***Pristiorhynchus palmi* n. g., n. sp. (Cestoda: Trypanorhyncha) from sawfishes (Pristidae) off Australia, with redescrptions and new records of six species of the Obothrioidea Dollfus, 1942**

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Abstract A new genus of trypanorhynch cestodes, *Pristiorhynchus* n. g. (Obothrioidea: Obothriidae), is described from two species of modern sawfishes (Pristidae) from off northern Australia. *Pristiorhynchus palmi* n. g., n. sp. is characterised by an acraspedote scolex with two bothria, paired bothrial pits on the posterior margins of each bothrium, the absence of gland-cells within the bulbs and prebulbar organs, a retractor muscle inserting at the posterior region of the elongate bulbs, a characteristic basal tentacular armature with dispersed billhooks and a heteroacanthous atypical metabasal armature with five principle and three intercalary hooks. Furthermore, redescrptions are provided for *Symbothriorhynchus tigaminacantha* Palm, 2004, *Parotobothrium balli* (Southwell, 1929) and *Pseudotobothrium arii* (Bilqees & Shaukat, 1976). Observations of adult worms revealed novel information on the segment morphology, which has not been described for these three species. Specimens of *Proemotobothrium linstowi* (Southwell, 1924), *Pr. southwelli* Beveridge & Campbell, 2001 and *Fossobothrium perplexum* Beveridge & Campbell, 2005 collected from elasmobranchs from several sampling localities off Australia revealed additional information on host range and geographical distribution.

Introduction

Originally, the superfamily Obothrioidea Dollfus, 1942 combined species with an atypical heteroacanthous armature and a scolex with two bothria and paired bothrial pits on the bothrial margins [as ‘Hétéracanthes atypica’, *sensu* Dollfus (1942)]. In later taxonomic treatments of trypanorhynch cestodes (Campbell & Beveridge, 1994; Palm, 1995), the main focus changed from either oncotaxy (Campbell & Beveridge, 1994) or the presence of bothrial pits (Palm, 1995) as defining features for the superfamily. The Obothrioidea, as defined by Palm (2004), is composed of the families Paranybeliniidae Schmidt, 1970, Pseudotobothriidae Dollfus, 1942 (originally a subgenus) and Obothriidae Dollfus, 1942, which are united by the possession of bothrial pits. However, some obothrioids either lack bothrial pits [*Ancipirhynchus afossalis* Schaeffner, Gasser & Beveridge, 2011 and *Obothrium curtum* (Linton, 1909); see Schaeffner et al. (2011) and Beveridge & Justine (2007)] or have pits in a reduced state [*Symbothriorhynchus tigaminacantha* Palm, 2004; see Palm (2004)]. The most recent rearrangement of families in the Obothrioidea applied a combination of both the presence of bothrial pits and microthrix shapes on different scolex parts (see Palm, 2008), which allocated the Paranybeliniidae to the Tentacularioidea Poche, 1926. In a molecular phylogenetic study of the Trypanorhyncha (Olson et al., 2010), the bothrial pits were identified as a morphological synapomorphy for the Obothrioidea, although none of the species currently allocated to the superfamily which lack this feature was included in this study. As a consequence, the morphological features defining the Obothrioidea remain unclear. In this paper, we describe a new obothriid genus and redescribe a number of obothrioid species with the expectation that additionally detailed studies of the morphology of these cestodes may eventually provide a reliable morphological basis for defining the genera and families of this superfamily. At present, species of the Pseudotobothriidae have been described solely based on larval stages and, due to the absence of adult worms, knowledge of the segment morphology is lacking. Redescriptions with particular emphasis on the segment morphology are provided for *Parotobothrium balli* (Southwell, 1929) and *Pseudotobothrium arii* (Bilqees & Shaukat, 1976), providing novel information for this family. Moreover, we provide a redescription of *S. tigaminacantha*, a species for which adult specimens were previously unknown. New host and geographical records are added for both species of *Proemotobothrium* Beveridge & Campbell, 2001 and for the monotypic genus *Fossobothrium* Beveridge & Campbell, 2005.

