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Three new genera of trypanorhynch cestodes from Australian elasmobranch fishes

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Abstract

Three new genera of trypanorhynch cestodes from Australian elasmobranch fishes collected in the Arafura Sea, off the Northern Territory, are described. *Fossobothrium perplexum* n. g., n. sp. (Otobothriidae), from the spiral valves of *Anoxypristis cuspidata* (Latham) and *Pristis zijsron* Bleeker, is similar to the otobothriid genera *Pseudotobothrium* Dollfus, 1942 and *Poecilancistrium* Dollfus, 1929 in possessing bothrial pits and a band of hooks on the tentacle, but differs from all known otobothriid genera in having the pits joined by a prominent velum. *Iobothrium elegans* n. g., n. sp. (Otobothriidae), from the spiral valve of *Himantura jenkinsi* (Annandale), is placed in the Otobothriidae because it possesses bothrial pits, but differs from *Otobothrium* Linton, 1890 and other genera in lacking intercalary hooks between the principal rows and in possessing a chainette on the external surface of the tentacle in the metabasal region. *Oncomegoides celatus* n. g., n. sp. (Eutetrarhynchidae), from the spiral valve of *Dasyatis microps* (Annandale) and *Himantura jenkinsi*, resembles *Oncomegas* Dollfus, 1929 in possessing two bothria and a megahook on the bothrial surface of the basal armature, but differs in possessing an extra row consisting of four intercalary hooks formed by the overlapping of two intercalary hooks on the external tentacular surface between each of the opposing principal rows and is therefore an atypical heteroacanth.

Introduction

Australian waters are inhabited by a diverse array of elasmobranch fishes, with the most recent estimates suggesting the presence of 296 species, of which 97 are currently un-named (Last & Stevens, 1994). In addition, more than half of the Australian chondrichthyan fauna is endemic (Last & Stevens, 1994). Studies of their parasite fauna are limited, particularly in the northern Australian region, where species with a broad Indo-West Pacific distribution mix with endemic elements (Beveridge & Jones, 2002). It might therefore be expected that studies of elasmobranchs in this region will reveal diverse and novel parasite taxa. Collections of elasmobranchs in the Arafura Sea off northern Australia undertaken by Dr Kirsten Jensen of the University of Connecticut in 1999 have revealed a significant number of undescribed trypanorhynch genera and species. Here, in an initial contribution to investigating the cestode parasites of the region, three new genera, belonging to the trypanorhynchan cestode families Otobothriidae and Eutetrarhynchidae are described.

Materials and methods

Spiral valves were removed from elasmobranchs, opened with a longitudinal incision, placed in fixative, ususally 10% formalin, and shaken vigorously. In the laboratory, cestodes were removed and stored in 70% ethanol. For study, tentacles were removed from scoleces with a scalpel blade and mounted in glycerine jelly. Strobilae and scoleces were stained in celestine blue, differentiated in acid alcohol, dehydrated in a series of ethanols, cleared in methyl salicylate and mounted in Canada balsam. Where available, mature segments were embedded in paraffin-wax and serially sectioned in transverse and longitudinal planes at a thickness of 5 μm. Sections were stained using haematoxylin and eosin. Drawings were made with a drawing tube attached to an Olympus microscope. Terminology for morphological features follows Dollfus (1942) and Campbell & Beveridge (1994), with the exception that the attachment organs are termed bothria, following Jones et al. (2004). In otobothriid cestodes, the term 'bothrial pit' is used for the invaginations of the bothrial margin containing modified microtriches (Jones, 2000; Jones et al., 2004). Vitelline follicles are shown on the lateral margins of segments only. Measurements are given in micrometres, unless otherwise indicated, with the mean followed, in parentheses, by the range and the number of measurements. Hooks on the antibothrial surface of the tentacle, in rows beginning on the internal surface and terminating on the external surface, were distinguished by Dollfus (1942) from those on the bothrial surface by the addition of a prime to the hook number. In the descriptions which follow below, hook rows may begin on the antibothrial surface and terminate on the bothrial surface. In the former case, the hooks of the external surface are distinguished by a prime. Wherever possible the orientation of the tentacles illustrated is indicated. However, in specimens in which tentacles were detached for examination, it was not possible to identify all surfaces. Specimens have been deposited in the South Australian Museum, Adelaide (SAM), The Natural History Museum, London (BMNH), the United States National Parasite Collection, Beltsville (USNPC) and the Lawrence R. Penner Parasitology Collection, Department of Ecology and Evolutionary Biology, University of Connecticut, Storrs, Connecticut, USA (LRP). Host nomenclature follows Last & Stevens (1994).

Fossobothrium n. g.

Diagnosis

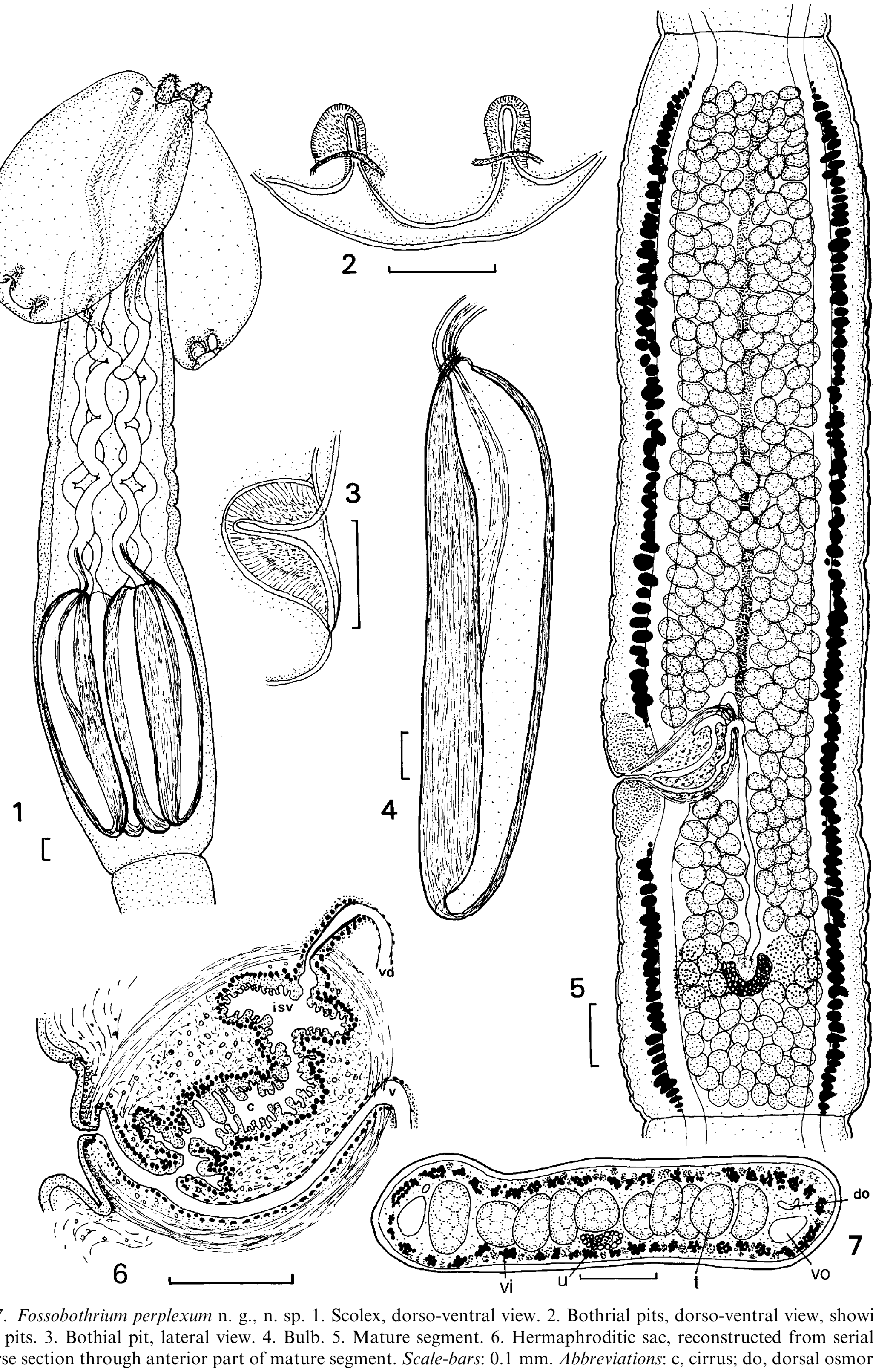
Otobothriidae Dollfus, 1942. Scolex acraspedote; 2 bothria with pits on posterior margin; pits joined by prominent velum. Pars vaginalis longer than pars bothrialis. Bulbs elongate, lacking prebulbar organ and internal gland-cells. Retractor muscle originates in middle of bulb. Tentacles without distinctive basal armature or swelling. Armature heteroacanthous, heteromorphous; hooks hollow. Prominent space separates hook files 1 and 1'. Hook rows begin on bothrial surface of tentacle, terminate on antibothrial surface. Antibothrial surface with band of regularly arranged hooks with 2 rows of band hooks per principal row. Segments longer than wide, acraspedote or very slightly craspedote. Genital pores on lateral margins of segments, alternating irregularly. Testes numerous, pre- and post-ovarian. Hermaphroditic sac present. Internal seminal vesicle present; external seminal vesicle absent. Uterus median, linear without preformed uterine pore. Vitelline follicles circumcortical. Parasitic in sawfishes (Pristidae). Type-species: *F. perplexum* n. sp.

