Floriparicapitus, a new genus of lecanicephalidean tapeworm (Cestoda) from sawfishes (Pristidae) and guitarfishes (Rhinobatidae) in the Indo-West Pacific

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2013

Journal of Parasitology

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--Manuscript Draft--

Manuscript Number:	13-468R1
Full Title:	FLORIPARICAPITUS, A NEW GENUS OF LECANICEPHALIDEAN TAPEWORM (CESTODA) FROM SAWFISHES (PRISTIDAE) AND GUITARFISHES (RHINOBATIDAE) IN THE INDO-WEST PACIFIC
Short Title:	NEW LECANICEPHALIDEAN GENUS FROM SAWFISHES AND GUITARFISHES
Article Type:	Regular Article
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Abstract: *Floriparicapitus* n. gen. (Cestoda: Lecanicephalidea), with *F. euzeti* n. gen. n. sp. as its type, is erected to house 3 new tapeworm species and 2 known species that are transferred to the new genus, all parasitizing sawfishes and guitarfishes (order Rhinopristiformes) in Indo-Pacific waters. The new genus differs from the 20 valid lecanicephalidean genera in its possession of a large scolex bearing a laterally expanded apical organ in the form of a rugose sheet in combination with a cirrus conspicuously armed with spinitriches and 3 pairs of excretory vessels. It most closely resembles *Lecanicephalum*, but differs conspicuously in its possession of 3, rather than 1, pair of excretory vessels. Two new species are described from sawfishes: *Floriparicapitus euzeti* n. sp., from *Pristis clavata* and *Floriparicapitus juliani* n. sp. from *Pristis microdon*, both from Australia. *Floriparicapitus plicatilis* n. sp. is described from the guitarfish *Glaucostegus typus* in Australia and the guitarfish *Glaucostegus thouin* in Malaysian Borneo. Two species formerly assigned to *Cephalobothrium* are transferred to the new genus; *Floriparicapitus variabilis* (Southwell, 1911) n. comb. from the sawfish *Anoxypristis cuspidata* in Sri Lanka and *Floriparicapitus rhinobatidis* (Subhapradha, 1955) n. comb. from the guitarfish

Glaucostegus granulatus in India. The species from guitarfish differ conspicuously from those parasitizing sawfish in their possession of only 4 (*F. plicatilis* n. sp.) or 5 (*F. rhinobatidis* n. comb.) testes per proglottid, versus 9 or more in the 3 sawfish-parasitizing species. The latter 3 species differ from one another in scolex width, acetabular size, number of proglottids, and cirrus sac size. As it stands, the new genus appears to be restricted to a subclade of the Rhinopristiformes consisting of the sawfishes and species of *Glaucostegus*.

Sawfishes (family Pristidae) are some of the most recognizable elasmobranchs because of their distinctive, long rostrum bearing bilateral teeth. Their affinity for estuarine and freshwater habitats, coupled with their large size (up to 7 m in length and 1 metric ton in weight) has made them highly vulnerable, both to fishing pressure (as targets and by-catch of fisheries) and to habitat loss (see Simpfendorfer, 2000; Peverell, 2005; Phillips et al., 2011). In fact, they are now the focus of formal conservation efforts by both CITES (Appendix I; 12 June 2013) and the IUCN (2013). Relatively little is known about the tapeworms parasitizing any of the 7 species in either genus of sawfishes. At present, cestode records consist entirely of 6 accepted trypanorhynch species (see Campbell and Beveridge, 1996; Beveridge and Campbell, 2001, 2005; Schaeffner and Beveridge, 2012, 2013) and 2 tetraphyllidean species (see Woodland, 1934; Watson and Thorson, 1976). As members of the Rhinopristiformes (sensu Naylor, Caira, Jensen, Rosana, White, and Last, 2012) occurring in the Indo-Pacific, sawfishes are particularly likely candidates as hosts of lecanicephalideans, yet only a single member of this order, *Cephalobothrium variabile* Southwell, 1911, has been reported from sawfishes. Southwell described this species in 1911 from 47 specimens he found parasitizing the knifetooth sawfish, *Anoxypristis cuspidata* (Latham) (as *Pristis cuspidata* Latham), from the Pearl Banks of Ceylon (now Sri Lanka). He described *C. variabile* as an unusually large and curious cestode that

exhibited "… remarkable variability, hence the specific name" (pg. 221; Southwell, 1911), presumably referring to the variability in form of the scolex and particularly the proglottids illustrated in the figures accompanying the original description (fig. 5c; Southwell, 1911). The distinctive scolex of *C. variabile* is laterally expanded and bears a large apical organ in the form of a rugose sheet giving it a frilled appearance. Its proglottid morphology remains poorly understood.

Collections of tapeworms from sawfishes throughout the Indo-West Pacific between 1996 and 2003 yielded specimens resembling *Cephalobothrium variabile* from *Anoxypristis cuspidata* in Australia. Cestodes of this general form were also collected from 3 additional sawfish species and from 2 guitarfish species. Examination of this new material led to the realization that *Cephalobothrium variabile* differs substantially in morphology from *Cephalobothrium* Shipley and Hornell, 1906, as typified by *Cephalobothrium aetobatidis* Shipley and Hornell, 1906 (see Shipley and Hornell, 1906; Jensen, 2005; Cielocha and Jensen, 2011) described from the spotted eagleray, *Aetobatus ocellatus* (Kuhl) (as *Aetobatus narinari* [Euphrasen]) (Myliobatiformes: Myliobatidae). As a consequence, a new genus is established to accommodate species parasitizing rhinopristiform hosts. *Cephalobothrium variabile* and *Cephalobothrium rhinobatidis* Subhapradha, 1955 are transferred to the new genus. *Cephalobothrium variabile* is redescribed from type specimens found in the collection of L. Euzet and voucher specimens newly collected from the type host. Three new species are described, 1 each from the sawfishes *Pristis clavata* Garman and *Pristis microdon* Latham, and 1 from the guitarfishes *Glaucostegus thouin* (Anonymous [Lacepède]) and *G. typus* (Anonymous [Bennett]).

MATERIALS AND METHODS

For this study, specimens of the new genus were collected from 19 host individuals. These consisted of 4 specimens of *Pristis clavata* collected in August 1997 (1 female, 98 cm in total length [TL], and 3 males, 90, 152, and 200 cm in TL), 2 specimens of *Pristis zijsron* Bleeker collected in August 1997 (2 females, 244 and 542 cm in TL), 1 specimen of *Pristis microdon* collected in July 2002 (unknown sex and TL), 3 specimens of *Anoxypristis cuspidata* collected in November 1999 (3 females, 209, 308, and 317 cm in TL), 7 specimens of *Glaucostegus typus* in August 1996 and 1997, and May 2004, all from Australia (3 females, unknown, 65, and 117 in TL, and 4 males, 49.5, 52, 86, and 103 cm in TL), and 2 specimens of *Glaucostegus thouin* collected in May 2003 and November 2006 (1 female, 112 cm in TL and 1 male, 67.5 cm in TL), from Borneo. Host specimen Collection Codes and Numbers, and locality details are given in Table I. Images and additional host specimen information can be accessed using host specimen Collection Codes and Numbers in the Elasmobranch Specimen Database (http://elasmobranchs.tapewormdb.uconn.edu) of the Global Cestode Database (GCDB). Also examined was a specimen of the new genus from a single individual of *Pristis pectinata* Latham collected by Lawrence R. Penner in July 1967 (unknown sex and TL), in the Myakka River, on Rt. 41, Florida (host code P-Pp[1]-67).

The spiral intestine was removed from each host specimen and opened with a longitudinal incision. Each spiral intestine was fixed in 10% formalin buffered with seawater and subsequently transferred to 70% ethanol for storage. In the laboratory, spiral intestines were examined for tapeworms using a dissecting microscope. Tapeworms found attached to the spiral intestine were removed and cleaned of host tissue. Specimens were prepared for examination by light microscopy according to the following protocol. Whole mounts were hydrated in distilled water, stained with Delafield's haematoxylin, dehydrated in a graded series of ethanols, cleared

in methyl salicylate, and mounted in Canada balsam on glass-slides under cover-slips. Specimens for histological sections (longitudinal, cross, and in situ) were processed as follows: they were dehydrated in a graded series of ethanols, cleared in xylene, and embedded in paraffin according to standard techniques. Serial sections of proglottids and scoleces embedded in paraffin were cut at a thickness of 7 μm on a TBS CUT 4060 Microtome. Sections were floated on glass slides using 3% sodium silicate and allowed to air-dry. Sections were subsequently deparaffinized in xylene, hydrated in a graded series of ethanols, stained with Delafield's haematoxylin, counterstained with eosin, dehydrated in a graded ethanol series, cleared in xylene, and mounted in Canada balsam. Additional specimens prepared as histological sections were embedded in Technovit H7100 Glycol Methacrylate (GMA) and processed according to manufacturer's directions for embedding soft tissues (available at www.emsdiasum.com) with the following modifications: dehydration for 30 min. each in 70%, 95%, and 100% ethanol; final dehydration for 1 hr in 100% ethanol; infiltration for 2 hr at 4 C in a 1:1 solution of 100% ethanol and Infiltration Solution; and infiltration overnight at 4 C in 100% Infiltration Solution. Specimens were subsequently embedded in polymerized GMA in plastic block holders. Specimens embedded in GMA were cut with glass knives on the above mentioned microtome at a thickness of 4 μm. Individual sections were floated on ca. 10 μl drops of de-ionized water on *Superfrost* (Fisherbrand) microscope slides and allowed to dry on a slide warmer at 40 C. Sections were stained with Delafield's haematoxylin, counterstained with eosin, rinsed with 95% ethanol, air-dried, and mounted in Canada balsam. Specimens prepared as whole mounts and for histological sections were examined with a Zeiss Axioskop 2 Plus compound microscope. Scoleces observed with scanning electron microscopy (SEM) were prepared as follows. Scoleces were removed from the strobila and hydrated in distilled water, fixed in 1% osmium tetroxide overnight,

dehydrated in a graded ethanol series, transferred to hexamethyldisilizane (HMDS) for 30 min, air-dried, and mounted on aluminum stubs with double-sided adhesive carbon tape. They were then sputter coated with ca. 35 nm of gold and examined with a Zeiss LEO 1550 field emission scanning electron microscope. Strobilar vouchers were mounted according to the protocol described above for whole-mounted specimens. Line drawings were made using a drawing tube attached to the above-mentioned compound microscope.

Measurements of reproductive organs were taken from mature proglottids unless otherwise specified. All measurements are reported in micrometers (μm) with the exception of total length, which is reported in millimeters (mm). The range is given in the text; mean, standard deviation, number of worms examined, and total number of measurements if more than one measurement was taken per worm are presented in Table II. In the redescription of *C. variabile*, measurements from the original description of Southwell (1911) are presented in bold. Microthrix terminology follows Chervy (2009). Museum abbreviations used are as follows: LRP, Lawrence R. Penner Collection, Department of Ecology and Evolutionary Biology, University of Connecticut, Storrs, Connecticut, USA; MZUM(P), Muzium Zoologi, Universiti Malaya, Kuala Lumpur, Malaysia; NHMUK (and BMNH) Natural History Museum, London, United Kingdom; QM, Queensland Museum, Brisbane, Australia; SBC, Sarawak Biodiversity Center, Kuching, Sarawak, Malaysia; USNPC, U.S. National Parasite Collection, Beltsville, Maryland, USA. Host classification follows Naylor, Caira, Jensen, Rosana, White, and Last (2012) and identifications of most host specimens follow Naylor, Caira, Jensen, Rosana, Straube, and Lakner (2012).

DESCRIPTIONS

Floriparicapitus n. gen.