Materials and methods

Specimens were collected from several sampling localities off Australia, Malaysia and New Caledonia. Australian sampling localities were: the Arafura Sea off Weipa, Queensland (12°35'S, 141°42'E); off the Wessel Islands (eastern part), Northern Territory (11°17'S, 136°59'E); the Coral Sea off Balgal (18°59'S, 146°27'E); off Heron Island, Queensland (23°26'S, 151°54'E); the Indian Ocean off Geraldton (28°46'S, 114°36'E) and in Nickol Bay (20°42'S, 116°51'E), Western Australia; the Timor Sea near Darwin (Buffalo Creek), Northern Territory (12°20'S, 130°54'E); and Tommy Cut Creek, Northern Territory (12°16'S, 131°42'E). Sampling localities in Malaysian waters were as follows: the South China Sea off Mukah, Sarawak (02°53'N, 112°05'E) and Sematan, Sarawak (01°48'N, 109°46'E). Sampling off New Caledonia was conducted in the Coral Sea off Nouméa (22°40'S, 165°58'E). Most cestodes were fixed in 10% formalin for morphological observations and later transferred into 70% ethanol. Other specimens were provided by colleagues and the fixation methods used are not known. All specimens were stained with Celestine Blue. For morphological observation they were processed as described in Schaeffner et al. (2011). Selected mature segments were embedded in paraffin for serial histological sections, cut in the longitudinal plane and stained with haematoxylin and eosin. Line drawings were made using an Olympus BH-2 microscope with a drawing attachment and differential interference contrast optics. Measurements are in micrometres (μm), unless otherwise indicated, and are given as the range followed in parentheses by the mean, standard deviation and the number of specimens measured. For two-dimensional measurements, length is given before breadth. Specimens selected for scanning electron microscopy (SEM) were dehydrated, placed in hexamethyldisilazane (HMDS) and allowed to air dry. They were mounted on stubs and coated with gold. Scanning electron micrographs were taken using a Hitachi S-570 scanning electron microscope (Hitachi Ltd) with Spectrum V.3.0 software (Dindima Group Pty Ltd). Vitelline follicles are shown on the lateral margins of segments only, unless otherwise indicated. Morphological characteristics used for the description follow the terminology of Pintner (1913), Dollfus (1942) and Campbell & Beveridge (1994). Microthrix terminology follows Chervy (2009). Specimens have been deposited in the Lawrence R. Penner Parasitology Collection, Department of Ecology and Evolutionary Biology, University of Connecticut, Storrs, Connecticut, USA (LRP), the Natural History Museum, London, UK (BMNH), the Muséum national d'Histoire naturelle, Paris, France (MNHN), the South Australian Museum, Adelaide,

Australia (SAM) and the United States National Parasite Collection, Beltsville, Maryland, USA (USNPC). Additional comparative material was examined from the Meguro Parasitological Museum, Tokyo, Japan (MPM), BMNH and MNHN. Host nomenclature follows Naylor et al. (2012), such that provisional identifications of host specimens belonging to a species complex [e.g. *Sphyrna mokarran* (Rüppell)] are indicated by a numeral. Although morphologically similar, these host species [e.g. *Sphyrna mokarran* 2, *sensu* Naylor et al. (2012)] were shown to be distinct based on their molecular phylogeny (data from Naylor et al., 2012). Host higher classification follows Naylor et al. (2012). Abbreviations used for individual host specimens are as follows: AU, CM03 and NT for specimens from off northern Australia; BO for specimens from off Malaysian Borneo. Additional information on these hosts is available from the Global Cestode Database (<http://elasmobranchs.tapewormdb.uconn.edu/>).

