanthuroidei, which includes the Ephippidae as its basal member (Winterbottom, 1993). Meanwhile, Tang et al. (1999) suggested that the Ephippidae may share a close evolutionary relationship with the Scatophagidae (with four species in two genera) and the Drepaneidae based on analyses of 12S and 16S ribosomal mtDNA sequences. Whereas dactylogyrids recorded from scatophagids have been assigned to *Metahaliotrema* Yamaguti, 1953, whose members show only minor similarity with *Parancylodiscoides* spp., those from drepaneids are more comparable to those assigned to *Parancylodiscoides* as amended herein.

Known dactylogyrids from drepaneid hosts include *Ancyrocephalus parspinicirrus* Mamaev, 1970, *Haliotrema bilobatum* (Yamaguti, 1953) Bychowsky & Nagibina, 1970 (emend.), *H. magnihamus* Bychowsky & Nagibina, 1970, *H. neobilobatum* Bychowsky & Nagibina, 1970 (emend.), *H. parvihamus* Bychowsky & Nagibina, 1970 and *H. spinicirrus* (Yamaguti, 1953) Bychowsky & Nagibina, 1970, all from the spotted sicklefish *Drepane punctata* (Linnaeus) in the western Pacific Ocean (Yamaguti, 1953; Bychowsky & Nagibina, 1970; Mamaev, 1970). *Haliotrema bilobatum* (as *Ancyrocephalus bilobatus*) was also reported from the concertina fish *Drepane longimana* (Bloch & Schneider) in the western Pacific by Mamaev (1970). Only a single feature, the vaginal pore being dextromarginal, apparently distinguishes

this group of species from those of *Parancylodiscoides* (verified in specimens on the MPM slide MPM 23648; see list of species in the ‘Materials and methods’). That a dextromarginal vaginal pore occurs in most marine dactylogyrids suggests that the dextroventral and sinistroventral vaginal pores of *Parancylodiscoides* and *Sundatrema* species represent secondary developments and that the species recorded from drepaneid hosts will eventually be transferred to *Parancylodiscoides*. Other features, such as the bifurcate ends of the dorsal bar, occurring in some species infecting other fishes assigned to the Acanthuroidei, suggest that an even wider concept of *Parancylodiscoides* may be necessary once the diversity of dactylogyrids on marine fishes, particularly those of the Acanthuroidei, is fully understood.

Acknowledgements Support from the following individuals is gratefully acknowledged: Robin Overstreet (Gulf Coast Research Laboratory [GCRL]) hosted the author and furnished laboratory supplies, space, equipment and logistical support and Ash Bullard and Jody Peterson (GCRL) assisted during the collection of Atlantic spadefish from the Gulf of Mexico; Eileen Harris (NHMUK), Pat Pilit (USNPC), Eric Hoberg (USNPC), Luis García Prieto (CNHE) and Jun Araki (MPM) allowed access to museum specimens under their care; Walter Boeger (Universidade Federal do Paraná, Brazil) collected and provided specimens of *Parancylodiscoides longiphallus* from Brazilian waters and permitted their deposition in the USNPC; and Ernest (Bert) Williams, Jr (University of Puerto Rico) gave permission to report the record of *P. longiphallus* from off Puerto Rico based on specimens that he had deposited in the USNPC.

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