Diagnosis: Worms euapolytic. Scolex laterally expanded, bearing 4 acetabula, apical modification of scolex proper, and apical organ. Acetabula in form of suckers. Apical modification with extensive aperture at apex, expandable, bearing apical organ. Apical organ in form of extensive, wide, muscular and glandular sheet, usually highly folded, may appear rugose, sometimes retractable into apical modification of scolex proper. Cephalic peduncle absent. Proglottids craspedote. Longitudinal muscle bundles conspicuous, cortical. Testes medial, arranged in 1 or 2 irregular columns, extending to level of ovary. Vas deferens sinuous, extensive, extending from ootype region to anterior margin of cirrus sac, may be expanded to form external seminal vesicle. Internal seminal vesicle absent. Cirrus sac pyriform to panduriform. Cirrus with conspicuous spinitriches, surrounded by prominent gland-like cells. Ovary consisting of multiple irregular lobes on each lateral side, essentially H-shaped in dorso-ventral view, tetralobed in cross-section. Vagina curving to sinuous, extending along midline of proglottid, opening into genital atrium posterior to, at the level of, or anterior to cirrus sac. Genital pores lateral, irregularly alternating. Vitellarium follicular; follicles arranged in multiple columns on each lateral margin of proglottid, extending from near anterior margin of proglottid to posterior margin of proglottid, sometimes interrupted by ovary. Excretory ducts in 3 pairs, central pair expanded. Uterus medial, saccate. Eggs not observed. Parasites of Rhinopristiformes.

Taxonomic summary

Type species: Floriparicapitus euzeti n. sp.

Additional species: Floriparicapitus juliani n. sp., *Floriparicapitus plicatilis* n. sp., *Floriparicapitus variabilis* (Southwell, 1911) n. comb., *Floriparicapitus rhinobatidis* (Subhapradha, 1955) n. comb.

Etymology: *Floriparus*, L. (m.), flower-bearing; *caput*, L., head. The generic name refers to the shape of the apical organ resembling a flower.

Remarks

The new genus is readily distinguished from 19 of the 20 recognized genera of lecanicephalideans based largely on the configuration of the apical features of its scolex. Unlike *Aberrapex* Jensen, 2001 and *Paraberrapex* Jensen, 2001 it possesses, rather than lacks, an apical organ. Unlike those of *Anteropora* Subhaprada, 1955, *Eniochobothrium* Shipley and Hornell, 1906, *Healyum* Jensen, 2001, *Hornellobothrium* Shipley and Hornell, 1906, *Quadcuspibothrium* Jensen, 2001, and *Sesquipedalapex* Jensen, Nikolov, and Caira, 2011, its apical organ is external, rather than entirely internal. Its apical organ is in the form of a wide continuous sheet of tissue, rather than tentacles or multiple projections as seen in *Polypocephalus* Braun, 1878 and *Rexapex* Koch, Jensen, and Caira, 2012, respectively, or a thick muscular organ or sucker as in *Corrugatocephalum* Caira, Jensen, and Yamane, 1997, *Cephalobothrium*, *Hexacanalis* Perrenoud, 1931, *Stoibocephalum* Cielocha and Jensen, 2013, *Tetragonocephalum* Shipley and Hornell, 1905, and *Tylocephalum* Linton, 1890, or a transverse, thick, oval pad as in *Collicocephalus* Koch, Jensen, and Caira, 2012. *Floriparicapitus* n. gen. lacks the cylindrical, partially invaginable apical modification of the scolex proper seen in *Elicilacunosus* Koch, Jensen and Caira, 2012. Finally, it lacks the multi-tiered apical structure seen in the most recently described genus, *Seussapex* Jensen and Russell, in press.

The new genus can be further distinguished from the 19 genera mentioned above in its possession of the following strobilar features: non-laciniate rather than laciniate proglottids as in *Aberrapex* and *Collicocephalus*; testes in a single layer rather than 2 or more layers as in *Cephalobothrium*, *Corrugatocephalum*, *Hexacanalis*, *Quadcuspibothrium*, *Stoibocephalum*,

Tetragonocephalum, and *Tylocephalum*; the presence of conspicuous cirrus spinitriches, rather than lack of cirrus spinitriches, as seen in *Elicilacunosus*, *Healyum*, *Paraberrapex*, and *Rexapex*; anterior proglottids are not expanded laterally as they are in *Eniochobothrium* and *Hornellobothrium*; possession of distinct cortical longitudinal muscle bundles, which are absent in *Anteropora*, *Polypocephalus*, *Sesquipedalapex*, and *Seussapex*.

Floriparicapitus n. gen. most closely resembles *Lecanicephalum*. However, it can be distinguished from *Lecanicephalum* in lacking the conspicuous circular muscle bundle of the apical organ; this muscle bundle is presumably responsible for the degree of constriction of the apical organ when invaginated in species of *Lecanicephalum* (see Jensen, 2005). In addition, whereas the apical organ of *Lecanicephalum* is in the form of a circular expanded sheet, that of the new genus is expanded laterally and is highly folded, the rugose surface of which interdigitates with the host's intestinal mucosa.

We note that *Floriparicapitus* was the genus referred to as New genus 5 in the molecular phylogeny of Caira et al. (2014).

***Floriparicapitus euzeti* n. sp.**

(Figs. 1–3, 6–11)

Description (based on 30 specimens: 27 whole mounts of mature worms, scolex frontal and mature proglottid cross-sections of 1 specimen, scolex frontal sections of 1 specimen, and 1 scolex prepared for SEM): Worms 11–30 mm long; euapolytic; maximum width of strobila 205–310 in posterior-most mature proglottids; proglottids 130–227 in number, craspedote. Scolex laterally expanded, consisting of scolex proper bearing 4 acetabula, apical modification of scolex proper, and apical organ. Scolex proper 73–148 long by 474–743 wide. Acetabula in form of suckers, 95–133 in diameter. Apical modification of scolex proper with extensive aperture at

apex. Apical organ retractable, in form of extensive, wide, muscular and glandular, folded sheet, 82–150 long by 584–1,504 wide, overlapping apical modification of scolex proper.

Scolex proper (Fig. 9) and scolex proper surrounding suckers (Fig. 10) covered with capilliform filitriches and coniform spinitriches. Surface of suckers not observed. Apical modification of scolex proper (Fig. 8) covered with acicular filitriches. Apical organ (Fig. 7) covered with possibly papilliform filitriches. Strobila (Fig. 11) covered with capilliform filitriches.

Cephalic peduncle absent. Longitudinal muscle bundles in cortex conspicuous. Immature proglottids 100–267 in number, initially much wider than long, becoming square, and then longer than wide with maturity; posterior-most immature proglottid 126–229 long by 122–264 wide. Mature proglottids 19–62 in number, 471–787 long by 182–286 wide; often with sizeable gap between anterior margin of proglottid and internal organs. Testes 9–14 in number, 21–54 long by 26–52 wide, extending from anterior margin of proglottid to level of ovary, may be degenerated in terminal mature proglottid(s) (Fig. 1), 2 columns in dorso-ventral view, 1 layer deep in cross-section. Vas deferens extending medially from level of ootype to anterior margin of cirrus sac, not expanded to form external seminal vesicle. Internal seminal vesicle absent. Cirrus sac pyriform, angled anteriorly, 102–169 long by 74–123 wide, containing coiled cirrus. Cirrus armed with spinitriches, expanded near genital pore. Ovary consisting of multiple irregular lobes on each lateral side, essentially H-shaped in dorso-ventral view, tetralobed in cross-section, 100–181 long by 120–200 wide; ovarian bridge at mid-level of ovary. Mehlis' gland posterior to ovarian bridge. Vagina wide, sinuous, extending medially from ootype region to genital atrium, opening into genital atrium posterior to cirrus sac. Genital pores lateral, irregularly alternating, 43–70 % of proglottid length from posterior margin of proglottid. Vitellarium follicular; follicles

arranged in 2 columns on each lateral margin of proglottid, extending from near anterior margin of proglottid to posterior margin of proglottid, interrupted by ovary, 17–59 long by 27–61 wide. Excretory ducts in 3 pairs; central pair expanded, passing through ovarian lobes. Uterus saccate, extending medially from level of ovarian bridge to level of anterior-most vitelline follicles. Eggs not observed.

Taxonomic summary

Type and only known host: Pristis clavata Garman, dwarf sawfish, (Rhinopristiformes: "Pristidae").

Type locality: Darwin (12°20'11"S, 130°54'39"E), Buffalo Creek, Northern Territory, Australia, Timor Sea, Indian Ocean.

Additional localities: None.

Site of infection: Spiral intestine.

Specimens deposited: Holotype (QM G234394; whole worm) and 13 paratypes (QM G234395–G234407; 12 whole worms, and scolex frontal and mature proglottid cross-sections with strobila voucher), 8 paratypes (USNPC 108154.00–108157.00; 7 whole worms, and scolex frontal sections with strobila voucher), 7 paratypes (LRP 8457–8462; whole worms); 1 scolex prepared for SEM with strobila voucher retained with KJ at the University of Kansas.

Etymology: This species is named in honor of Professor Louis Euzet for providing the authors with the type series of *Cephalobothrium variabile* and for his contributions to the field of elasmobranch cestode taxonomy, particularly those relating to the Lecanicephalidea.

Remarks

The scolex of *F. euzeti* n. sp. shows a substantial amount of variation in size; most conspicuously, apical organ width ranged from 584 to 1,504 µm among specimens. While this

degree of variation is not altogether unusual in lecanicephalideans (e.g. Mojica et al., 2013), it warrants at least some mention here.

***Floriparicapitus juliani* n. sp.**

(Figs. 4, 5, 12–17)

Description (based on 14 specimens: 11 whole mounts of mature worms, scolex frontal and mature proglottid cross-sections of 1 specimen, scolex frontal and immature and mature proglottid cross-sections of 1 specimen, and 1 scolex prepared for SEM): Worms 18–46 mm long; euapolytic; maximum width of strobila 235–388, in posterior-most mature proglottids; proglottids 75–149 in number, craspedote. Scolex laterally expanded, consisting of scolex proper bearing 4 acetabula, apical modification of scolex proper, and apical organ. Scolex proper 263–420 long by 995–1,356 wide. Acetabula in form of suckers, 161–212 in diameter. Apical modification of scolex proper with extensive aperture at apex. Apical organ in form of extensive, wide, muscular and glandular, rugose sheet, 255–290 long by 1,330–1,653 wide. Scolex microtriches not examined.

Cephalic peduncle absent. Longitudinal muscle bundles in cortex particularly conspicuous in immature proglottids. Immature proglottids 50–96 in number, initially much wider than long, becoming square and then longer than wide with maturity; posterior-most immature proglottid 188–322 long by 160–277 wide. Mature proglottids 23–68 in number; 690–1,185 long by 211–388 wide; often with sizeable gap between anterior margin of proglottid and internal organs. Testes 10–14 in number, 22–61 long by 23–51 wide, extending from anterior margin of proglottid to level of ovary, may be degenerated in terminal mature proglottid(s), loosely arranged in 2 irregular columns in dorso-ventral view, 1 layer deep in cross section. Vas deferens, extensive, extending medially from level of ootype to anterior margin of cirrus sac.

Internal seminal vesicle absent. Cirrus sac pyriform to panduriform, angled anteriorly, 171–225 long by 110–142 wide, containing coiled cirrus (Fig. 14). Cirrus armed with spinitriches. Ovary consisting of multiple irregular lobes on each side, essentially H-shaped in dorso-ventral view (Fig. 5), tetralobed in cross-section (Fig. 16), 130–218 long by 152–225 wide; ovarian bridge at mid-level of ovary. Mehlis' gland posterior to ovarian bridge. Vagina wide, sinuous, extending medially from ootype region to genital atrium, crossing cirrus sac, opening into genital atrium just posterior to, at same level as (Fig. 14), or anterior to cirrus sac (Fig. 5). Genital pores lateral, irregularly alternating, 49-61% of proglottid length from posterior margin of proglottid. Vitellarium follicular; follicles arranged in 2–3 irregular columns on each lateral margin of proglottid (Figs. 12, 15), extending from near anterior margin of proglottid (Fig. 12) to posterior margin of proglottid (Fig. 17), interrupted by cirrus sac (Fig. 14) on poral side and to some extent by ovary (Fig. 16), 32–76 long by 30–70 wide. Excretory ducts in 3 pairs (Fig. 16); central pair expanded, passing through ovarian lobes. Uterus saccate, extending medially in proglottid from level of ovarian bridge to level of anterior-most vitelline follicles (Fig. 12). Eggs not observed.

Taxonomic summary

Type and only known host: Pristis microdon Latham, freshwater sawfish (Rhinopristiformes: "Pristidae").

Type locality: Off Queensland, Australia, Pacific Ocean.

Additional localities: None.

Site of infection: Spiral intestine.