***Pristiorhynchus* n. g.**

Generic diagnosis

Otobothriidae Dollfus, 1942. Scolex acraspedote; maximum width at level of pars bothrialis. Bothria two in number, subcircular; paired bothrial pits on posterior margin; pars vaginalis longer than pars bothrialis; tentacle sheaths sinuous; prebulbar organs and gland-cells absent; bulbs elongate; retractor muscle originates in posterior third of bulb; pars post-bulbosa and velum absent. Basal armature present, with dispersed billhooks; basal tentacular swelling absent. Metabasal armature heteroacanthous, atypical; hooks heteromorphous, hollow; five hooks per principle row; space between hook files 1 and 1'; hook files commence on bothrial surface of tentacle, terminate on antibothrial surface; three intercalary hooks present. Mature segments acraspedote, elongate; genital pores alternate irregularly, postequatorial; hermaphroditic sac elongate; internal seminal vesicle present; external seminal vesicle absent; cirrus unarmed; testes occupy complete intervascular space, in two columns; ovarian lobes elongate; vitelline follicles circumcortical; uterus median, tubular, pre-formed; uterine pore absent. Parasitic in sawfishes (family Pristidae).

Type- and only species: P. palmi n. g., n. sp.

***Pristiorhynchus palmi* n. g., n. sp.**

Type-host: *Anoxypristis cuspidata* (Latham) (Rajiformes: Pristidae) (NT-58, NT-65, NT-89).

Additional host: *Pristis zijsron* Bleeker (Rajiformes: Pristidae) (AU-33).

Type-locality: Arafura Sea off the Wessel Islands (eastern part), Northern Territory, Australia, coll. J. N. Caira and K. Jensen, 13.xi.1999.

Additional locality: Timor Sea off Darwin (Buffalo Creek), Northern Territory, coll. J. N. Caira and K. Jensen, 6.viii.1997; Coral Sea off Balgal, Queensland, Australia, coll. B. G. Robertson, 13.ix.1985.

Site of infection: Spiral intestine.

Type-material: Holotype in SAM (AHC 35587). Paratypes in BMNH (2012.5.14.1–7), LRP (7896–7901), USNPC (105631–33), and SAM (AHC 35588–600).

Etymology: The generic name alludes to the host group (Pristidae - modern sawfishes). The specific name is for Prof. H. W. Palm in recognition of his contribution to the systematics of trypanorhynch cestodes.

Description (Figs. 1–3)

[Based on 64 whole-mounts, 1 specimen in glycerine, 6 specimens used for SEM, 3 longitudinally sectioned specimens.] Mature cestodes small, 1.0–3.2 (2.3 ± 0.6 ; $n = 15$) mm long, with 5–12 (7 ± 2 ; $n = 15$) segments; gravid segments not present. Scolex acraspedote (Figs. 1A,B, 3A), 350–755 (571 ± 122 ; $n = 19$) long; maximum width at level of pars bothriialis 150–260 (217 ± 26 ; $n = 16$); pars bothriialis 130–210 (161 ± 20 ; $n = 19$) long. Bothria 2 in number, subcircular (Figs. 1B, 3A,C), 120–220 (168 ± 31 ; $n = 9$) $\times$ 110–180 (153 ± 29 ; $n = 9$); distal bothrial surface covered with trifid spinitriches (Fig. 3D); proximal bothrial surface covered with trifid spinitriches (Fig. 3F); paired bothrial pits present on posterior margin of bothria (Fig. 1A,B). Pars vaginalis longer than pars bothriialis, 225–555 (349 ± 80 ; $n = 19$) long, covered with papilliform to acicular filitriches (Fig. 3G); tentacle sheaths sinuous. Pars bulbosa 105–300 (219 ± 58 ; $n = 19$) $\times$ 75–140 (107 ± 14 ; $n = 19$); prebulbar organs and gland-cells within bulbs absent; bulbs elongate (Fig. 1A,B,D), 95–290 (204 ± 57 ; $n = 31$) $\times$ 35–60 (46 ± 6 ; $n = 31$); bulb width/length ratio 1.0 : 3.2–6.5 (5.1 ± 0.9 ; $n = 31$); retractor muscle originates in posterior third of bulb; pars post-bulbosa absent; bulbs extend into pars proliferans in most specimens; velum absent. Scolex ratio (pars bothriialis/pars vaginalis/pars bulbosa) 1.0 : 1.6–2.6 : 0.8–1.9 (1.0 : 2.2 $\pm$ 0.3 : 1.4 $\pm$ 0.3; $n = 19$).