Fossobothrium perplexum n. sp.

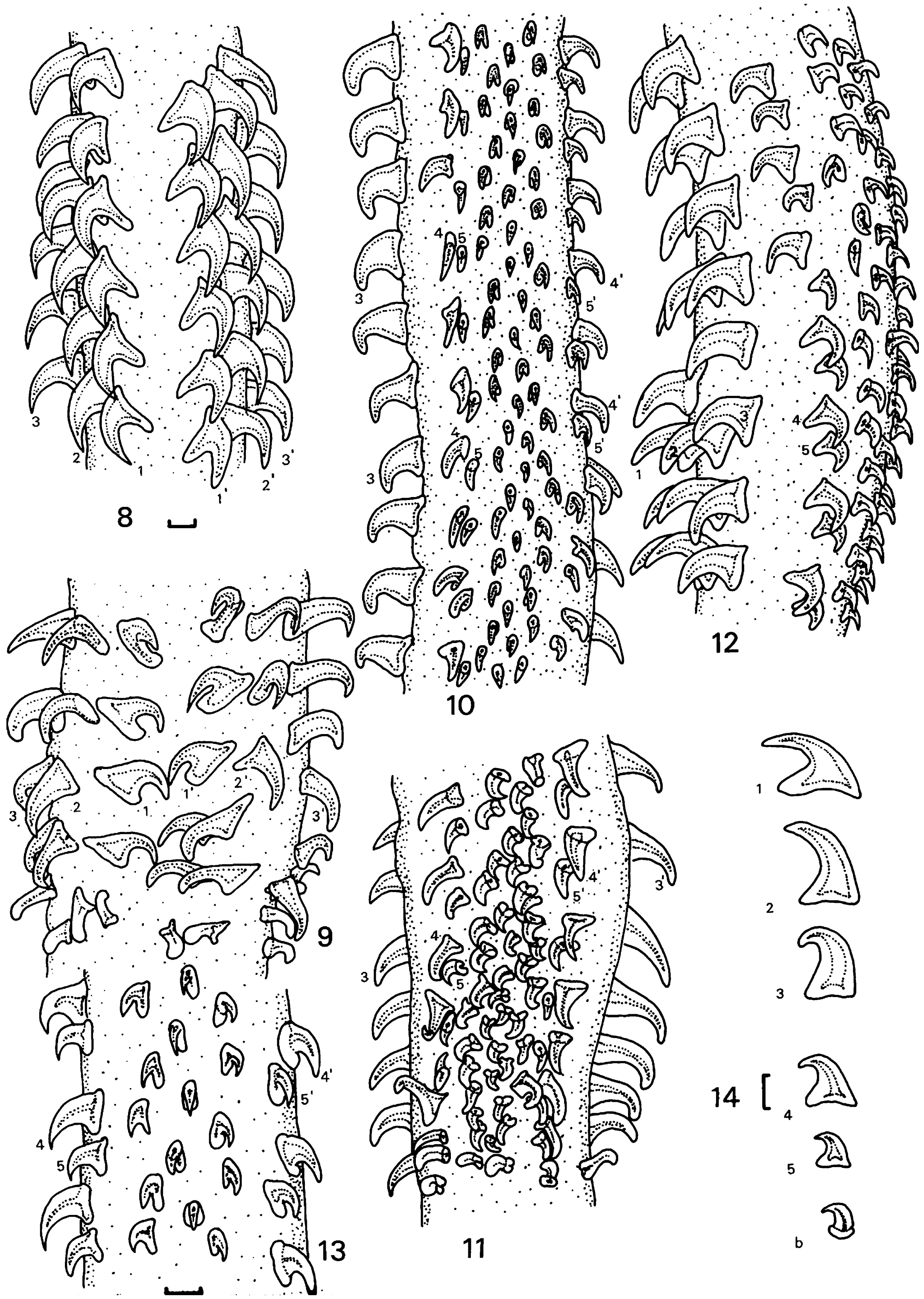
Type-material: Holotype from spiral valve of *Anoxypristis cuspidata* (Latham) (narrow sawfish), Arafura Sea, off Northern Territory, Australia, 14.ix.1999, coll. K. Jensen, SAM 28636; 3 paratypes, same data, SAM 28637–9; serial sections of paratypes SAM 28640; 1 paratype BMNH 2004.7.12.5; 1 paratype USNPC 94895; 1 paratype LRP 3714.
Other specimens examined: 2 specimens from *Pristis zijsron* Bleeker (green sawfish), Balgal, Queensland, Australia, coll. B.G. Robertson, 23.ix.1985, SAM 28641–2; tentacles mounted in glycerine jelly SAM 28643.
Etymology: The generic name alludes to the bothrial pits or fossae. The specific name indicates the unusual morphological arrangement of the pits.

Description (Figures 1–14)

Cestodes 55–107 mm (70, $n = 5$) long. Scolex acraspedote, 2.89–4.67 mm (3.37, $n = 5$) long, maximum width of pars bothrialis scolecis in region of bulbs 0.53–0.72 mm (0.61, $n = 5$). Pars bothrialis 1.18–1.52 mm (1.32, $n = 5$) long; 2 elongate, pyriform bothria with weak margins, wider posteriorly, 0.51–0.95 mm (0.72, $n = 5$) in width; 2 prominent pits present on posterior



Figures 1–7. Fossobothrium perplexum n. g., n. sp. 1. Scolex, dorso-ventral view. 2. Bothrial pits, dorso-ventral view, showing velum joining the pits. 3. Bothial pit, lateral view. 4. Bulb. 5. Mature segment. 6. Hermaphroditic sac, reconstructed from serial sections. 7. Transverse section through anterior part of mature segment. *Scale-bars*: 0.1 mm. *Abbreviations*: c, cirrus; do, dorsal osmoregulatory canal; isv, internal seminal vesicle; t, testis; u, uterus; v, vagina; vi, vitelline follicle; vo, ventral osmoregulatory canal.