Specimens deposited: Holotype (QM G234408; whole worm) and 5 paratypes (QM G234409–G234413; 4 whole worms, and scolex frontal and mature proglottid cross-sections with strobila voucher); 4 paratypes (USNPC 108158.00; 3 whole worms, and scolex frontal and immature and

mature proglottid cross-sections with strobila voucher); 3 paratypes (LRP 8475–8477; whole worms); 1 scolex prepared for SEM with strobila voucher retained with KJ at the University of Kansas.

Etymology: This species is named in honor of Julian Baggio, of Cairns Marine, Australia, for his collecting efforts including that of the type host specimen of *F. juliani* n. sp., *Pristis microdon* (CMJ-10).

Remarks

Whole-mounted specimens of *F. juliani* n. sp. were unusually clear and allowed for unambiguous interpretation of internal anatomical structures. This species differs from the type of the genus, *F. euzeti*, in possessing much larger scolex elements. For example, its scolex proper is almost twice as wide (995–1,356 vs. 474–743) and its acetabula are 1.3–1.5 times larger in diameter (161–216 vs. 95–133). Furthermore, it has a longer cirrus sac (171–225 vs. 102–169).

***Floriparicapitus plicatilis* n. sp.**

(Figs. 18–30)

Description (based on 29 specimens: 21 whole mounts of mature worms, scolex frontal sections of 3 specimens, scolex frontal sections of 1 specimen in situ, proglottid cross-sections of 3 specimens, and 1 scolex prepared for SEM): Worms 12–52 mm long; euapolytic; maximum width of strobila 132–255, generally at level of mature proglottids; proglottids 355–784 in number, craspedote. Scolex laterally expanded, consisting of scolex proper bearing 4 acetabula, apical modification of scolex proper, and apical organ. Scolex proper 140–317 long by 435–960 wide. Acetabula in form of suckers, 59–99 in diameter. Apical modification of scolex proper with extensive aperture at apex. Apical organ retractable, in form of extensive, wide, muscular and glandular, rugose sheet, 116–173 long by 512–1,123 wide.

Scolex proper (Fig. 23) and scolex proper surrounding suckers (Fig. 25) covered with capilliform filitriches and coniform spinitriches. Surface of suckers not observed. Apical modification of scolex proper (Fig. 24) covered with papilliform filitriches anteriorly, and capilliform filitriches and coniform spinitriches posteriorly, separated by region devoid of microtriches. Apical organ (Fig. 22) covered with papilliform filitriches. Strobila (Fig. 26) covered with capilliform filitriches.

Cephalic peduncle absent. Longitudinal muscle bundles in cortex conspicuous (Fig. 28). Immature proglottids 292–698 in number, wider than long; posterior-most immature proglottid 64–125 long by 113–248 wide. Mature proglottids 30–168 in number, 232–502 long by 98–192 wide; often with sizeable gap between anterior margin of proglottid and internal organs. Testes 4 in number, 13–31 long by 14–42 wide, extending from anterior margin of proglottid to level of ovary, degenerated in terminal mature proglottid(s), 1 column in dorso-ventral view, 1 layer deep in cross-section. Vas deferens extending medially from level of ootype to anterior margin of cirrus sac, not expanded to form external seminal vesicle. Internal seminal vesicle absent. Cirrus sac pyriform, angled slightly anterior, 60–86 long by 41–59 wide, containing coiled cirrus. Cirrus armed with spinitriches. Ovary consisting of multiple irregular lobes on each lateral side, essentially H-shaped in dorso-ventral view, tetralobed in cross-section (Fig. 30), 37–84 long by 62–123 wide in mature proglottids; ovarian bridge at mid-level of ovary. Mehlis' gland posterior to ovarian bridge. Vagina wide, curving along its extent, extending medially from ootype region to genital atrium, opening into genital atrium at same level as cirrus sac (Fig. 29). Genital pores lateral, irregularly alternating, 55–76% of proglottid length from posterior margin of proglottid. Vitellarium follicular; follicles arranged in 2–3 irregular columns on each lateral margin of proglottid, extending from near anterior margin of proglottid to posterior margin of proglottid,

interrupted by cirrus sac on poral side and somewhat by ovary; vitelline follicles 15–41 long by 19–48 wide. Excretory ducts in 3 pairs (Fig. 28); central pair expanded, passing through ovarian lobes (Fig. 30). Uterus saccate, extending medially from level of ovarian bridge to level of anterior-most vitelline follicles. Eggs not observed.

Taxonomic summary

Type host: Glaucostegus typus (Anonymous [Bennett]), giant shovelnose ray, (Rhinopristiformes: "Rhinobatidae").

Additional hosts: Glaucostegus thouin Anonymous [Lacepède], clubnose guitarfish, (Rhinopristiformes: "Rhinobatidae").

Type locality: Dundee Beach (12°45'33"S, 130°21'7"E), Fog Bay, Northern Territory, Australia, Timor Sea, Indian Ocean.

Additional localities: Lee Point (12°20'11"S, 130°54'39"E), Fog Bay, Northern Territory, Australia, Timor Sea, Indian Ocean (*G. typus*); Weipa (12°35'11"S, 141°42'34"E), Queensland, Australia, Arafura Sea, Pacific Ocean (*G. typus*); Scarborough Beach (27°S, 153°E), Brisbane, Queensland, Australia, Pacific Ocean (*G. typus*); Sematan (1°48'15.45"N, 109°46'47.17"E), Sarawak, Borneo, Malaysia, South China Sea, Pacific Ocean (*G. thouin*).

Site of infection: Spiral intestine.

Specimens deposited: Holotype (QM G234414; whole worm) and 12 paratypes (QM G234415–G234426; 8 whole worms, scolex frontal sections *in situ* with strobila voucher, scolex frontal sections with strobila voucher, 2 proglottid cross-section series with strobila and scolex voucher); 1 paratype (MZUM[P]-2014.2(P); whole worm); 1 paratype (SBC-P-00066; whole worm); 7 paratypes (USNPC 108159.00–108162.00; 5 whole worms, scolex frontal sections with strobila voucher, and proglottid cross-sections with strobila and scolex voucher); 6 paratypes (LRP 8464–

8474; 5 whole worms and scolex frontal sections with strobila voucher); 1 scolex prepared for SEM with strobila voucher retained with KJ at the University of Kansas.

Etymology: This species is named for its highly folded apical organ; *plicatilis* (L.) meaning foldable, pliable.

Remarks

Floriparicapitus plicatilis n. sp. differs most conspicuously from both *F. euzeti* and *F. juliani* in its possession of only 4 testes (vs. 9–14 and 10–14, respectively) per proglottid and also in its greater number of proglottids (355–784 vs. 130–227 and 75–149, respectively). Curiously, despite this large number of proglottids, specimens of *F. plicatilis* n. sp. include the shortest (12 mm) and longest (52 mm) specimens of all 3 new species in the genus. In addition, the apical organ of *F. plicatilis* is conspicuously rugose rather than unwrinkled as in F. *euzeti*, and much smaller than that of *F. juliani* (116–173 long by 512–1,123 wide vs. 255–290 long by 1,330–1,653 wide, respectively). We note that *F. plicatilis* n. sp. was referred to as New genus 5 n. sp. 1 in the molecular analyses of Caira et al. (2014).

Sections of the host mucosa with specimens of *F. plicatilis* n. sp. in situ, show a remarkably close association between the apical organ and the mucosal surface. It appears the elaborate folds of the apical organ allow this taxon to interdigitate with the intestinal villi of its host (Fig. 27). It seems likely this will be found to be the mode of attachment of all members of the genus given the similarity in overall morphology of their respective apical organs.

Floriparicapitus plicatilis n. sp. is the only member of its genus known to date to parasitize 2 different species of rhinopristiform hosts. It was found to parasitize 2 closely related taxa in this order, both members of the genus *Glaucostegus* Bonaparte. *Floriparicapitus plicatilis*

was found to parasitize specimens of *G. typus* in northern and eastern Australia, and *G. thouin* in Malaysian and Indonesian Borneo, where *G. typus* was not found to host this species.

***Floriparicapitus rhinobatidis* (Subhapradha, 1955) n. comb.**

Synonym: *Cephalobothrium rhinobatidis* Subhapradha, 1955.

Taxonomic summary

Type and only known host: Glaucostegus granulatus (Latham) [as *Rhinobatus* [sic] *granulatus*], sharpnose guitarfish (Rhinopristiformes: "Rhinobatidae").

Type locality: Madras Coast, eastern coast of India, Bay of Bengal, Indian Ocean.

Site of infection: Spiral intestine.

Specimens deposited: Unknown.

Remarks

Subhapradha's (1955) description and illustrations of *Cephalobothrium rhinobatidis* show it to be fully consistent in both scolex morphology and proglottid anatomy with the diagnosis of *Floriparicapitus*. It is thus, hereby transferred to this new genus, formally establishing the new combination *Floriparicapitus rhinobatidis* (Subhapradha, 1955) n. comb. Because the type specimens were unavailable for study, a redescription was not possible. However, this species is easily distinguished from *F. euzeti*, *F. juliani*, and *F. plicatilis*, in its possession of 5 testes per proglottid (vs. 9–14, 10–14, and 4, respectively) (see Subhapradha, 1955). *Floriparicapitus rhinobatidis* n. comb. further differs from the 3 new species described here in its greater total length (64 vs. 11–30, 18–46, and 12–52 mm) and greater number of proglottids (>800 vs. 130–227, 75–149, and 355–784) for *F. euzeti*, *F. juliani*, and *F. plicatilis*, respectively.

The host identity for *F. rhinobatidis* n. comb. remains to be verified. The distribution of *Glaucostegus granulatus* (reported as *Rhinobatus granulatus* by Subhapradha in 1955) is not fully understood (e.g. Compagno and Last, 1999). More than 10 species of *Rhinobatos* and *Glaucostegus* have been reported from Indian waters (Talwar and Jhingran, 1991; Compagno and Last, 1999; Raje et al., 2007) and the correct identification of guitarfish in both genera is often problematic (Last et al., 2004; Naylor, Caira, Jensen, Rosana, Straube, and Lakner, 2012). As a consequence, new collections of *F. rhinobatidis* n. comb. from *G. granulatus* in the Bay of Bengal along the east coast of India are needed to confirm this host-parasite association.

Complicating the situation, *Cephalobothrium gogadevensis* Pramanik and Manna, 2005, also was described from *G. granulatus* (as *Rhinobatus* [sic] *granulatus*) from the Digha coast, in the Bay of Bengal (Pramanik and Manna, 2005). Although the description is relatively complete, the images presented consist entirely of 2 photomicrographs of exceptionally poor quality that lack detail and inquiries reveal that the whereabouts of the type material is unknown. Moreover, the host identity is highly suspect (P. Kumar Kar, pers. comm.). While Pramanik and Manna (2005) did distinguish their species from *C. rhinobatidis* (now *F. rhinobatidis* n. comb.) mainly based on total length, number of segments, and testes count, we propose their species be considered a *species inquirendum*. Given the limitations of the original description, unavailability of type material (P. Kumar Kar, pers. comm.), and suspect host identification, we have little hope for the resolution of the identity of *Cephalobothrium gogadevensis*.

***Floriparicapitus variabilis* (Southwell, 1911) n. comb.**

Synonyms: *Cephalobothrium variabile* Southwell, 1911; *Hexacanalis variabilis* (Southwell, 1911) Yamaguti, 1959.

(Figs. 31–43)

Redescription (based on 25 specimens: lectotype and 15 paralectotypes [previously syntypes] consisting of 14 whole mounts [6 whole mounts of complete worms, 8 whole mounts of incomplete worms], proglottid frontal sections of 1 specimen, and proglottid cross-sections of 1 specimen; Southwell's non-type proglottid frontal sections of 1 specimen and proglottid mixed sections of 1 specimen; 7 non-type specimens from newly collected material consisting of 4 whole mounts of mature worms, scolex frontal sections series of 1 specimen, proglottid cross-sections of 1 specimen, and 1 scolex prepared for SEM): Worms 29–77 [**130**] mm long, euapolytic; maximum width of strobila 271–536 [**<500**], in posterior-most mature proglottids; proglottids 439–1,088 [**>400**] in number, craspedote. Scolex laterally expanded, consisting of scolex proper bearing 4 acetabula, apical modification of scolex proper, and apical organ. Scolex proper 207–235 long by 556–712 wide in scoleces with expanded apical organ, 689–895 long by 638–940 wide in scoleces with retracted apical organs. Acetabula in form of suckers, 85–135 in diameter. Apical modification of scolex proper with extensive aperture at apex (Fig. 33). Apical organ retractable (Fig. 31), in form of extensive, wide, muscular and glandular, rugose sheet (Fig. 33), 175–336 long by 686–1,424 wide [**1,000**].