Everted tentacles $c.590$ ($n = 1$) long; diameter 13–16 (14 ± 1 ; $n = 3$) at base, 16–20 (19 ± 2 ; $n = 3$) in region of billhooks, 13–18 (16 ± 2 ; $n = 8$) in metabasal region. Metabasal armature heteroacanthous, heteromorphous; hooks hollow. Hook files begin on bothrial surface of tentacle (Fig. 2B), terminate on antibothrial surface (Fig. 2C,E); 5 hooks per principle row (Fig. 2A,D); prominent space between hook files 1 and 1' (Fig. 2B). Hooks 1(1') uncinat, 7–9 (8 ± 1 ; $n = 10$) long, base 5–6 (6; $n = 10$) long; hooks 2(2') falcate, larger, 11–13 (12 ± 1 ; $n = 16$) long, base narrower, 3–4 (4; $n = 16$) long; hooks 3(3') falcate, with erect tip, 10–13 (12 ± 1 ; $n = 8$) long, base 3–4 (4; $n = 8$) long; hooks 4(4') falcate, smaller, 7–9 (8 ± 1 ; $n = 12$) long, base 2–3 (3; $n = 12$) long; hooks 5(5') falcate, smaller, 3–8 (4 ± 2 ; $n = 12$) long, base 1–3 (1 ± 1 ; $n = 10$) long; intercalary hook row present, with three hooks a(a')–c(c') (Fig. 2C,E); hooks a(a') falcate, posterior to hooks 4(4'), 2–5 (3 ± 1 ; $n = 11$) long, base 1–2 (1; $n = 11$) long; hooks b(b') falcate, posterior between hooks 5(5') and 6(6'), 2–3 (3; $n = 8$) long, base 1 ($n = 8$) long; hooks c(c') falcate, 2–3 (3; $n = 7$) long, base 1 ($n = 7$) long.

Distinctive basal armature present; initial hook rows of base with falcate hooks, 10 ($n = 3$) long, base 3–4 (3; $n = 3$) long; tentacle increases in width to form slight basal swelling; swelling with dispersed billhooks (Figs. 2A–D, 3B,E), 6–10 (7 ± 1 ; $n = 9$) long, base 2–4 (3; $n = 9$) long. Initial principle rows with hooks 1(1') not separated by space (Fig. 2B).

Segments acraspedote; first mature segments 120–250 (166 ± 42 ; $n = 11$) $\times$ 50–100 (76 ± 17 ; $n = 11$); terminal mature segments 685–1,290 ($1,090 \pm 172$; $n = 13$) $\times$ 85–145 (112 ± 18 ; $n = 13$) (Fig. 1C). Genital pores alternate irregularly, in posterior third of segment (Fig. 1C); pore inconspicuous. Hermaphroditic sac elongate (Fig. 1C), 110–158 (136 ± 16 ; $n = 8$) $\times$ 60–85 (71 ± 8 ; $n = 8$); internal and external seminal vesicles absent; cirrus joins vagina at proximal pole of hermaphroditic sac, unarmed. Vas deferens coils posteriorly to ovarian isthmus. Testes occupy complete intervascular space, in 2 columns, 38–58 (48 ± 7 ; $n = 10$) $\times$ 30–40 (35 ± 3 ; $n = 10$); testes 24–39 (33 ± 4 ; $n = 11$) in number (Fig. 1C), 21–33 (27 ± 3 ; $n = 11$) preporal, 3–9 (5 ± 2 ; $n = 11$) postporal; 1–5 (2 ± 1 ; $n = 10$) testes postovarian or between posterior regions of ovarian lobes (Fig. 1C). Vagina penetrates proximal pole of hermaphroditic sac; cirrus runs posteriorly towards Mehlis' gland, thin-walled, $c.5$ ($n = 1$) wide. Seminal receptacle absent. Ovary anterior to posterior end of segment; ovarian lobes elongate, 160–198 (180 ± 12 ; $n = 10$) $\times$ 20–38 (29 ± 7 ; $n = 10$). Mehlis' gland 23–40 (30 ± 6 ; $n = 6$) in diameter. Vitelline follicles small, circumcortical, 10–13 (11 ± 1 ; $n = 10$) in diameter. Uterus median, tubular; uterine pore absent.