Figures 8–14. Fossobothrium perplexum n. g., n. sp. Tentacular armature 8. Metabasal region, bothrial surface. 9. Basal region, bothrial surface. 10. Metabasal region, antibothrial surface. 11. Basal region, antibothrial surface. 12. Metabasal region, internal surface. 13. Metabasal region, antibothrial surface, showing detail of band of hooks. 14. Profiles of hooks 1–5 and band hooks (b). *Scale-bars*: 0.01 mm.

margin of each bothrium, joined by distinctive velum, within posterior margin of bothrium. Pars vaginalis 1.74–2.18 mm (1.97, $n = 5$) long; tentacle sheaths sinuous; bulbs elongate, 0.91–1.13 mm (1.04, $n = 5$) long, 0.17–0.22 (0.20) wide, length/width ratio 1:4.14–5.88 (5.20, $n = 5$); retractor muscle originates in middle of bulb; prebulbar organ absent, ring of muscles encircles entry of sheath into bulb; pars postbulbosa 0.16–0.30 mm (0.22, $n = 5$) long; posterior end of scolex truncate. Tentacles of uniform diameter, without basal swelling or distinctive armature, 60–70 (64, $n = 5$) in basal region, 60–70 (64, $n = 5$) in distal region; extended tentacles up to 1.25 mm long with 55 principal rows of hooks.

Armature heteromorphous, heteroacanthous; hooks hollow, arranged in ascending half rows; rows begin on bothrial surface, terminate on antibothrial surface; distinct space between hooks 1 and 1' on bothrial surface; 5 hooks per principal row, all erect, uncinate. Hooks of basal region similar in shape to those of metabasal region, but smaller and with blunt tips. Metabasal hooks 1(1') 30–55 (47, $n = 10$) long, with elongate base 28–45 (34, $n = 10$); hooks 2(2') longer, 30–40 (36, $n = 10$) long, with slightly shorter base of 23–30 (26, $n = 10$); hooks 3(3') slightly smaller, 25–33 (31, $n = 10$) long, base 23–28 (24, $n = 10$); hooks 4(4'), 5(5') separated from hooks 3(3') by distinct space, arranged in satellite position that is with hooks 4(4') anterior to hooks 5(5'), uncinate; hooks 4(4') 20–28 (25, $n = 10$) long, base 15–18 (16, $n = 10$); hooks 5(5') 13–20 (16, $n = 10$) long, base 10–15 (13). Principal rows separated from band of hooks on antibothrial surface of tentacle; band composed of regularly arranged files of uncinate hooks 10–12 (11, $n = 10$) long, base 5–10 (8, $n = 10$); 2 rows of band hooks present for each principal row, 3–4 files of hooks in band.

Mature segments acraspedote, longer than wide, 1.21–1.95 mm (1.45, $n = 10$) long, 0.40–0.76 mm (0.63, $n = 10$) wide; genital atrium in posterior third of lateral segment margin, 0.37–0.62 mm (0.48, $n = 10$) from posterior end; genital pores alternate irregularly. Tegument around atrium slightly elevated to form projections of lateral margin of segment anterior and posterior to atrium; sub-tegumental tissues around atrium thickened, deeply staining; atrium shallow. Hermaphoditic sac 172–273 (232, $n = 10$) long, 78–156 (140, $n = 10$) wide, extends anteromedially from atrium, almost reaching mid-line of segment; sac lies ventral to osmoregulatory canals. Cirrus unarmed, with thick, highly sinuous wall, extends to crescentic internal seminal vesicle at anterior pole of hermaphoditic sac; lining of vesicle rugose. External seminal vesicle absent; proximal region of vas deferens distal to hermaphroditic sac thick-walled; remainder of vas deferens thin walled, extends anteriorly from proximal pole of hermaphroditic sac, then turns posteriorly. Testes intervascular, 38–82 (59, $n = 10$) long, 20–35 (27, $n = 10$) wide, 345–485 (425, $n = 5$) per segment, confluent posterior to ovary, fill medulla except for region of hermaphroditic sac; testes in single dorso-ventral layer. Vagina joins cirrus within hermaphroditic sac close to genital atrium, runs along internal posterior margin of sac, penetrating wall at proximal pole; proximal vagina sinuous, directed posteriorly. Ovary 4-lobed in transverse section; ovarian lobes ovoid in dorso-ventral view, 101–250 (163, $n = 10$) long, 62–156 (104, $n = 10$) wide; Mehlis' gland 62–140 (110, $n = 10$) in diameter. Uterus median, sinuous, extends to near anterior end of segment; vitelline follicles encircle medulla, distributed between feeble longitudinal muscle bundles; vitelline follicles irregular in shape, maximum diameter 23–78 (35, $n = 10$). Near-gravid segments acraspedote or slightly craspedote, 2.15–3.06 mm (2.43, $n = 5$) long, 0.53–0.71 mm (0.64, $n = 5$) wide; genital pore 0.74–1.15 mm (0.87, $n = 5$) from posterior end of segment. Hermaphroditic sac 250–312 (280, $n = 5$) long, 164–296 (218, $n = 5$) wide; vitelline follicles completely obscure remaining internal organs.

Remarks

Fossobothrium perplexum n. g., n. sp. belongs within the Otobothriidae since it possesses paired pits on the posterior margin of the bothrium. It resembles *Pseudotobothrium dipsacum* (Linton, 1897) and *Poecilancistrium caryophyllum* (Diesing, 1850), the respective type-species of their genera, in lacking a distinctive basal armature and in having a band of hooks on the side of the tentacle at the termination of the principal rows (Beveridge & Campbell, 1996; Beveridge et al., 2000) and differs from *Otobothrium* Linton, 1890, which possesses a single intercalary hook between each principal row, and *Proemotobothrium* Beveridge & Campbell, 2001, which possesses distinct files of hooks on the external surface of the tentacle. It differs from *Poecilacanthum* Palm, 1995 in lacking a chainette composed of triangular elements at the base of the tentacle and from *Diplootobothrium* Chandler, 1942 in possessing only a single set of genitalia per segment. It differs from *Ps. dipsacum* in having only five hooks in each principal row compared with numerous hooks in the latter species and from *Po. caryophyllum* in lacking intercalary hook rows. It also resembles *Ps. arii* (Bilqees & Shaukat, 1976) in that the final files of hooks (4(4') and 5(5')) are separated from the preceeding file (3(3')) and the band of hooks on the antibothrial surface consists of three to four files of hooks (Beveridge et al., 2000). It differs from *Ps. arii* in that there are twice as many rows of hooks on the antibothrial surface as there are on the bothrial surface. *F. perplexum* is also distinctive in the form of the pits on the posterior margins of the bothria. The pits are joined by a distinctive velum internal to the margin of the bothrium, a feature known in no other otobothriid cestode species. Thus, while described from only a very limited number of specimens, the new species is readily distinguishable and adds novel features to the Otobothriidae. An hermaphroditic sac has not been reported previously in other members of the Otobothriidae. This may represent an additional distinguishing feature of the new genus, but a more detailed examination of the terminal genitalia of other otobothriids would be needed before this character could be used with confidence.

Iobothrium n. g.

Diagnosis

Otobothriidae Dollfus, 1942. Scolex acraspedote; 2 bothria with bothrial pits on posterior margin. Pars vaginalis longer than pars bothrialis. Bulbs elongate, lacking prebulbar organ and internal gland cells. Retractor muscle originates in middle of bulb. Tentacles without distinctive basal armature or swelling. Armature poeciloacanthous, heteromorphous; hooks hollow. Prominent space separates hook files 1 and 1'. Hook rows begin on internal surface of tentacle, terminate on external surface; final hook of each principal row distinctive in shape, forming chainette on external surface of tentacle. Segments acraspedote. Parasitic in sting-rays (Dasyatididae). Type-species: *I. elegans* n. sp.