Scolex proper (Fig. 35) covered with coniform spinitriches and possibly capilliform filitriches. Surface of suckers not observed. Apical modification of scolex proper (Fig. 36) covered with coniform spinitriches and capilliform filitriches. Apical organ covered with papilliform filitriches (Fig. 37) and sensory cilia (Fig. 34). Strobila covered with capilliform filitriches (Fig. 38).

Cephalic peduncle absent. Longitudinal muscle bundles conspicuous, cortical. Immature proglottids 353–1,006 in number, initially wider than long, becoming longer than wide with maturity; posterior-most immature proglottid 164–290 long by 206–683 wide. Mature proglottids

15–98 in number, 295–931 long by 256–622 wide, lacking gap between anterior margin of proglottid and internal organs. Testes 13–17 in number, 27–77 long by 32–81 wide, extending from anterior margin of proglottid to level of ovary, degenerated in terminal mature proglottid(s), loosely arranged in 2 columns in dorso-ventral view, 1 layer deep in cross-section. Vas deferens extending medially from level of ootype to anterior margin of cirrus sac, expanded to form external seminal vesicle (Fig. 42) in mature proglottids in which testes may be degenerated. Internal seminal vesicle absent. Cirrus sac pyriform, angled posteriorly, 140–279 long by 120–230 wide, containing coiled cirrus. Cirrus armed with spinitriches; expanded near genital pore. Ovary consisting of multiple irregular lobes on each lateral side, essentially H-shaped in dorso-ventral view, tetralobed in cross-section, 179–459 long by 101–237; ovarian bridge at mid-level of ovary. Mehlis' gland posterior to ovarian bridge. Vagina curving, extending medially from ootype region to genital atrium, opening into genital atrium anterior to cirrus sac (Figs. 32, 39). Genital pores lateral, irregularly alternating, 70–86% of proglottid length from posterior margin of proglottid. Vitellarium follicular; follicles arranged in 5–6 irregular columns on each lateral margin of proglottid, extending from near anterior margin of proglottid to posterior margin of proglottid, partially interrupted by ovary, 17–63 long by 34–87 wide. Excretory ducts in 3 pairs (Fig. 40); central pair expanded, passing through ovarian lobes (Fig. 43). Uterus saccate, extending medially in proglottid from level of ovarian bridge to level of anterior-most vitelline follicles. Eggs not observed.

Taxonomic summary

Type and only known host: Anoxypristis cuspidata (Latham) (as *Pristis cuspidata*), knifetooth sawfish (Rhinopristiformes: "Pristidae").

Type locality: Portugal Bay, Ceylon (now Sri Lanka) (see Southwell, 1911).

Additional localities: east of Wessel Islands (11°17'44"S, 136°59'48"E), Northern Territory, Australia, Arafura Sea, Indian Ocean.

Site of infection: Spiral intestine.

Specimens deposited: Lectotype (NHMUK 2014.5.19.1; whole worm) and 15 paralectotypes (NHMUK 2014.5.19.2–16; 13 complete or incomplete worms, proglottid frontal sections, and proglottid cross sections (Southwell's syntypes); 2 non-types (NHMUK 0000.0.00.00–00; 1 slide of proglottid frontal sections and 3 slides of proglottid mixed sections) from Southwell's collection dated 1922; 6 non-types (QM G234427–G234432; 4 whole worms, scolex frontal sections without strobila voucher, proglottid cross-sections without strobila voucher); 1 scolex prepared for SEM with strobila voucher retained with KJ at the University of Kansas.

Etymology: The specific epithet *variable* refers to the "…remarkable variability, hence the specific name" (Southwell, 1911).

Remarks

The discovery of 18 of Southwell's 47 type slides of *Cephalobothrium variabile* helped clarify some of the confusion surrounding the identity of this species particularly with respect to details of its proglottid and scolex morphology, and thus its affiliation with *Floriparicapitus*. Furthermore, although Southwell (1911) originally described *C. variabile* from the sawfish "*Pristis cuspidatus*" (=*Anoxypristis cuspidata*), he (Southwell, 1912) subsequently reported it from the stingray "*Trygon kuhli*" (=*Neotrygon kuhlii* [Müller & Henle]). Six slides that appear to have been the source of Southwell's 1912 report for they bear labels that read "*Cephalobothrium variabile* Southwell, 1911; *Dasybatus kuhli*, Ceylon" were available at the Natural History Museum in London (BNHM 1965.2.23.201–206). (We note that *Dasybatus* is one of several generic names used at the turn of the 20th century for this stingray species). The availability of

type material allowed for a direct evaluation of their conspecificity with *C. variabile* and, thus, for an evaluation of *N. kuhlii* as an additional host for *C. variabile.*

Owing to the taxonomic confusion surrounding *C. variabile* (see Jensen, 2005), we have formally designated a lectotype from Southwell's original series and it has been deposited at the Natural History Museum in London (NHMUK 2014.5.19.1). The remaining 15 specimens were designated as paralectotypes and they too have been deposited (NHMUK 2014.5.19.2–16). Examination of the type and newly collected material from *A. cuspidata* using light and scanning electron microscopy not only facilitated a complete redescription of this species, but it also confirmed its membership in *Floriparicapitus*.

Overall, the measurements reported by Southwell (1911) in the original description based on 47 specimens fall within the ranges reported in this redescription, with the exception of total length. The discrepancy in total length (i.e., 29–77 reported herein vs. 130 mm in Southwell [1911]) can likely be attributed to the fact that the subset of type specimens available for study did not include these longest specimens. Moreover, the description of *C. variabile* by Southwell (1911) as possessing only 2 suckers on the scolex proper, rather than 4, is likely an oversight due to their small size, as clarified by Southwell (1925) and observed herein.

Floriparicapitus variable n. comb. differs from its 4 congeners in possessing 5–6 irregular columns of vitelleria on each proglottid margin (vs. 2 or 2–3 irregular columns) and from the 3 new species described herein in possessing vitelline follicles that extend to the anterior margin of the proglottid rather than stopping short of the anterior margin of the proglottid. In addition, the cirrus sac of *F. variabilis* n. comb. is angled posteriorly rather than anteriorly as seen in the other known congeners.

Although Southwell's specimens from *N. kuhlii* are in poor condition, it seems apparent that they are not conspecific with *F. variabilis*, and, in fact, differ in a number of important respects from the diagnosis of *Floriparicapitus*, suggesting they do not belong in that genus. Most convincingly, 1 slide bears histological sections of a scolex with a large oval, muscular apical organ, rather than a wide, muscular and glandular, rugose sheet that is thus clearly inconsistent with *Floriparicapitus*. Among known lecanicephalidean genera, these specimens from *N. kuhlii* most closely resemble *Hexacanalis* Perrenoud, 1931, but this remains to be confirmed. Nonetheless, we believe this host species should be removed from the list of hosts for the new genus at this time.

DISCUSSION

Species of *Floriparicapitus* n. gen. are unusual among lecanicephalideans in the position of the opening of the vagina relative to the cirrus sac. The majority of lecanicephalideans have been described as possessing a vagina that enters the genital atrium posterior to the cirrus. Exceptions include species of *Anteropora*, *Polypocephalus*, and *Sesquipedalapex*, which have been described with a vagina that opens into the genital atrium posterior to or at the same level as the cirrus sac (see Jensen, 2005; Jensen et al., 2011), and species of *Hornellobothrium*, which possess a vagina that opens into the genital atrium anterior to the cirrus sac (see Jensen, 2005). *Floriparicapitus* n. gen. is unique among elasmobranch tapeworm genera in that it includes species in which the vagina opens posterior to, at the same level as, and anterior to the cirrus sac, even within the same individual (e.g. in *F. juliani*).

Floriparicapitus shows notable affinities with *Lecanicephalum* in both strobilar and scolex morphology. For example, both genera possess conspicuously armed cirri and testes arranged in 1 or 2 columns, both also exhibit scoleces bearing an apical organ in the form of a

muscular and glandular sheet of tissue. However, they also differ in a number of important respects. For example, the scolex of *Floriparicapitus* lacks the conspicuous muscle bundles of the apical organ observed in *Lecanicephalum*. Whereas *Lecanicephalum* species have been described as possessing only a single pair of excretory vessels (Jensen, 2005), species of the former genus exhibit 3 pairs of excretory vessels. In this respect members of *Floriparicapitus* resemble those of *Hexacanalis* and *Stoibocephalum* which also possess 3 pairs of excretory vessels (see Cielocha and Jensen, 2011 and Cielocha and Jensen, 2013, respectively). In the molecular phylogeny of Caira et al. (2014), *Floriparicapitus plicatilis* (as New genus 5 n. sp. 1) grouped most closely with the 2 included species of *Eniochobothrium*, as sister taxon to a clade consisting of the exemplars of *Adelobothrium* Shipley, 1900 and *Cephalobothrium*. However, the affinities between *Floriparicapitus* and *Eniochobothrium* and also with *Cephalobothrium* + *Adelobothrium* were not well supported. Furthermore, the 3 genera that are arguably key to understanding the relationships of *Floriparicapitus* (i.e., *Lecanicephalum*, *Hexacanalis*, and *Stoibocephalum*) were not included in the analyses of Caira et al. (2014). As a consequence, the affinities of *Floriparicapitus* remain to be assessed in the larger context of lecanicephalidean diversity. Also of interest to explore further in a phylogenetic context is the observation that while species of *Floriparicapitus* parasitizing sawfish exhibit 9 or more testes per proglottid, those parasitizing species of the guitarfish genus *Glaucostegus* bear only 4 or 5.

Recent studies focusing on the relationships among batoids, using morphological and/or molecular data (Aschliman et al., 2012; Naylor, Caira, Jensen, Rosana, White, and Last, 2012), although not completely congruent in their results, have done much to shed light on batoid phylogenetic relationships. Deviating from traditional classification of major batoid groups, Naylor, Caira, Jensen, Rosana, White, and Last, (2012) found significant support for a clade

uniting guitarfishes and sawfishes in the single order Rhinopristiformes. Within this order, their work also revealed potential issues with the monophyly of the guitarfish family Rhinobatidae as traditionally recognized, for it was shown to consist of as many as 4 distinct lineages. Curiously, Naylor et al.'s work also called into question the monophyly of the sawfish because the monotypic genus *Anoxypristis* was found to group more closely with species of the guitarfish genus *Glaucostegus*, than to the remaining sawfish (i.e., *Pristis*), suggesting instead that there exists a larger clade comprised of sawfishes and *Glaucostegus* species. The host associations of *Floriparicapitus* are particularly intriguing in light of that topology for the genus appears to be restricted to the latter subclade of rhinopristiformes. With respect to sawfishes, here we describe new species of *Floriparicapitus* from *P. clavata* and *P. microdon*, and in transferring *Cephalobothrium variabile* report a species from *A. cuspidatus*. In addition, although not formally described owing to the unavailability of sufficient material, 3 specimens collected from *P. zijsron* (*Floriparicapitus* sp. 1) off Australia and 1 specimen collected from *P. pectinata* (*Floriparicapitus* sp. 2) in the western Atlantic Ocean off Florida have been deposited in the LRP (8478–8479 and 8480, respectively) to document these host records (see Table III). Tapeworms have not been examined from the one remaining pristid host, *Pristis pristis* (Linnaeus). It is interesting to note that *P. microdon* and *P. clavata* are parasitized by different species of *Floriparicapitus* in Australia where they occur sympatrically. With respect to *Glaucostegus*, here we describe a new species from *G. thouin* and *G. typus* and, in transferring *F. rhinobatidis*, also recognize *G. granulatus* as an appropriate host. Among guitarfishes, the 5 remaining species of *Glaucostegus* (i.e., *G. cemiculus* [St. Hilaire], *G. halavi* [Forsskål], *G. micropthalmus* Teng, *G. obtusus* [Müller and Henle], and *G. spinosus* [Günther]) are the most likely candidates as hosts of additional species of *Floriparicapitus*. We have less confidence in

species of rhinopristiform genera outside of this clade (i.e., *Aptychotrema* Norman, *Rhina* Bloch, *Rhinobatos* Linck, *Rhynchobatus* Philippi, *Trygonorrhina* Müller and Henle, or *Zapteryx* Jordan) for despite records of cestodes from members of many of these genera (e.g., Ostrowski de Núñez, 1971; Butler, 1987; Campbell and Beveridge, 2002; Jensen, 2005; Cielocha and Jensen, 2013; Caira et al., 2013), species consistent with *Floriparicapitus* have not yet been found.