Remarks

The new species is a member the Otophthriidae, since it possesses an acraspedote scolex, two sub-circular bothria with paired bothrial pits, no gland-cells within the bulbs, no prebulbar organs, a heteroacanthous, heteromorphous tentacular armature with five hooks per principle row and an intercalary hook row of three hooks. The acraspedote scolex resembles the scolex shape of species of *Proemotobothrium*. However, species of this genus are characterised by four hooks per principle row, a single intercalary hook and either two [in *Pr. linstowi* (Southwell, 1912)] or three [in *Pr. southwelli* Beveridge & Campbell, 2001] “extra hooks” (*sensu* Beveridge & Campbell, 2001) arranged in tandem arrays on the external surface of each tentacle. Palm (2004) applied a different numbering system in which both species possess five or six principle and two intercalary hooks to match it with other otophthriid species (see below). The new species differs from the pattern in oncotaxy of *Proemotobothrium* spp., regardless of which numbering system is applied. Apart from features of the oncotaxy, additional morphological characters differentiate the new species from *Proemotobothrium*. The present specimens possess a much smaller body size, fewer segments and testes, different ratios of individual scolex regions, a heterogeneous arrangement of testes and an origin of the retractor muscle in the basal region of the bulb.

The oncotaxy of the new species resembles species of *Otophthrium* Linton, 1890, with a distinctive basal armature and a metabasal tentacular armature with an intercalary row posterior to each principle hook row. However, species of *Otophthrium* possess a craspedote scolex. Bulbs are either short and compact forming a velum covering the anterior part of the pars proliferans scolecis or are elongate with an almost laterally directed posterior extremity terminating at the postero-lateral margins of the velum. In contrast, *Pristiorhynchus palmi* n. g., n. sp. possesses an acraspedote scolex lacking a velum and a pars bulbosa of a similar width as the pars proliferans scolecis. It furthermore differs from *Otophthrium* spp. in the origin of the retractor muscle, the arrangement and size of internal organs and the shape of the segment.

The mature segment of *P. palmi* is of an almost eutetrarhynchoid appearance, not seen in other taxa of the Otophthrioidea. The shape of the segment is elongate and about nine times longer than the maximum width. Testes are relatively few in number, arranged in a single layer and in two longitudinal columns. Very few testes are located posterior to the ovary. The ovarian lobes are elongate and extend almost to the posterior margin of the segment. However, the paired bothrial pits and lack of both prebulbar organs and gland-cells inside the bulbs indicate its affinities with the Otophthriidae.

For these reasons we consider the species to represent a unique taxon within the Otophriidae, combining morphological characteristics not seen in other genera. Therefore, we feel obliged to erect a new genus, *Pristiorhynchus*, to accommodate the single species *P. palmi* n. g., n. sp.

***Symbothriorhynchus tigaminacantha* Palm, 2004**

Syn. *Otophrium* sp. of Kardousha (1999)

Type-host: *Uranoscopus* sp. (Perciformes: Uranoscopidae) (*intermediate host*).

Additional hosts: *Nemipterus japonicus* (Bloch) (Perciformes: Nemipteridae) (*intermediate host*); *Parupeneus cyclostomus* (Lacépède) (Perciformes: Mullidae) (*intermediate host*).

Type-locality: Indian Ocean off Pelabuhan Ratu, Indonesia (07°01'S, 106°28'E).

Additional locality: Arabian Gulf off Dubai, United Arab Emirates (25°18'N, 55°14'E).