Iobothrium elegans n. sp.

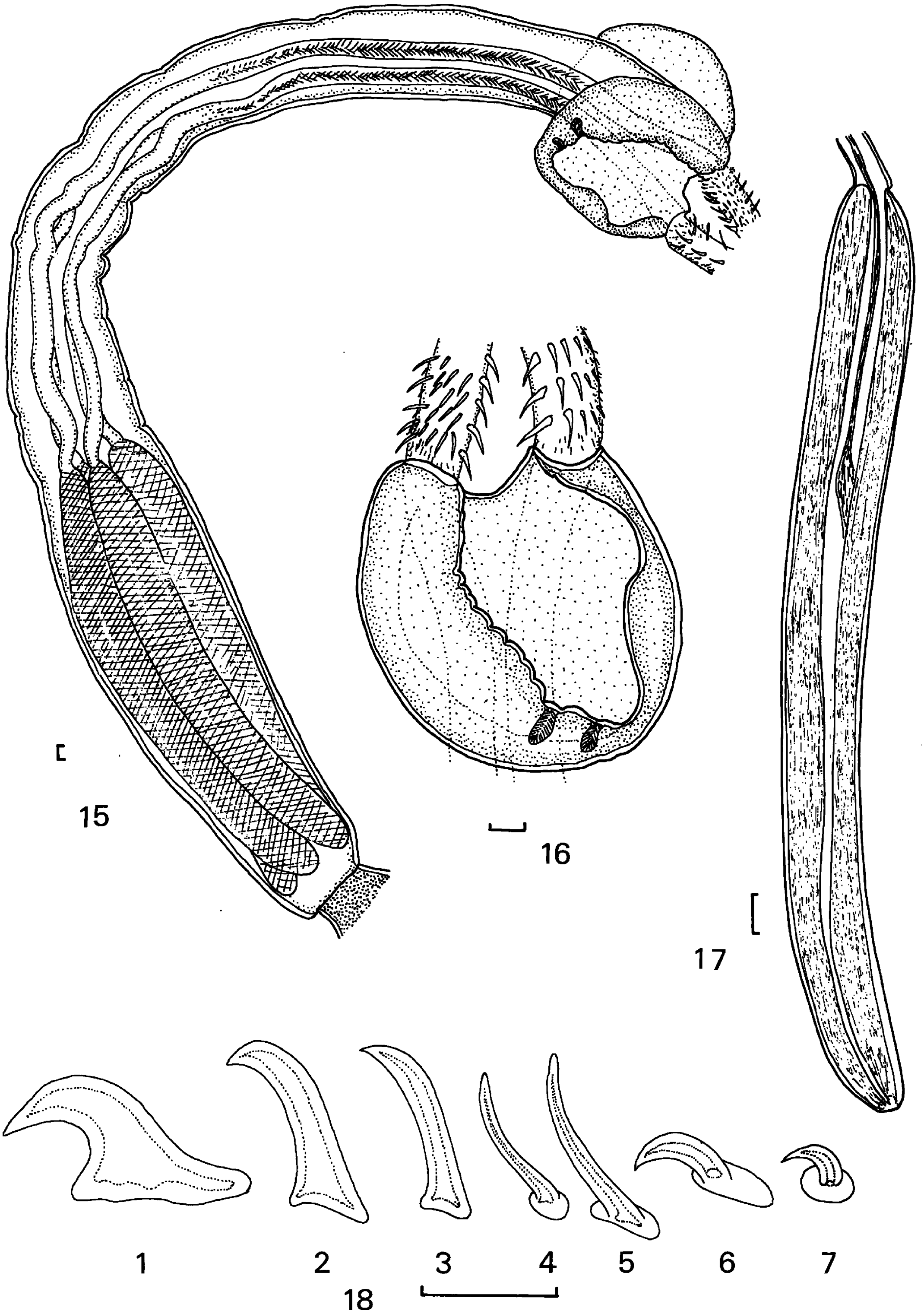
Type-material: Holotype from spiral valve of *Himantura jenkinsi* (Annandale) (Jenkins' whipray), Arafura Sea, off Northern Territory, Australia, 12.ix.1999, coll. K. Jensen, scolex SAM 28634, tentacles in glycerine jelly SAM 28635.

Etymology: The generic name *Iobothrium* is proposed after Io, a classical Greek deity with a singularly unusual history (Stapleton, 1978), and the specific name reflects the worm's perceived elegance.

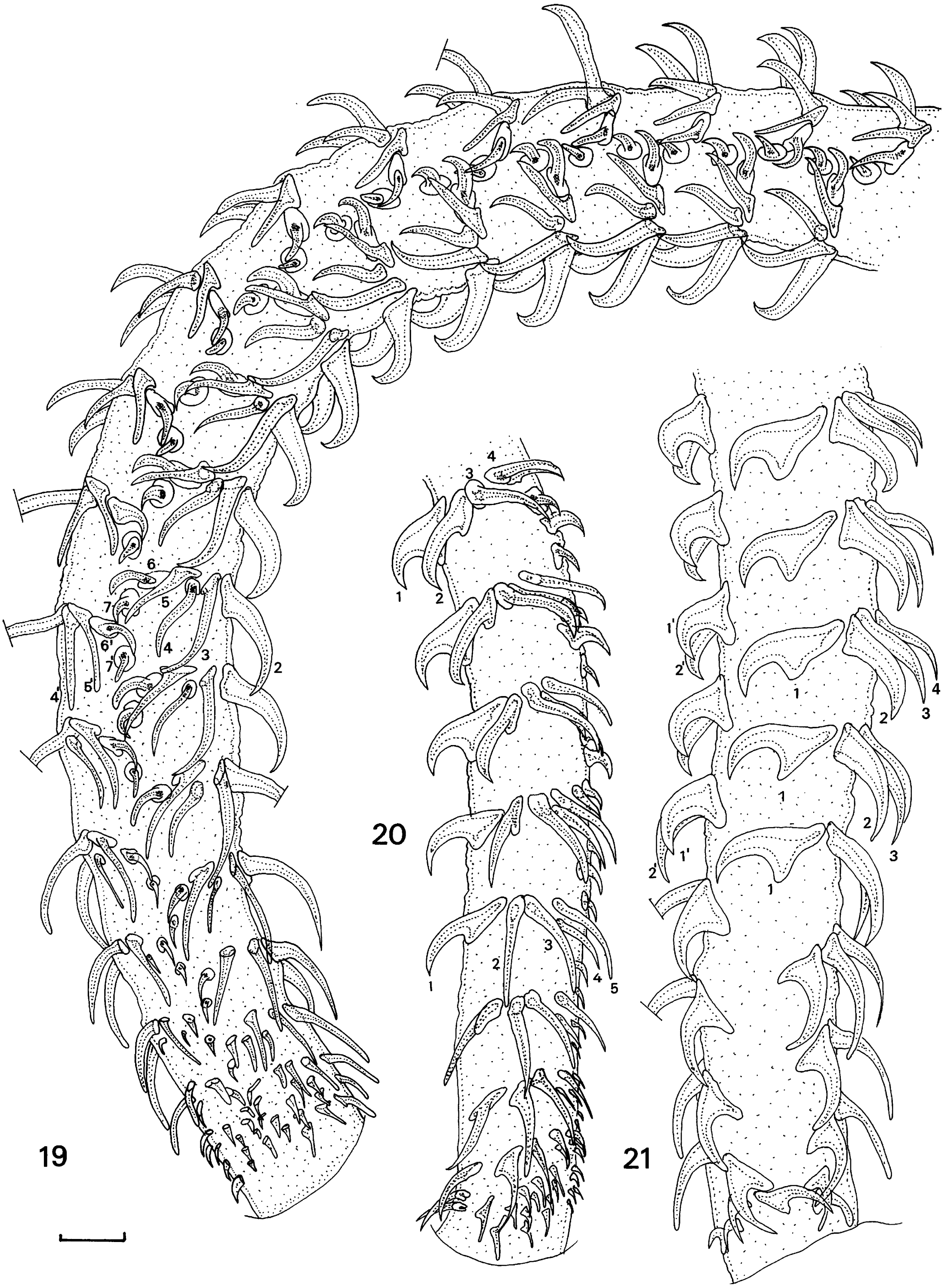
Description (Figures 15–21)