Greater diversity of *Floriparicapitus* parasitizing host species confirmed herein is anticipated because specimens of what appears to be a second species (*Floriparicapitus* sp. 3), distinct from *F. plicatilis*, were found parasitizing an individual of *G. thouin* from Indonesian Borneo. They too have been deposited in the LRP (8481–8483) to document this record. However, additional specimens and observations are required to formally describe these 3 species. Though these species are not formally described, these reports provide further insight into the prevalence of *Floriparicapitus* in sawfish and guitarfish, especially in the Indo-Pacific region as well as the Western Atlantic and allude to greater species diversity in the genus.

Lecanicephalidean genera vary in their affinities for elasmobranch host taxa. Some exhibit a relatively relaxed host-choice. For example, collectively species of *Polypocephalus* parasitize a broad spectrum of batoid families including the rhinopristiform families Rhinobatidae and Rhynchobatidae and the myliobatiform families Dasyatidae, Myliobatidae, Rhinopteridae, and Urolophidae (see Jensen, 2005). The host associations of other genera are much more restricted. For example, species of *Hexacanalis* each parasitize only a single species of butterfly ray of the genus *Gymnura* (see Cielocha and Jensen, 2011). Valid members of the *Lecanicephalum* are known only from stingrays of the genus *Dasyatis*. Species of *Eniochobothrium* parasitize only cownose rays in the genus *Rhinoptera* Cuvier (see Jensen,

2005). *Floriparicapitus* appears to be more catholic in its host associations given that its species collectively parasitize 3 different rhinopristiform genera.

However, at the individual species level, its members exhibit much more fidelity. Most species of *Floriparicapitus* are oioxenous sensu Euzet and Combes (1980), parasitizing only a single species of host. This phenomenon is certainly not uncommon among lecanicephalidean species (Jensen, 2001, 2005). The exception is *F. plicatilis*, which appears to parasitize 2 species of *Glaucostegus* and thus exhibits mesostenoxenous specificity sensu Caira et al. (2003). Interestingly, this is not the first tapeworm species reported to parasitize more than a single species of *Glaucostegus*. Ivanov and Caira (2012) described the diphyllidean *Echinobothrium weipaense* Ivanov and Caira, 2012 from *G. typus*, but reported specimens that were generally consistent with their new species also parasitizing *G. thouin* albeit differing in several minor respects from specimens collected from *G. typus* (e.g., longer in total length [0.70–1.15 mm vs. 0.46–0.88 mm] and differences in spines per row on the cephalic peduncle [9–11 vs. 9–10]). Similar small differences were seen here between specimens of *Floriparicapitus* parasitizing *G. typus* and *G. thouin*. For example, in general, specimens of *F. plicatilis* collected from *G. thouin* in Malaysian Borneo exhibited a slightly wider strobila and scolex than seen in those from *G. typus* in northern Australia (212–255 µm vs. 132–230 µm and 752–960 µm vs. 435–837 µm, respectively). Despite the subtle morphological differences observed for these specimens, conspecificity is assumed. We note that many of these cestodes came from the same host specimens examined by Ivanov and Caira (2012).

ACKNOWLEDGMENTS

We are grateful for the assistance of many colleagues who either contributed to host collections or facilitated the collecting process. Julian Baggio, of Cairns Marine, Australia,

collected the specimen of *Pristis microdon* (GCDB Collection Code: CMJ). We are grateful to Captain Hamri bin Hji-Kating and his son Sebli bin Hamri for assistance with the collection of specimens of *Glaucostegus thouin* (BO) from the waters of Malaysian Borneo. We thank Tom Cribb and Rob Adlard for "grabbing" a specimen of *Glaucostegus typus* at Moreton Bay (DF), Richard Mounsey and Julie Lloyd, formerly of Darwin Fisheries, for arranging for the collection of specimens of *Glaucostegus typus* from the Timor Sea (AU), Lyle Squires of Cairns Marine for assistance with the collection of specimens of *Glaucostegus* from the Gulf of Carpentaria (CM03), and we are grateful to Bill and Ray Passey for allowing JNC and KJ to collect on the *F.V. Ocean Harvest* in November 1999, during which time specimens of *Anoxypristis cuspidata* (NT) were examined. Collections in Sarawak were conducted under collecting permit No. UPE:40/200/19SJ.924 from the Economic Planning unit in Kuala Lumpur and research agreement No. SBC-RA-0050-JNC from the Sarawak Biodiversity Center in Kuching. Collections in Queensland, Australia were conducted under Queensland Fisheries Service permit PRM03834B. Collections in the Northern Territory, Australia were conducted in collaboration with the Fisheries Division of the Department of Primary Industry and Fisheries in Darwin, NT. This work has been partially funded by NSF BS&I grants DEB 0103640, DEB 0542846, and DEB 0542941, NSF PB&I grants DEB 0818696 and DEB 0818823, and NSF DDIG grant DEB 1110468.

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Figures 1–5. Line drawings of species of *Floriparicapitus* (**1–3**). *Floriparicapitus euzeti* n. sp. from *Pristis clavata*. (1) Whole worm (paratype, QM G234397). (2) Scolex (paratype, QM G234404). (3) Mature proglottid (holotype, QM G234394). (**4–5**) *Floriparicapitus juliani* n. sp. from *Pristis microdon*. (4) Scolex (paratype, QM G234410). (5) Mature proglottid (holotype, QM G234408); arrowheads indicate level at which sections in Figs. 12–17 were taken.

Figures 6–11. Scanning electron micrographs of *Floriparicapitus euzeti* n. sp. from *Pristis clavata*. (**6**) Scolex; small numbers indicate location of detail in Figs. 7–11. (**7**) Apical organ possibly with papilliform filitriches. (**8**) Transition between apical modification of scolex proper (AMSP) and scolex proper; AMSP with acicular filitriches and scolex proper with capilliform

filitriches and coniform spinitriches. (**9**) Scolex proper with capilliform filitriches and coniform spinitriches. (**10**) Scolex proper surrounding suckers with capilliform filitriches and coniform spinitriches. (**11**) Strobila with capilliform filitriches.

Figures 12–17. Cross-sections through mature proglottid (in which testes are degenerated) of *Floriparicapitus juliani* n. sp. (paratype, QM G234413); embedded in glycol methacrylate. (**12**) Anterior-most part of proglottid. (**13**) At level anterior to genital pore showing expanded uterus, external seminal vesicle, and anteriorly projected cirrus sac. (**14**) At level of genital pore; note that vagina and cirrus are at the same level. (**15**) At level posterior to cirrus sac showing vas deferens and expanded vagina. (**16**) At level of ovary; excretory vessels are indicated by arrowheads. (**17**) At level posterior to ovary. Abbreviations: C, cirrus; CM, cirrus microtriches; CS, cirrus sac; GP, genital pore; MG, Mehlis' gland; OV, ovary; OC, ovicapt; OD, oviduct; UD, uterine duct; U, uterus; VA, vagina; VD, vas deferens; VF, vitelline follicle.

Figures 18–20. Line drawings of *Floriparicapitus plicatilis* n. sp. from *Glaucostegus typus*. (**18**) Whole worm (holotype, QM G234414). (**19**) Scolex (paratype, QM G234421). (**20**) Mature proglottid in which testes are degenerated (holotype, QM G234414). Arrowheads indicate level at which sections in Figs. 28–30 were taken.

Figures 21–26. Scanning electron micrographs of *Floriparicapitus plicatilis* n. sp. from *Glaucostegus typus*. (**21**) Scolex; small numbers indicate location of detail in Figs. 22–26. (**22**) Apical organ with papilliform filitriches. (**23**) Scolex proper between suckers with capilliform filitriches and coniform spinitriches. (**24**) Microthrix variation of apical modification of scolex proper (AMSP); anterior AMSP with papilliform filitriches and posterior AMSP with capilliform filitriches and coniform spinitriches, separated by region devoid of microtriches. (**25**) Scolex

proper surrounding suckers with capilliform filitriches and coniform spinitriches. (**26**) Strobila with capilliform filitriches.

Figure 27. Frontal section of scolex of *Floriparicapitus plicatilis* n. sp. in situ; embedded in paraffin. (**A**) Scolex attached to chamber wall, showing intimate association between apical organ and host intestinal mucosa (paratype, QM G234416); black outline indicates region shown in B. (**B**) Close-up of attached scolex; arrowhead indicates boundary of apical organ and apical modification of scolex proper. Abbreviation: AMSP, apical modification of scolex proper.

FIGURES 28–30. Proglottid cross-sections of *Floriparicapitus plicatilis* n. sp.; embedded in paraffin. (**28**) Through anterior region of strobila showing six excretory vessels (arrowheads) and discrete longitudinal muscle bundles (paratype, QM G234416). (**29**) Through mature proglottid at level of genital pore. Note vagina and cirrus opening at approximately same level (paratype, USNPC 108159.00). (**30**) Through mature proglottid at level of ovarian bridge (paratype, USNPC 108159.00). Note expanded size of medial pair of excretory vessels (arrowheads). Abbreviations: C, cirrus; CS, cirrus sac; GP, genital pore; LM, longitudinal muscle bundles; MG, Mehlis' gland; OV, ovary; OC, ovicapt; OD, oviduct; T, testis; U, uterus; UD, uterine duct; VA, vagina; VF, vitelline follicle; VD, vas deferens.

Figures 31, 32. Line drawings of *Floriparicapitus variabilis* n. comb. from *Anoxypristis cuspidata*. (**31**) Scolex; apical organ retracted (paralectotype, NHMUK 2014.5.19.2). (**32**) Mature proglottid in which most testes are degenerated (lectotype, NHMUK 2014.5.19.1).

Figures 33–38. Scanning electron micrographs of *Floriparicapitus variabilis* n. comb. from *Anoxypristis cuspidata*. (**33**) Scolex; small numbers indicate location of detail in Figs. 34–38. (**34**) Apical organ with papilliform filitriches and sensory cilium. (**35**) Scolex proper with coniform spinitriches and possibly capilliform filitriches. (**36**) Transition between apical organ

and apical modification of scolex proper (AMSP); apical organ possibly with papilliform filitriches and AMSP with capilliform filitriches and coniform spinitriches. (**37**) Apical organ with papilliform filitriches. (**38**) Strobila with capilliform filitriches.

Figures 39–43. Light micrographs of mature proglottid of *Floriparicapitus variabilis* n. comb. **(39**) Whole mount showing vagina entering into genital atrium anterior to cirrus (paratype, QM G234430); arrowheads indicate level at which sections in Figs. 40–43 were taken. (**40**) Cross-section near anterior extremity with remnants of testes (paratype, QM G234432); excretory vessels are indicated by arrowheads. (**41**) Cross-section immediately anterior to genital pore (paratype, QM G234432). (**42**) Cross-section between cirrus sac and ovary showing vas deferens expanded to form external seminal vesicle (paratype, QM G234432). (**43**) Cross-section at level of ovarian bridge (paratype, QM G234432). Abbreviations: CS, cirrus sac; ESV, external seminal vesicle; LM, longitudinal muscle bundles; MG, Mehlis' gland; OV, ovary; OD, oviduct; T, testis; U, uterus; VA, vagina; VF, vitelline follicle.