Material examined: 1 plerocercus from the intestine of *Platycephalus bassensis* Cuvier (Scorpaeniformes: Platycephalidae) off Heron Island, Queensland, Australia, coll. J. Reddick, Jan., 1997 (QM G233885); 7 voucher specimens from *Sphyrna lewini* (Griffith & Smith) (Carcharhiniformes: Sphyrnidae) in Nickol Bay (SAM AHC 35601) and off Geraldton (SAM AHC 35602), Western Australia, Australia, coll. B. G. Robertson, 11.xi.1986 and 24.xi.1986, and the Coral Sea off Nouméa (JNC 1628), New Caledonia, coll. L. Euzet, 6.xi.1995 (MNHN JNC1628A1–A3; serial sections in MNHN JNC1628A4–A6); 5 voucher specimens from *Sphyrna mokarran* 2 [*sensu* Naylor et al. (2012)] (Carcharhiniformes: Sphyrnidae) (CM03-64; CM03-78) off Weipa, Queensland, Australia, coll. J. N. Caira and K. Jensen, 15.v.2004 (SAM AHC 35603–04).

Comparative material examined: Types of *Symbothriorhynchus uranoscopi* Yamaguti, 1952 from *Uranoscopus oligolepis* Bleeker off Kochi (Tosa Bay), Japan (33°26'N, 133°33'E) (MPM; SY50-71/22649).

Site of infection: Spiral intestine (for adults).

Redescription (Figs. 4–5, 6A)

[Based on 8 whole-mounts, 1 specimen used for SEM, 1 longitudinally sectioned specimen.]

Mature cestodes 9.0–13.6 (10.4 ± 2.1; n = 4) mm long, with 21–27 (24 ± 3; n = 4) segments; first mature segments appear posterior to segments 15–20 (18 ± 2; n = 4); gravid segments not

present. Scolex craspedote (Fig. 4A), 1,100–1,850 ($1,352 \pm 326$; $n = 5$) long, with thick tegument (Fig. 4A); maximum width of scolex at level of pars bulbosa 570–720 (646 ± 64 ; $n = 5$); pars bothrialis 250–310 (264 ± 26 ; $n = 5$) $\times$ *c.*400 ($n = 1$). Bothria 2 in number, patelliform (Fig. 4A), 230–260 (243 ± 13 ; $n = 6$) $\times$ 245–400 (325 ± 67 ; $n = 6$); paired bothrial pits absent (Fig. 4A). Pars vaginalis longer than pars bothrialis, 770–1,520 ($1,036 \pm 321$; $n = 5$) long; tentacle sheaths sinuous. Pars bulbosa 300–330 (314 ± 15 ; $n = 5$) long; prebulbar organs and gland-cells absent; bulbs ovoid (Fig. 4A,D), 310–370 (347 ± 18 ; $n = 15$) $\times$ 130–225 (154 ± 29 ; $n = 15$), surround pars proliferans scolecis; bulb width/length ratio 1.0 : 1.6–2.7 (2.3 ± 0.3 ; $n = 15$); retractor muscle originates in anterior region of bulb (Fig. 4D), occasionally forming internal loop (Fig. 4D); pars post-bulbosa absent; velum surrounds anterior 140–150 (145 ± 6 ; $n = 4$) of pars proliferans scolecis. Scolex ratio (pars bothrialis/pars vaginalis/pars bulbosa) 1.0 : 3.1–4.9 : 1.1–1.3 ($1.0 : 3.9 \pm 0.8 : 1.2 \pm 0.1$; $n = 5$).