Cestode 17 mm long, with 22 segments. Scolex acraspedote, 7.78 mm long. Pars bothrialis 0.93 long, bothrial width 0.93; pair of large bothrial pits on posterior margin of each bothrium. Pars vaginalis 5.09 mm long, 0.48 mm wide; tentacle sheaths weakly sinuous. Pars bulbosa 0.83 mm wide bulbs; 2.41 mm long, 0.30 mm wide, length/width ratio 1:8.03; prebulbar organ absent; gland-cells absent within bulb; origin of retractor in mid-bulb region; pars postbulbosa 0.20 mm; posterior end of scolex truncate. Everted tentacles up to 3.05 mm long; basal swelling and distinctive basal armature absent; diameter at base 170–200 (190, $n = 4$), diameter in metabasal region 170–200 (190, $n = 4$).

Armature poeciloacanthous, heteromorphous; hooks hollow. Hook rows begin on internal surface of tentacle, terminate on external surface. Hooks of first basal row small, uncinate on internal surface, becoming 3 rows on bothrial and antibothrial surfaces and terminating in array of 4 or 5 rows of small hooks on external surface, merging with simple chainette. Principal rows consist of 7 hooks; prominent space between hooks 1 and 1' on internal surface of tentacle. Hooks 1(1') large, uncinate with elongate base, 137–167 (155, $n = 10$) long, base 84–129 (108, $n = 10$); hooks 2(2') falcate, elongate, 137–171 (148, $n = 10$) long, with narrow base of 49–68 (62, $n = 10$); hooks 3(3') falcate, 118–182 (143, $n = 10$) long, with shorter base 34–46 (41, $n = 10$); hooks 4(4') small, falcate, 84–118 (98, $n = 10$) long, base 19–27 (22, $n = 10$); hooks 5(5') falcate, longer than 4(4') with broader base, 103–148 (116, $n = 10$) long, base 38–49 (42, $n = 10$); hooks 6(6') shorter, more robust with prominently elongate base, 80–114 (97, $n = 10$) long, base 53–76 (68, $n = 10$); hooks 7(7') with



Figures 15–18. *Iobothrium elegans* n. g., n. sp. 15. Scolex of holotype. 16. Bothrium of holotype showing bothrial pits on posterior margin. 17. Bulb. 18. Profiles of tentacular hooks 1–7. *Scale-bars*: 0.1 mm.



Figures 19–21. Iobothrium elegans n. g., n. sp. Tentacular armature. 19. Basal and metabasal regions, external surface. 20. Basal and metabasal regions, bothrial surface. 21. Basal and metabasal regions, internal surface. *Scale-bar*: 0.1 mm.

short blade and circular base, 46–53 (40, $n = 10$) long, diameter of base 30–42 (38, $n = 10$); hooks 7(7') form single file or chainette on external surface of tentacle.

Terminal segment immature 780 long, 800 wide; testes numerous, filling entire medulla, in single dorso-ventral layer.

Remarks

The new genus has been erected based on a single immature specimen. This action would not be warranted but for the fact that a complete description of the armature can be given and that the armature pattern itself is original and cannot be confused with any known existing genus or species. For this reason, it appears desirable to describe and name the cestode.

The cestode described above belongs to the Otobothriidae, since it possesses paired pits at the posterior margin of each bothrium. Of the known genera within this family, *Otobothrium* Linton, 1890 is characterised by an atypical heteroacanthous armature, with a single intercalary row of one or two hooks on the external surface of the tentacle (Campbell & Beveridge, 1994) compared with the lack of intercalary rows in the present species. *Proemotobothrium* Beveridge & Campbell, 2001 was characterised by a single intercalary hook associated with each principal row but with the hooks on the external surface arranged in two files. *Poecilancistrium* Dollfus, 1929 has a band of hooks on the external surface of the tentacle as well as intercalary rows of hooks (Campbell & Beveridge, 1994) while *Pseudotobothrium* Dollfus, 1942 exhibits a band of hooks without any intercalary rows (Beveridge et al., 2000). *Poecilacanthum* Palm, 1995 possesses a chainette of winged elements in the basal region of the tentacle, but the metabasal armature of this genus is not known (Palm, 1995).

The armature of the species described here is open to two possible interpretations. The simplest is that the armature is typical heteroacanthous in form with a single row of seven hooks and no intercalary hook rows or bands on the external surface of the tentacle. A typical heteroacanthous pattern of armature within the Otobothriidae is novel and would warrant recognition at the generic level. Alternatively, the file formed by hooks 7(7') on the external surface of the tentacle could be considered a chainette. Beveridge & Campbell (1989, p. 221) used as their definition of a chainette a file of hooks on the external surface of the tentacle contributed by but separated from the principal rows. Also implied in their definition was that the chainette hooks differed in shape from those of the principal rows. In the current case, the file of hooks on the external surface of the tentacle is contributed by each principal row and they are distinctive in shape, but are not separated from the principal rows. They do, however, form a distinctive file on the external surface of the tentacle and have therefore been designated a chainette. If the file of hooks is designated a chainette, the new species still differs from all other members of the family. The available information on *Poeciloacanthum* is limited, but it possesses a winged chainette in the basal region of the tentacle. *Iobothrium* n. g. differs in not having a distinctive basal armature and in having chainette elements which are not alate. The chainette elements with an almost circular base are similar to those found in *Pterobothrioides carvajali* Campbell & Beveridge, 1997. However the armature is interpreted, a new genus is considered warranted for this unusual cestode.

Oncomegoides n. g.

Diagnosis

Eutetrarhynchidae Guiart, 1927. Scolex acraspedote; 2 bothria. Pars vaginalis slightly shorter than pars bothrialis. Bulbs elongate, with prebulbar organ and internal gland cells. Retractor muscle originates at posterior end of bulb. Tentacles with distinctive basal armature or swelling; swelling with megahook on bothrial surface. Armature heteroacanthous, heteromorphous; hooks hollow. Prominent space separates hook files 1 and 1'. Hook rows begin on antibothrial surface of tentacle, terminate on bothrial surface; single row of intercalary hooks between each principal row. Hooks of principal rows largest on antibothrial surface, diminish in size towards bothrial surface. Segments acraspedote. Genital pores marginal, alternate irregularly; testes pre-ovarian arranged in 2 columns. Parasitic in stingrays (Dasyatididae). Type-species: *O. celatus* n. sp.

Oncomegoides celatus n. sp.

Type-material: Holotype from spiral valve of *Dasyatis microps* (Annandale), Arafura Sea, off Northern Territory, Australia, coll. K. Jensen, 20 ix.1999, SAM 28644; paratypes, same data, 23 specimens SAM 28645, 5 specimens BMNH 2004.7.12.6, 5 specimens USNPC 94896, 10 specimens LPP 3715–6.
Additional material examined: 3 specimens from spiral valve of *Himantura jenkinsi*, Arafura Sea, off Northern Territory, Australia, coll. J. Caira, 12 ix.1999, SAM 28648.
Etymology: The generic name *Oncomegoides* alludes to close similarities with *Oncomegas* and the specifc name 'celatus', Latin for concealed.