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Figures 1-5

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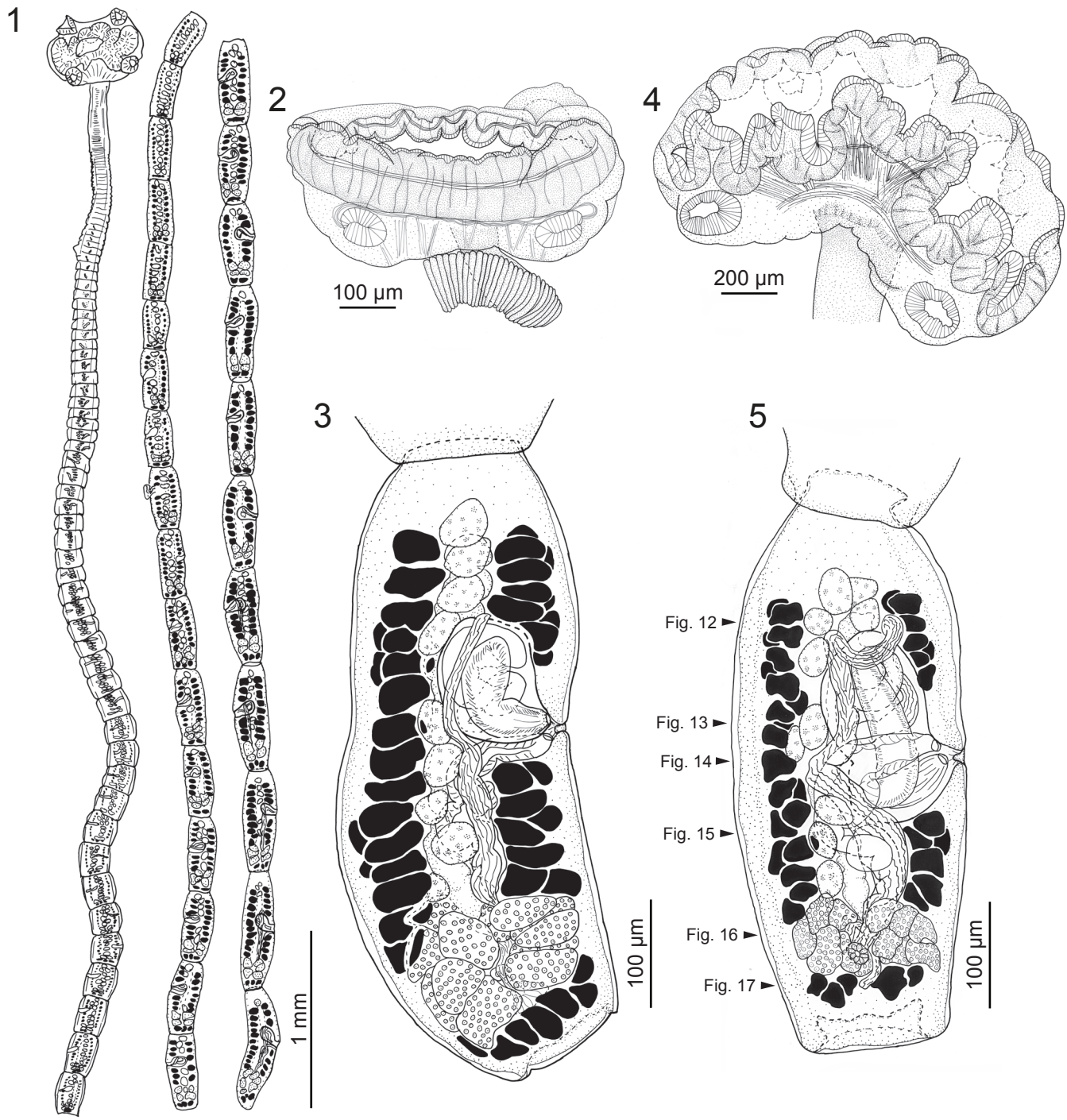

Figures 6-11

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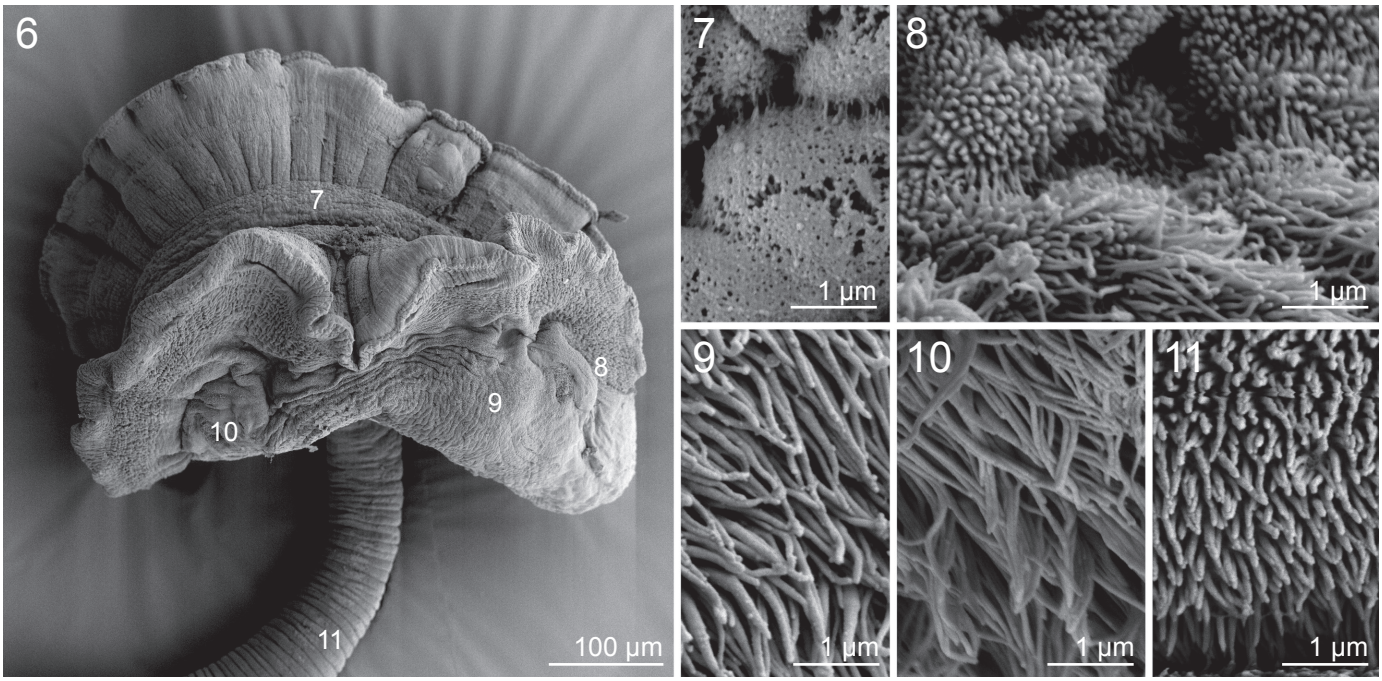

Figures 12-17

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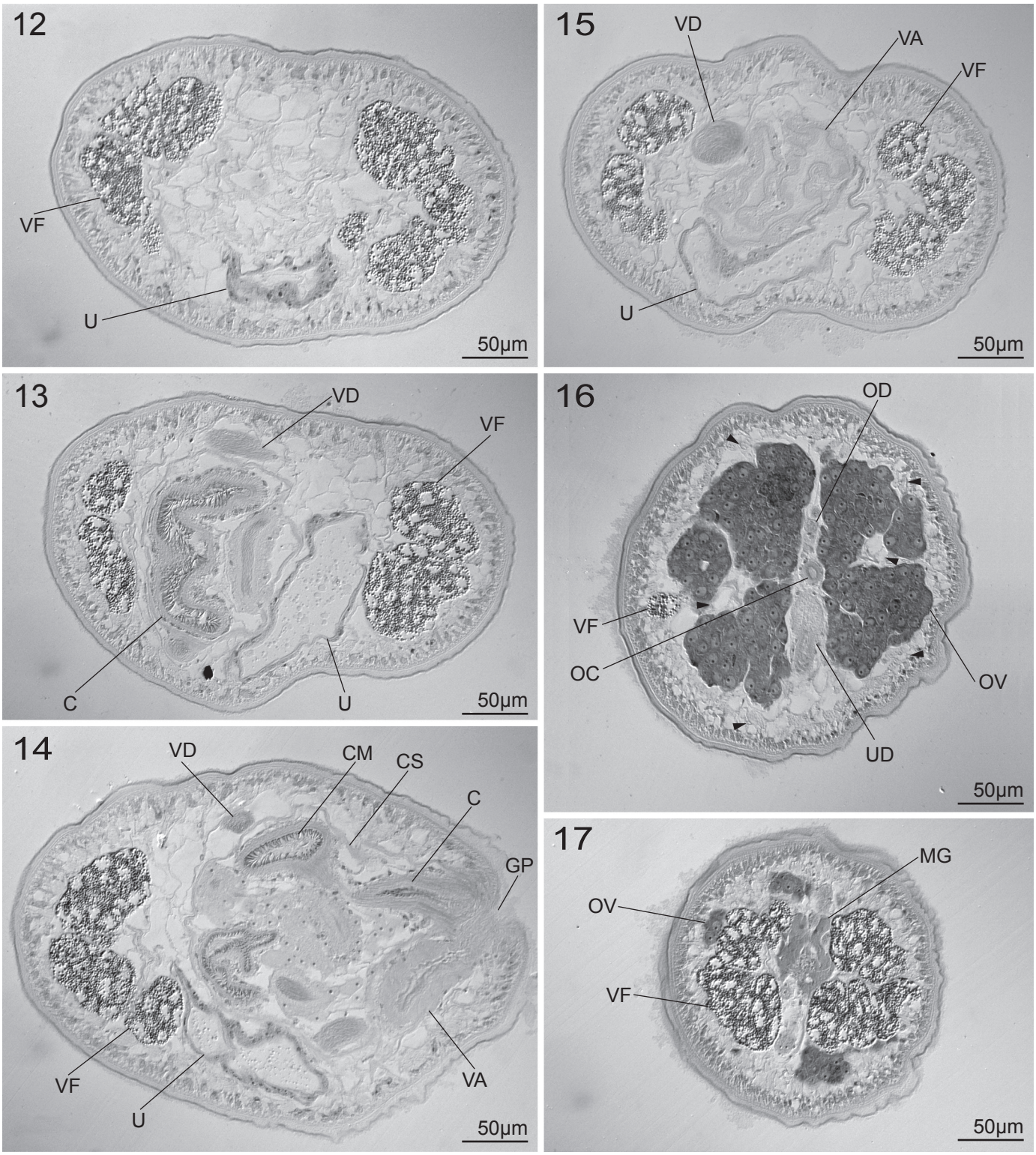

Figures 18-20
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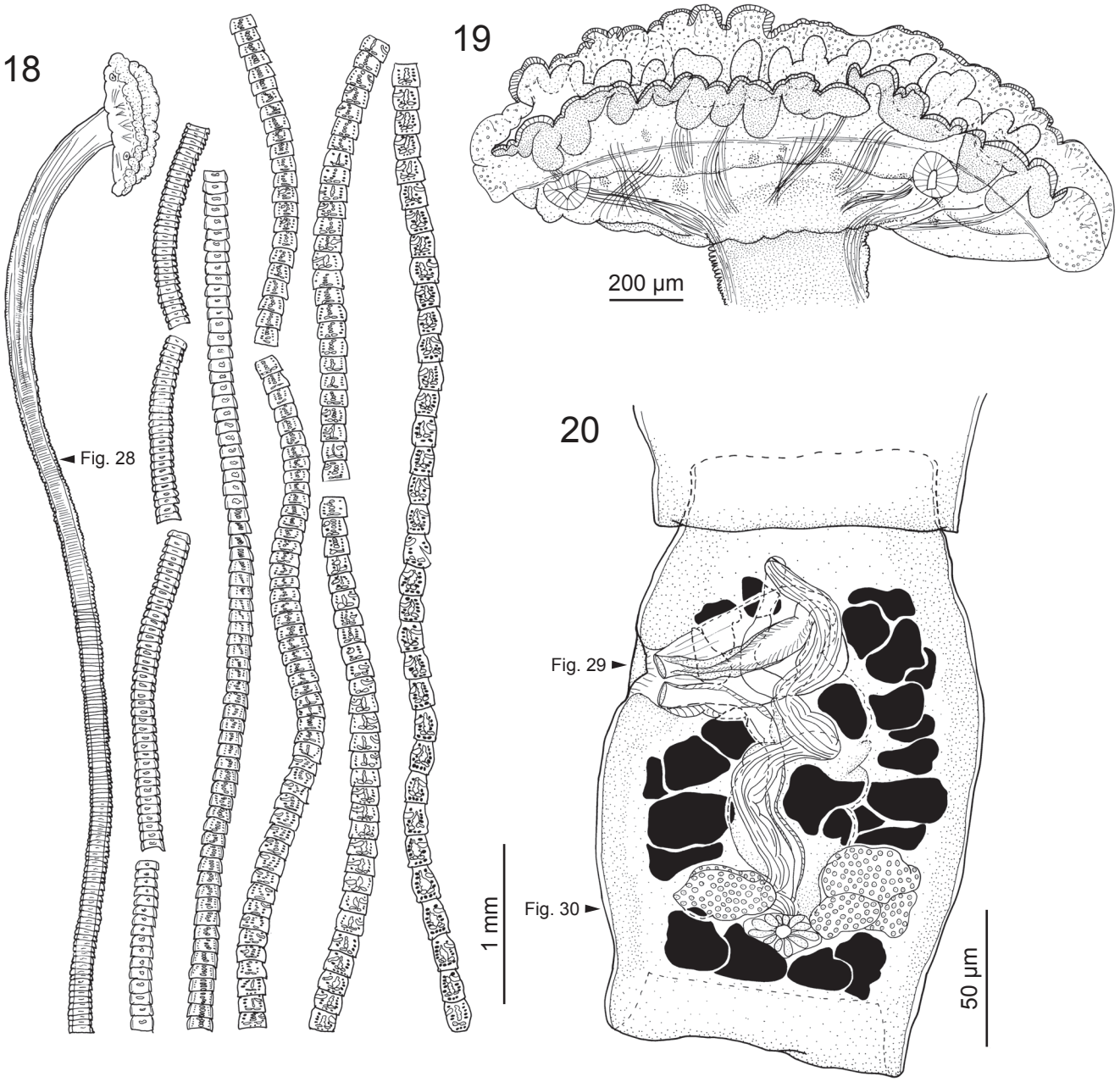

Figures 21-26

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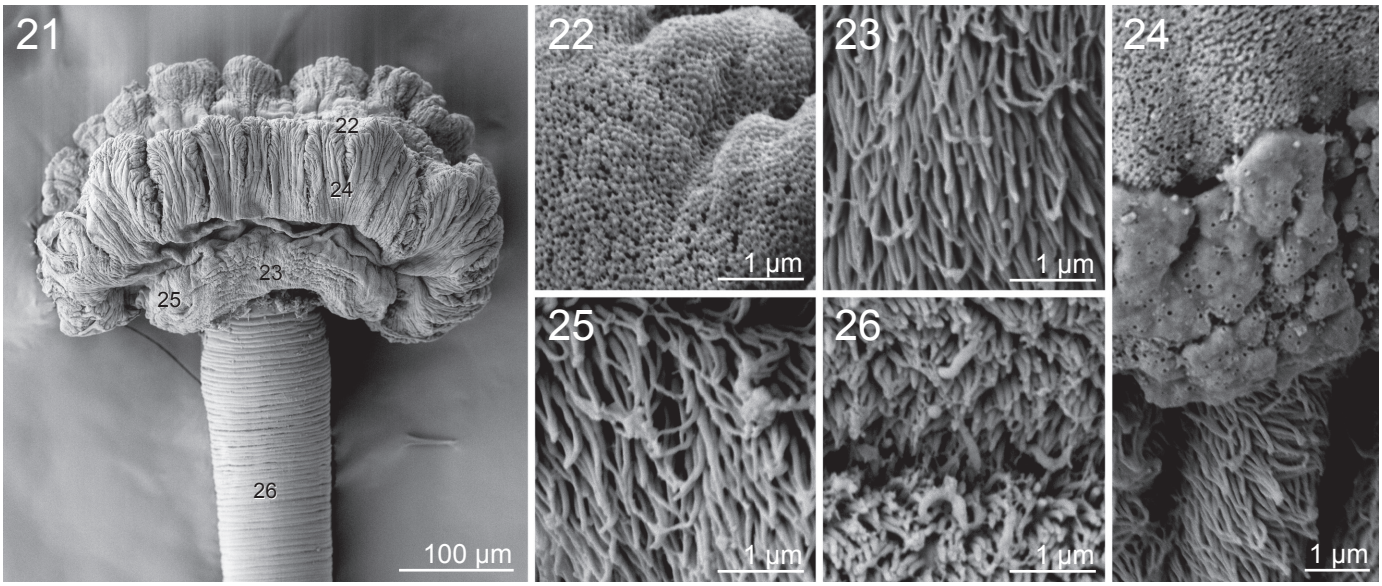

Figs27--revised

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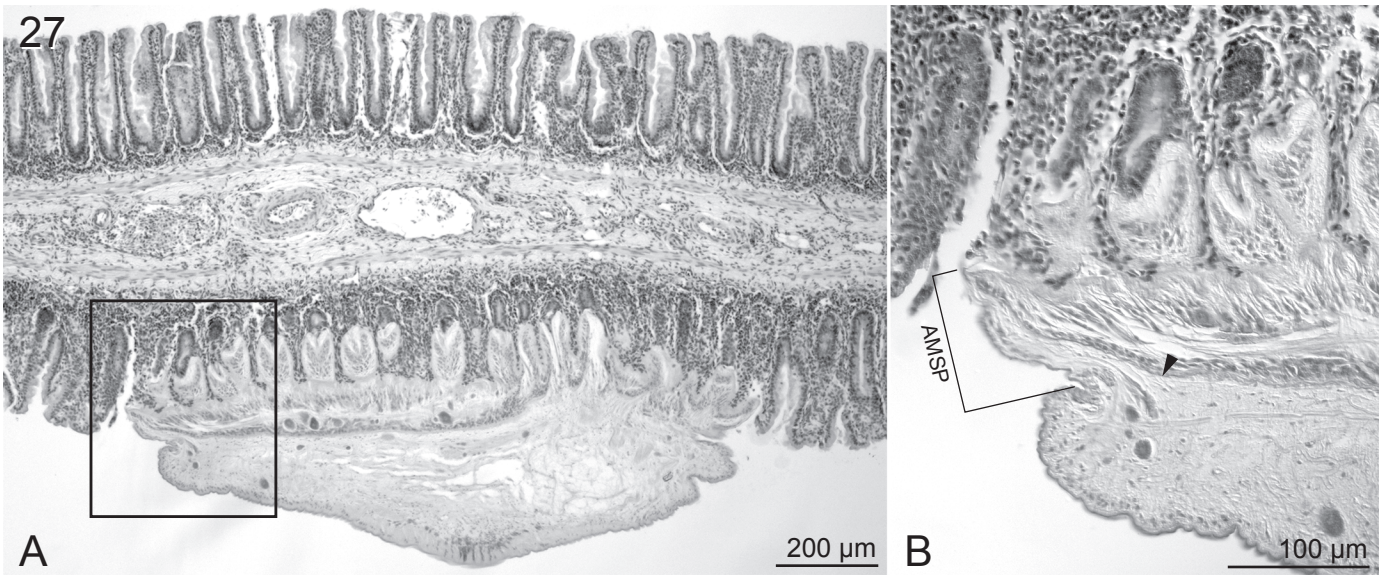

Figs28-30-revised
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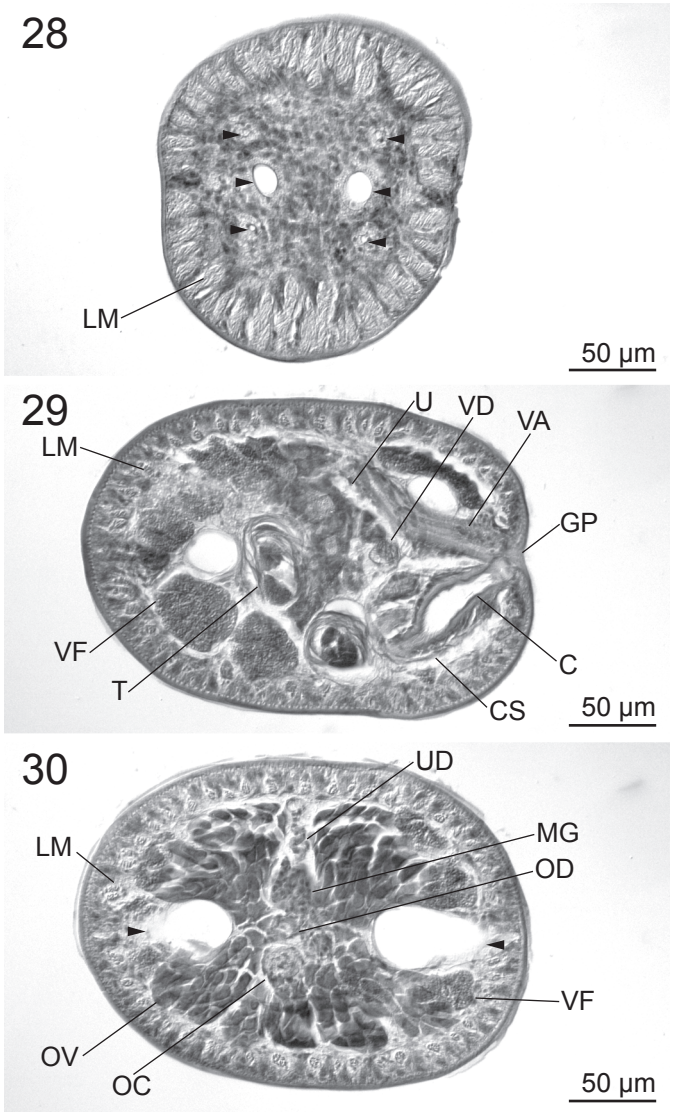

Figures 31-32
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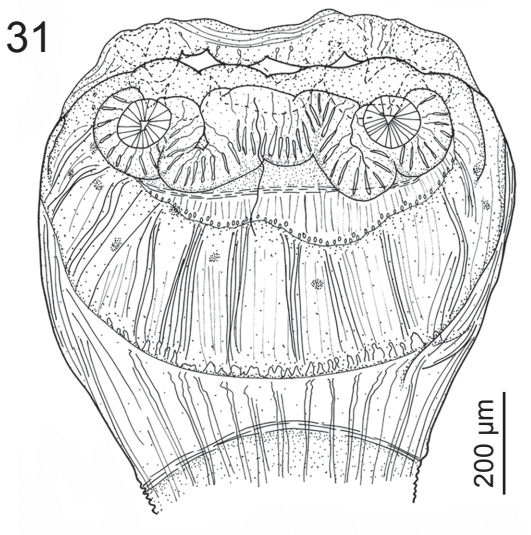

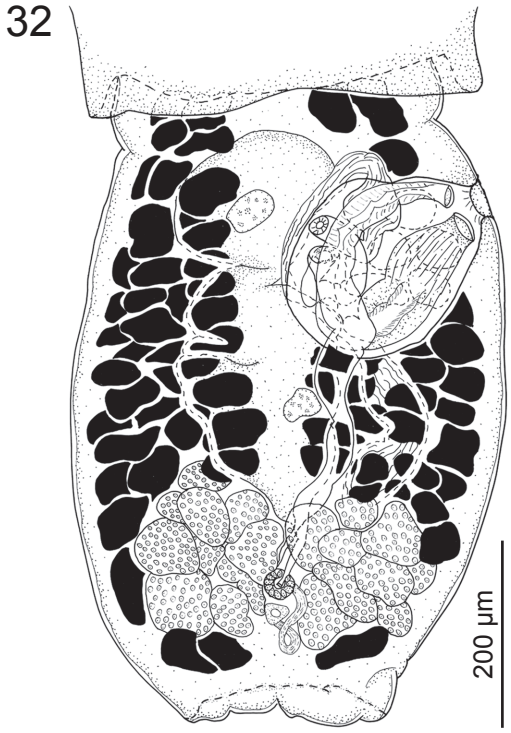

Figures 33-38
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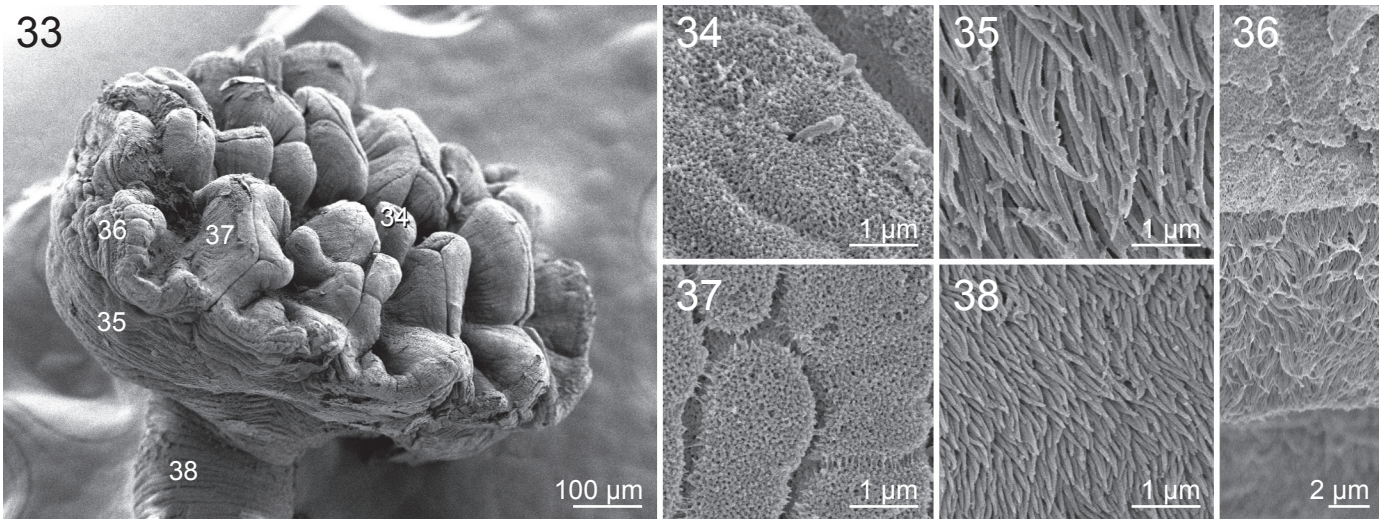