Description (Figures 22–30)

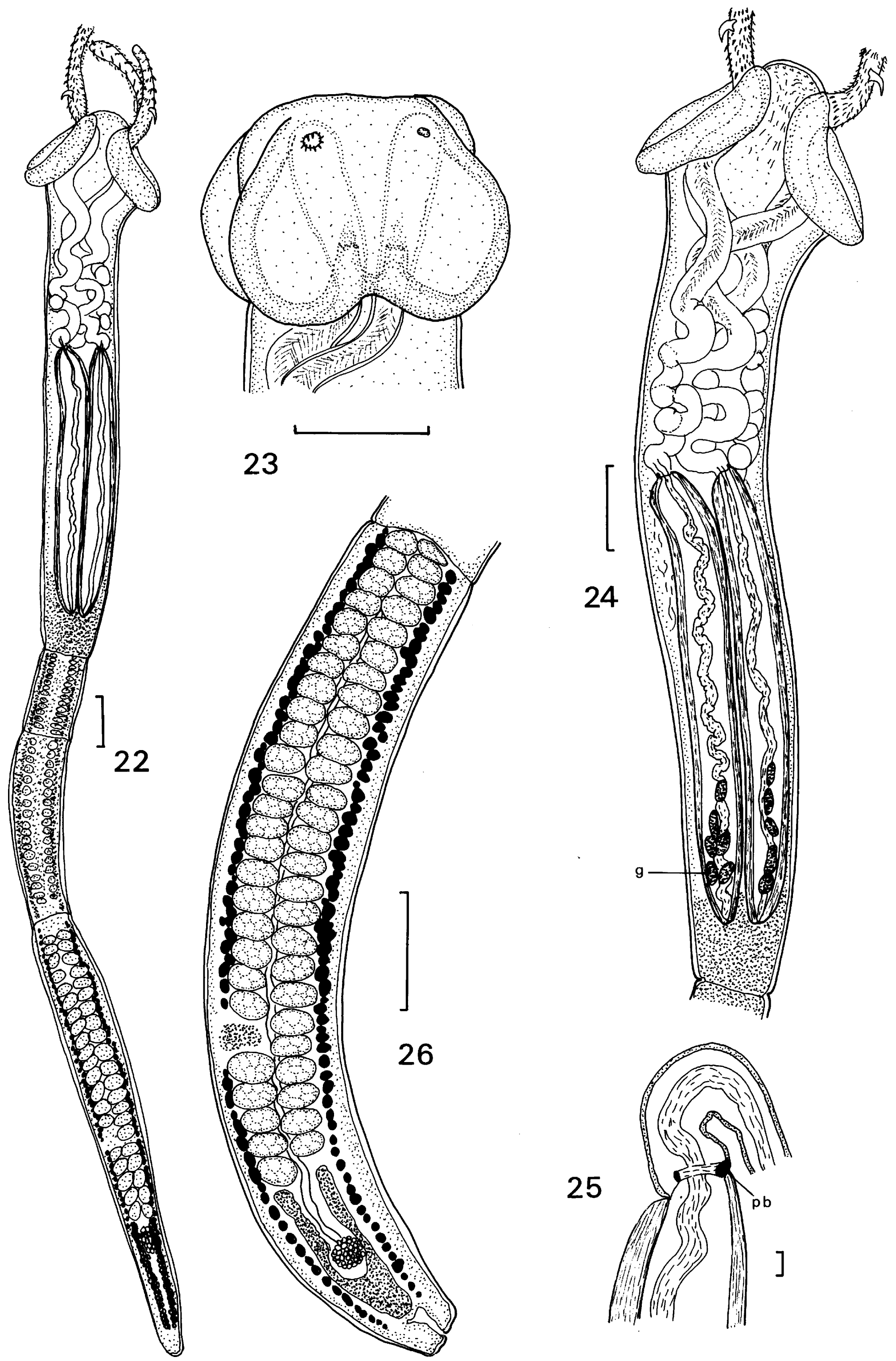
Small cestodes, mature specimens 1.87–2.78 mm (2.45, $n = 10$) long, with 3–5 (4, $n = 10$) segments. Scolex acraspedote, 780–1,100 (990, $n = 10$) long. Pars bothrialis 156–195 (168, $n = 10$) long; 2 cordiform bothria with slight indentation of posterior margin and median, bifid anterior projection subdividing posterior part of bothrium; width of bothrium 164–203 (187, $n = 5$). Pars vaginalis 328–452 (398, $n = 10$) long, width 140–180 (160, $n = 10$); sheaths sinuous. Bulbs 421–608 (463, $n = 10$) long, 47–70 (58, $n = 10$) wide, length/width ratio 1:9.3 (6.0–11.8, $n = 10$); prebulbar organ small, not visible in every specimen; few gland-cells within bulb, close to origin of retractor at base of bulb. Tentacles with prominent basal swelling and basal armature; diameter of tentacle at base 20–38 (30, $n = 10$), diameter in metabasal region 18–25 (21, $n = 10$).

Armature heteroacanthous, heteromorphous; hooks hollow. Initial rows of hooks on base uncinate, 10–13 (11, $n = 5$) long, base 6–10 (8, $n = 5$); on antibothrial side, hook rows 5–8 spiniform, 6–9 (8, $n = 5$) long, base 2–4 (3, $n = 5$); triangular array of closely packed uncinate hooks anterior to rows of spiniform hooks; array with *c.*9 hooks at base, diminishing to single hook at apex in middle of antibothrial surface; hooks of array 6–9 (8, $n = 5$) long, base 4–7 (6, $n = 5$). Ascending principal hook rows begin on antibothrial surface anterior to array. On bothrial surface, first 5 rows of hooks uncinate; single megahook in mid-line of bothrial surface, 20–25 (24, $n = 10$) long, base 10–18 (14, $n = 10$); anterior to megahook, hooks small, uncinate, arranged in *c.*6 ascending rows, meeting in mid-line of bothrial surface. Metabasal armature consisting of principal rows of 5 hooks beginning on antibothrial surface, terminating on bothrial surface; distinct space between hook files 1 and 1'. Hooks 1(1') large uncinate with elongate base, 16–21 (19, $n = 5$) long, base 15–20 (17, $n = 5$); hooks 2(2') uncinate, as long as hooks 1(1') but with slightly smaller base, 15–22 (19, $n = 5$) long, base 11–14 (13, $n = 5$); hooks 3(3'), elongate, falcate with narrow base, 18–24 (21, $n = 5$) long, base 6–11 (8, $n = 5$); hooks 4(4') falcate, smaller, 16–20 (18, $n = 5$) long, base 5–8 (6, $n = 5$); hooks 5(5') falcate smaller, 9–14 (12, $n = 5$) long, base 4–6 (5, $n = 5$). Two spiniform intercalary hooks (a(a'), b(b')) between each principal row; first intercalary hook posterior to hook 5, 5–8 (6, $n = 5$) long, base 2–5 (3, $n = 5$).