Figures 39-43
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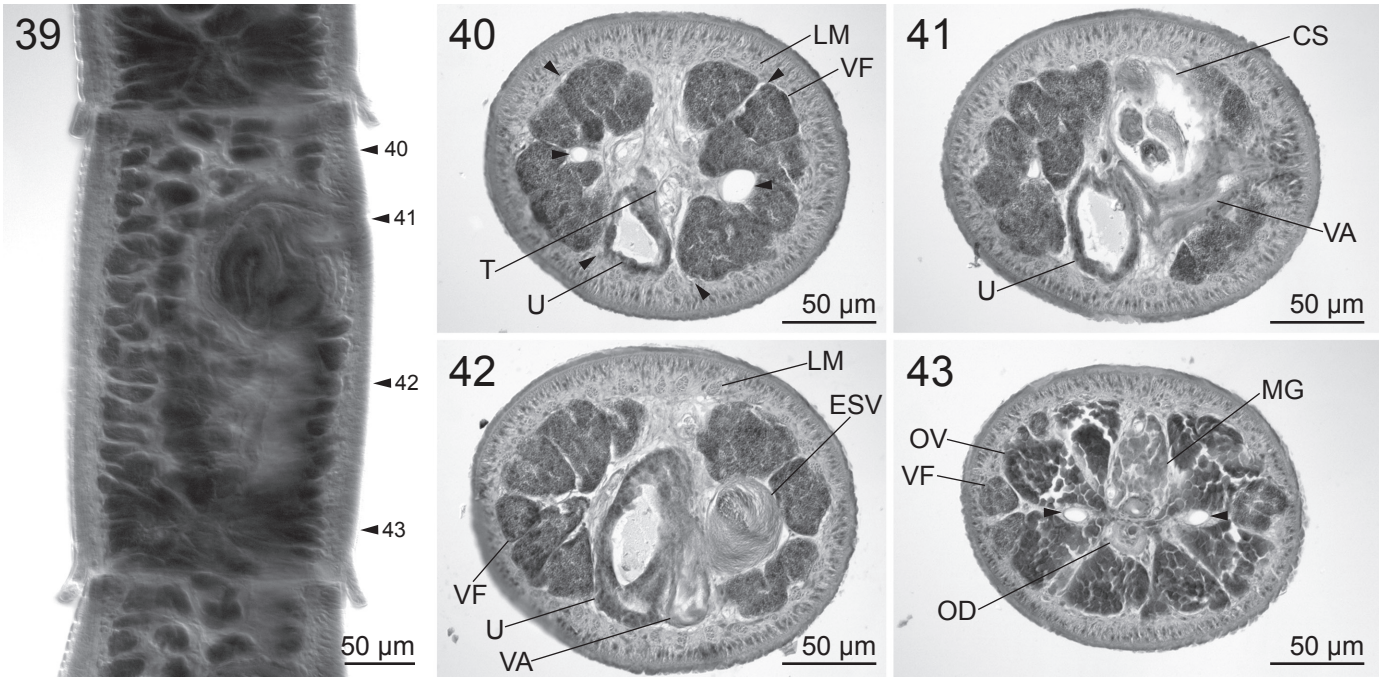

Table I. Host specimen locality data.

Host species	Locality (host specimens Collection Code and Number)
Family "Pristidae" sensu Naylor, Caira, Jensen, Rosana, White and Last (2012)	
Anoxypristis cuspidata Latham, narrow sawfish	AUSTRALIA: east of Wessel Islands (11°17'44"S, 136°59'48"E), Northern Territory, Arafura Sea, Indian Ocean (**NT-58*; NT-65*; NT-89**)
Pristis clavata Garman, dwarf sawfish	AUSTRALIA: Darwin (12°20'11"S, 130°54'39"E), Buffalo Creek, Northern Territory, Timor Sea, Indian Ocean **(AU-15*; AU-36*; AU-136*; AU-138***)
Pristis microdon Latham, freshwater sawfish	AUSTRALIA: off Queensland, Pacific Ocean (**CMJ-10)**
Pristis zijsron Bleeker, green sawfish	AUSTRALIA: Darwin (12°20'11"S, 130°54'39"E), Buffalo Creek, Northern Territory, Timor Sea, Indian Ocean (**DF-10*, AU-2***)
Family "Rhinobatidae" sensu Naylor, Caira, Jensen, Rosana, White and Last (2012)	
Glaucostegus thouin (Anonymous [Lacepède]), clubnose guitarfish	MALAYSIA: Sematan (1°48'15.45"N, 109°46'47.17"E), Sarawak, Borneo, South China Sea, Pacific Ocean (**BO-157***) INDONESIA: Pagatan (03°36'36.00"S, 115°54'59.40"E), South Kalimantan, Borneo, Makassar Straight, Pacific Ocean (**KA-70***)
Glaucostegus typus (Anonymous [Bennett]), giant shovelnose ray	AUSTRALIA: Lee Point (12°20'11"S, 130°54'39"E) (**AU-1***) and Dundee Beach (12°45'33"S, 130°21'7"E) (**AU-56*; AU-60*; AU-62***), Fog Bay, Northern Territory, Timor Sea, Indian Ocean; Weipa (12°35'11"S, 141°42'34"E), Queensland, Arafura Sea, Pacific Ocean (**CM03-60*; CM03-75***); Scarborough Beach (27°S, 153°E), Brisbane, Queensland, Pacific Ocean (**DF-2**)

* Specimens included in Naylor, Caira, Jensen, Rosana, White and Last (2012).

TableII-Revised
Click here to download Table: Cielochaetal_Table2-revised.pdf

Table II. Morphometric data* of species of *Floriparicapitus* n. gen.

Character	*F. euzeti* n. sp.	*F. juliani* n. sp.	*F. plicatilis* n. sp.	*F. variabilis* n. comb.‡
General Anatomy				
Total length (mm)	19 ± 6; 24	27 ± 8; 11	24 ± 9; 21	54 ± 12; 15
Maximum width of strobila	248 ± 32; 24	311 ± 49; 10	192 ± 38; 20	416 ± 100; 9
Position of maximum width	9 ± 7; 24	5 ± 6; 10	66 ± 62; 20	30 ± 12; 9
No. proglottids	172 ± 20; 24	123 ± 19; 11	604 ± 124; 21	728 ± 202; 11
Scolex				
Scolex proper length	111 ± 24; 9	345 ± 79; 3	201 ± 45; 14	221 ± 19; 2 (777 ± 88; 6)
Scolex proper width	565 ± 86; 10	1,222 ± 138; 9	670 ± 161; 17	616 ± 84; 3 (748 ± 123; 6)
Acetabulum diameter	112 ± 10; 23; 45	187 ± 14; 11; 22	73 ± 9; 21; 41	103 ± 13; 13; 26
Apical organ length	118 ± 19; 19	273 ± 17; 3	134 ± 16; 13	232 ± 51; 11
Apical organ width	950 ± 250; 13	1,516 ± 121; 10	818 ± 190; 13	976 ± 322; 4
Strobila				
No. immature proglottids	137 ± 30; 24	81 ± 12; 11	510 ± 104; 21	631 ± 199; 9
Immature proglottid length	180 ± 30; 24	238 ± 45; 11	85 ± 18; 21	211 ± 40; 13
Immature proglottid width	192 ± 31; 24	227 ± 32; 11	173 ± 42; 21	403 ± 131; 13
No. mature proglottids	39 ± 12; 24	42 ± 13; 11	86 ± 38; 21	68 ± 30; 10
Mature proglottid length	659 ± 89; 26	831 ± 150; 9	356 ± 70; 20	554 ± 188; 14
Mature proglottid width	226 ± 34; 26	298 ± 53; 9	142 ± 32; 20	410 ± 128; 14
No. testes	12 ± 1; 27; 81	12 ± 1; 10; 30	4 ± 0; 21; 63	14 ± 1; 17; 51
Testes length	32 ± 7; 27; 81	37 ± 9; 10; 30	19 ± 4; 21; 63	51 ± 12; 17; 51
Testes width	38 ± 6; 27; 81	36 ± 6; 10; 30	28 ± 6; 21; 63	61 ± 13; 17; 51
Cirrus sac length	140 ± 16; 26	196 ± 19; 8	74 ± 7; 20	202 ± 41; 14
Cirrus sac width	96 ± 12; 26	128 ± 9; 8	47 ± 6; 20	170 ± 32; 14
Ovary length	131 ± 21; 27	164 ± 27; 9	57 ± 12; 21	284 ± 102; 14
Ovary width	162 ± 25; 27	191 ± 21; 9	96 ± 22; 21	154 ± 42; 14
Genital pore position†	56 ± 6; 26	53 ± 4; 9	68 ± 6; 20	77 ± 4; 14
Vitelline follicle length	32 ± 9; 27; 81	46 ± 12; 9; 27	27 ± 6; 21; 63	35 ± 10; 14; 42
Vitelline follicle width	45 ± 7; 27; 81	48 ± 10; 9; 27	33 ± 7; 21; 63	52 ± 13; 14; 42
Host(s)	*Pristis clavata*	*Pristis microdon*	*Glaucostegus typus*, *Glaucostegus thouin*	*Anoxypristis cuspidata*

***** Measurements are as follows: mean, standard deviation, number of worms examined, and number of total observations made if more than 1 observation was taken per worm. All measurements are in micrometers (µm) except for total length which is reported in millimeters (mm).

† Genital pore position is given as a percentage from posterior margin of prolgottid.

‡ Parenthetical measurements represent those taken on scoleces in which the apical organ is retracted. These measurements, though the more common state observed for *F. variabile* n. comb., are not comparable to those measurements presented for scolex proper length and scolex proper width in other species, but are included for completeness.

Table III. *Floricapitus* species by host species.

Family “Pristidae” sensu Naylor, Caira, Jensen, Rosana, White, and Last (2012)

Anoxypristis cuspidata
- *Floriparicapitus variabilis* (Southwell, 1911) n. comb.

Pristis clavata
- *Floriparicapitus euzeti* n. sp. (type species)

Pristis microdon
- *Floriparicapitus juliani* n. sp.

Pristis pectinata
- *Floriparicapitus* sp. 2

Pristis zijsron
- *Floriparicapitus* sp. 1

Family “Rhinobatidae” sensu Naylor, Caira, Jensen, Rosana, White, and Last (2012)

Glaucostegus thouin
- *Floriparicapitus chordacistus* n. sp.
- *Floriparicapitus* sp. 3

Glaucostegus typus
- *Floriparicapitus chordacistus* n. sp.

Glaucostegus granulatus
- *Floriparicapitus rhinobatidis* (Subhapradha, 1955) n. comb.

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