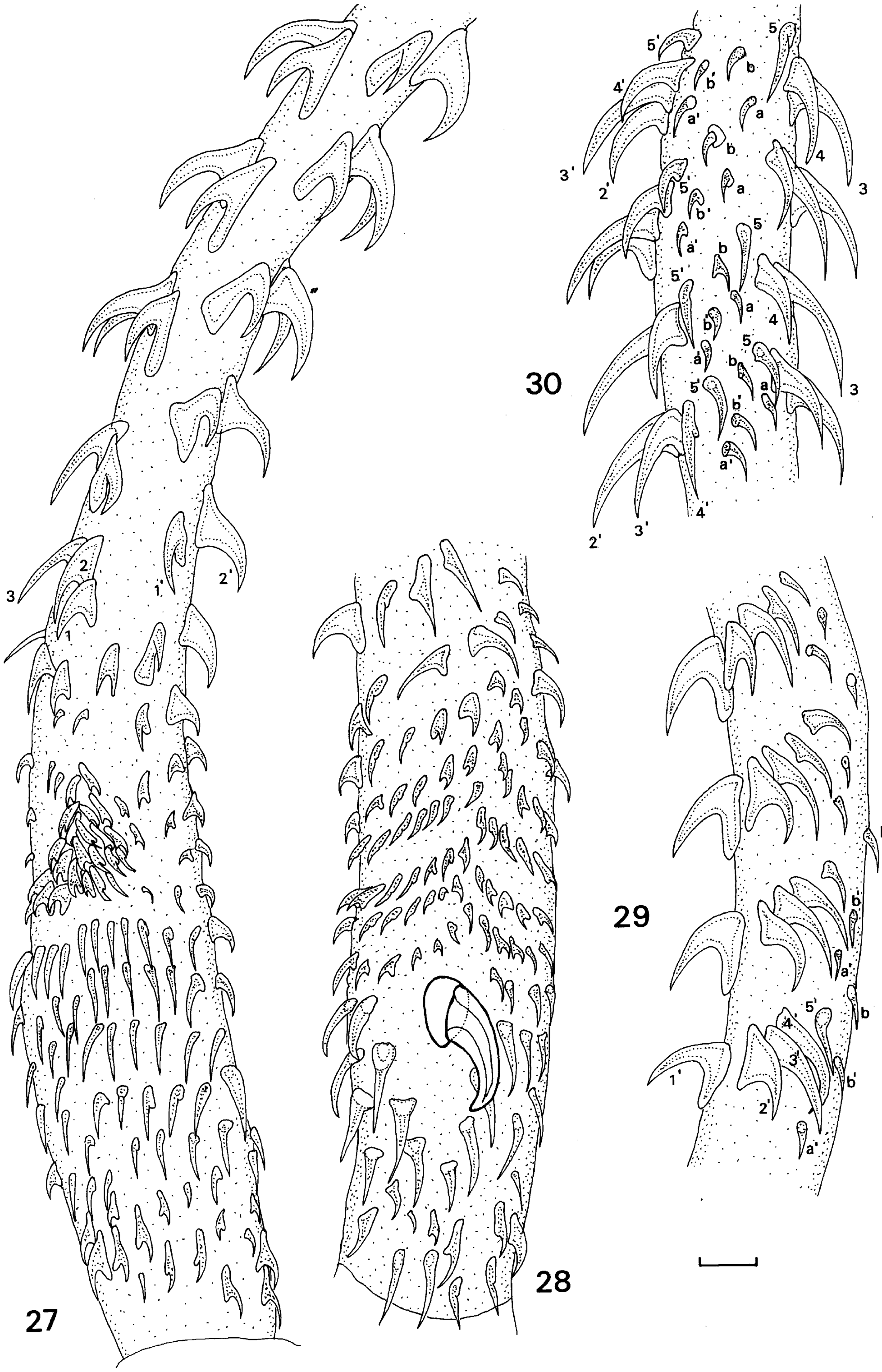
Pre-mature segments acraspedote, 647–1225 (842, $n = 5$) long, 117–140 (125, $n = 5$) wide; genital pores alternate irregularly, 234–484 (343, $n = 5$) from posterior end. Cirrus-sac not developed. Testes arranged in 2 columns; testes 35–59 (44, $n = 10$) long, 20–39 (26, $n = 10$) wide; number of testes per segment 39–53 (48, $n = 5$); 3–4 (4, $n = 5$) testes post-vaginal, 16–23 (19, $n = 5$) prevaginal, 20–27 (25, $n = 5$) antiporal; testes pre-ovarian. Ovarian lobes 133–273 (179, $n = 5$) long, 20–27 (24, $n = 5$) wide; Mehlis' gland between ovarian lobes, 27–35 (30, $n = 5$) in diameter; vitelline follicles encircle medulla, 8–23 (14, $n = 10$) in diameter. Gravid segments not present.

Remarks

The species described above is placed in the Eutetrarhynchidae, since it possesses two bothria, elongate bulbs, a prebulbar organ and gland-cells associated with the retractor muscle within the bulb, albeit in a reduced state. The latter characteristics were identified as being significant phylogenetically in the cladistic study of the order conducted by Beveridge et al. (1999). The presence of a megahook in the basal armature indicates close similarities with *Oncomegas* Dollfus, 1929 and *Paroncomegas* Campbell, Marques & Ivanov, 1999, the latter genus differing in the possession of a basal chainette. The species described in this paper differs from both of these genera in having highly heteromorphous hooks in the metabasal



Figures 22–26. *Oncomegoides celatus* n. g., n. sp. 22. Entire worm. 23. Bothria, dorso-ventral view. 24. Scolex, lateral view. 25. Anterior end of bulb showing prebulbar organ. 26. Pre-mature segment. *Scale-bars*: 22–24, 26, 0.1 mm; 25, 0.01 mm. *Abbreviations*: g, gland-cell; pb, prebulbar organ.



Figures 27–30. Oncomegoides celatus n. g., n. sp. Tentacular armature. 27. Basal and metabasal regions, antibothrial surface. 28. Basal region, bothrial surface. 29. Metabasal region, external surface. 30. Metabasal region, bothrial surface. *Scale-bars*: 0.01 mm.

armature, with rows originating on the antibothrial surface of the tentacle and terminating on the bothrial surface and with an intercalary row consisting of two hooks. An alternative explanation for the arrangement observed in the hook pattern could be that the intercalary hooks here designate a(a') and b(b') may represent hooks 6(6') and 7(7') separated by a space from the principal row. However, the latter interpretation would require that the hook row changes direction abruptly after hooks 5(5') and that the axis of the row becomes almost parallel with the axis of the tentacle. Instances of a sharp change in orientation of the hook row are not known within the trypanorhynchs and therefore the former explanation of an intercalary row of two hooks is preferred. Additional features which separates the species described above from *Oncomegas* are the separation of hook files 1 and 1' on the antibothridial surface of the tentacle and the gradual diminution of hook size along the row in *Oncomegoides celatus* n. g., n. sp. In species of *Oncomegas*, hook files 1 and 1' are not separated and hooks 1(1') are small with either an increase and a decrease in hook size along the row, as occurs in *Prochristianella* Dollfus, 1946, or hooks remaining similar in size along the row, as occurs in most species of *Dollfusiella* Campbell & Beveridge, 1994 (see Campbell & Beveridge, 1994). The triangular array of hooks on the base of the bothridial surface of the tentacle of *Oncomegoides celatus* also distinguishes the cestode from all species of *Oncomegas* (see Toth et al., 1992). In their descriptions of species of *Oncomegas*, Toth et al. (1992) described the bothria as having, on their adherent surface, a V-shaped ridge almost completely subdividing the bothrium. In *Oncomegoides celatus*, the ridge is incomplete, but its origins are clearly evident. Toth et al. (1992) described the hook rows of species of *Oncomegas* as originating on the internal surface of the tentacle. However, their illustrations of scoleces (Figures 12, 28, 46) suggest that the hook rows begin on the antibothrial surface of the tentacle, as described in *Oncomegoides celatus*.

This is the first instance in which a trypanorhynch cestode with a single megahook in the basal armature has been associated with an atypical armature in the metabasal region and as a consequence, a new genus has been erected for it. Additional characters such as the separation of hooks 1 and 1' on the antibothrial surface of the tentacle, the gradual reduction in hook size along the rows of principal hooks and the original arrangement of hooks on the bothrial surface of the base of the tentacle also indicate significant differences from the species of *Oncomegas*. The intercalary hook rows clearly differentiate the new genus from pre-existing genera. The inclusion of a cestode with an atypical armature within the Eutetrarhynchidae is not novel. Beveridge et al. (2004) presented evidence for the inclusion of *Progrillotia* Dollfus, 1946 in the Eutetrarhynchidae, even though it possesses a single row of intercalary hooks between each principal row. The addition of *Oncomegoides* to the Eutetrarhynchidae further supports the expanded definition of the family necessitated by the addition of *Paroncomegas* (with a chainette) and *Progrillotia* (with an intercalary row of hooks).

Discussion

Since the review of the genera of trypanorhynch cestodes of Campbell & Beveridge (1994), a number of new genera have been described which have expanded the variety of armature types known from the families Otobothriidae and Eutetrarhynchidae (*sensu* Campbell & Beveridge, 1994). In the Otobothriidae, delineated primarily by the possession of bothrial pits, Campbell & Beveridge (1994) recognised the genera *Diplootobothrium* Chandler, 1942 characterised by two sets of genitalia, *Otobothrium* Linton, 1890 characterised by an armature with a single intercalary hook row and *Poecilancistrium* Dollfus, 1929 with a band of hooks on the external surface of the tentacle. Subsequent redescriptions of *Pseudotobothrium dipsacum* (Linton, 1897) by Palm (1995) and Beveridge et al. (2000) elevated *Pseudotobothrium* Dollfus, 1942 from subgeneric to generic rank, based on the feature that there were no additional hook rows on the bothrial surface of the tentacle, a feature distinct from other genera of the Otobothriidae. Palm (1995) also erected *Poeciloacanthum* based on a plerocercus in which a chainette was present in the basal armature. The metabasal armature however remains unknown. Beveridge & Campbell (2001) erected *Proemotobothrium*, in which there was a single intercalary hook associated with each principal row, but the hooks of the external surface of the tentacle were arranged in tandem.

The two genera of the Otobothriidae described here considerably expand the range of morphological features exhibited within the family. *Fossobothrium* n. g. has an armature which resembles that of *Pseudotobothrium*, but differs from all other genera of the family in having the bothrial pits, on the posterior margin of the bothrium, joined by a distinctive velum. *Iobothrium* n. g., characterised by a chainette but lacking a distinctive basal armature, adds yet another distinctive armature type to the family. As additional genera with novel morphological features are added to the family, its definition changes, but the final definition and hence relationship with related families becomes more difficult to discern.

Similarly, the Eutetrarhynchidae was characterised by Campbell & Beveridge (1994) as a family with two bothria and a typical heteroacanthous armature. Since then, Campbell et al. (1999) have erected *Paroncomegas,* which posseses a chainette in the basal region of the armature and Beveridge et al. (2004) have provided evidence for the inclusion of *Progrillotia* Dollfus, 1946, with an atypical heteroacanthous metabasal armature, within the family. *Oncomegoides* n. g. adds an additional variation in tentacular armature in providing the first example of a eutetrarhynchid with a megahook in the basal region of the tentacle, exhibiting an atypical armature in the metabasal region, and contrasting with *Oncomegas* in which the metabasal armature is typical heteroacanthous (Toth et al., 1992).

The continuing discovery of novel forms or armature within currently defined families of trypanorhynch cestodes suggests that many additional forms await discovery and that attempts to define major taxonomic groupings within the Trypanorhyncha may be premature.

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References

Beveridge, I. & Campbell, R.A. (1989) *Chimaerarhynchus* n. g. and *Patellobothrium* n. g., two new genera of trypanorhynch cestodes with unique poeciloacanthous armatures, and a reorganisation of the poeciloacanthous trypanorhynch families. *Systematic Parasitology*, **14**, 209–225.

Beveridge, I. & Campbell, R.A. (1996) New records and descriptions of trypanorhynch cestodes from Australian fishes. *Records of the South Australian Museum*, **29**, 1–22.

Beveridge, I. & Campbell, R.A. (2001) *Proemotobothrium* n. g. (Cestoda: Trypanorhyncha), with the resdescription of *P. linstowi* (Southwell, 1912) n. comb. and description of *P. southwelli* n. sp. *Systematic Parasitology*, **48**, 223–233.

Beveridge, I., Campbell, R.A. & Jones, M.K. (2000) New records of the cestode genus *Pseudotobothrium* (Trypanorhyncha: Otobothriidae) from Australian fishes. *Transactions of the Royal Society of South Australia*, **124**, 151–162.

Beveridge, I., Campbell, R.A. & Palm, H. (1999) Preliminary cladistic analysis of genera of the cestode order Trypanorhyncha Diesing, 1863. *Systematic Parasitology*, **42**, 29–49.

Beveridge, I. & Jones, M.K. (2002) Diversity and biogeographical relationships of the Australian cestode fauna. *International Journal for Parasitology*, **32**, 343–351.

Beveridge, I., Neifar, L. & Euzet, L. (2004) Review of the genus *Progrillotia* Dollfus, 1946 (Cestoda: Trypanorhyncha), with a redescription of *Progrillotia pastinacae* Dollfus, 1946 and description of *P. dasyatidis* sp. n. *Folia Parasitologica*, **51**, 33–44.

Campbell, R.A. & Beveridge, I. (1994) Order Trypanorhyncha Diesing, 1863. *In*: Khalil, L.F., Jones, A. & Bray, R.A. (Eds) *Keys to the cestode parasites of vertebrates*. Wallingford: Commonwealth Agricultural Bureaux International, pp. 51–148.

Campbell, R.A., Marques, F. & Ivanov. V.A. (1999) *Paroncomegas araya* (Woodland, 1934) n. gen. et comb. (Cestoda: Trypanorhyncha: Eutetrarhynchidae) from the freshwater stingray *Pomatotrygon motoro* in South America. *Journal of Parasitology*, **85**, 313–320.

Dollfus, R.-P. (1942) Etudes critiques sur les Tétrarhynques du Muséum de Paris. *Archives du Muséum National d'Histoire Naturelle*, Paris, **19**, 1–466.

Jones, M.K. (2000) Ultrastructure of the scolex, rhyncheal system and bothridial pits of *Otobothrium mugilis* (Cestoda: Trypanorhyncha). *Folia Parasitologica*, **47**, 29–38.

Jones, M.K., Beveridge, I., Campbell, R.A. & Palm, H. (2004) Terminology of the sucker-like organs of the scolex of trypanorhynch cestodes. *Systematic Parasitology*, **59**, 121–126.

Last, P.R. & Stevens, J.D. (1994) *Sharks and rays of Australia*. Australia: C.S.I.R.O., 513 pp.

Palm, H. (1995) Untersuchungen zur Systematik von Rüsselbandwürmen (Cestoda: Trypanorhyncha) aus atlantischen Fischen. *Berichte aus dem Institut für Meereskunde an der Christian Albrechts Universität, Kiel*, **275**, 1–238.

Stapleton, M. (1978) *A dictionary of Greek and Roman mythology*. New York: Bell Publishing Company, 224 pp.

Toth, L.M., Campbell, R.A. & Schmidt, G.D. (1992) A revision of *Oncomegas* Dollfus, 1929 (Cestoda: Trypanorhyncha: Eutetrarhynchidae), the description of two new species and comments on its classification. *Systematic Parasitology*, **22**, 167–187.