Fully everted tentacles 1,060–1,135 ($1,098 \pm 32$; $n = 4$) long, slightly wider at base; diameter 40 ($n = 2$) at base, 55–63 (59 ± 5 ; $n = 2$) at basal swelling, 45–50 (47 ± 3 ; $n = 5$) in metabasal region, 23–30 (26 ± 3 ; $n = 5$) in apical region. Metabasal armature heteroacanthous, heteromorphous; hooks hollow, in ascending half spiral rows. Hook files begin on internal surface of tentacle (Fig. 5B), terminate on external surface (Fig. 5A); 5 hooks per principle row (Fig. 5C,D); prominent space between hook files 1 and 1' (Fig. 5B). Hooks 1(1') uncinata, 18–22 (19 ± 1 ; $n = 12$) long, base 15–21 (18 ± 2 ; $n = 10$) long; hooks 2(2') uncinata, slightly smaller, 14–21 (18 ± 2 ; $n = 14$) long, base 13–19 (18 ± 2 ; $n = 14$) long; hooks 3(3') uncinata, slightly larger, tip erect, 18–20 (19 ± 1 ; $n = 6$) long, base slightly narrower, 12–14 (13 ± 1 ; $n = 6$) long; hooks 4(4') falcate, 16–20 (18 ± 1 ; $n = 15$) long, base narrower, 6–9 (7 ± 1 ; $n = 15$) long; hooks 5(5') falcate, smaller, 12–20 (16 ± 3 ; $n = 7$) long, base narrower, 4–5 (5 ; $n = 7$) long; single intercalary hooks a(a') present (Fig. 5A,D), hooks a(a') falcate, in line with hooks 5(5'), 11–14 (13 ± 1 ; $n = 16$) long, base 2–4 (3 ± 1 ; $n = 16$) long; 3 longitudinal files of hooks on external surface, external hooks of same size and shape (Fig. 5D), uncinata, 6–8 (7 ± 1 ; $n = 20$) long, base 5–7 (6 ± 1 ; $n = 20$) long.

Distinctive basal armature present; spiniform hooks surround base of tentacle, with broad base in dorso-ventral view (Fig. 5C), *c.*15 ($n = 1$) long, base *c.*2 ($n = 1$) long, becoming more falcate and uncinata towards internal surface. Basal swelling present, with characteristic group of billhooks on external surface (Fig. 5C,D), 9–16 (12 ± 2 ; $n = 6$) long, base 3–5 (4 ± 1 ; $n = 6$) long; 2 greatly enlarged hooks on internal surface (Fig. 5D), uncinata, with tips apposed; larger hook slightly displaced towards bothrial surface, *c.*42 ($n = 1$) long, base *c.*26 ($n = 1$) long; second enlarged hook slightly smaller, *c.*29 ($n = 1$) long, base *c.*21 ($n = 1$) long.

Segments acraspedote; immature segments posterior to velum much wider than long (Fig. 4A), 20–35 (25 ± 7 ; $n = 4$) $\times$ 250–350 (304 ± 41 ; $n = 4$); first mature segments 400–550 (457 ± 81 ; $n = 3$) $\times$ 280–480 (400 ± 106 ; $n = 3$); mature segments become longer than wide (Fig. 4C); terminal mature segments 1,570–2,320 ($1,873 \pm 395$; $n = 3$) $\times$ 390–560 (502 ± 97 ; $n = 3$). Genital pores alternate irregularly, at mid-level of segment or slightly posterior to mid-level; pore inconspicuous; regions anterior and posterior to pore thickened (Fig. 4B,C). Hermaphroditic sac oval (Fig. 4B,C), 260–345 (295 ± 44 ; $n = 3$) $\times$ 200–210 (203 ± 6 ; $n = 3$); internal seminal vesicle present; cirrus joins vagina at distal pole of hermaphroditic sac, cirrus unarmed; external seminal vesicle absent. Vas deferens coils posteriorly to ovarian isthmus. Testes numerous, occupy complete intervascular space, in single layer (Fig. 4C), 75–100 (89 ± 7 ; $n = 20$) $\times$ 45–60 (54 ± 5 ; $n = 20$); testes 109–138 (124 ± 10 ; $n = 7$) in number, 62–84 (75 ± 9 ; $n = 7$) pre-ovarian, 45–55 (49 ± 4 ; $n = 7$) postovarian. Vagina penetrates proximal pole of hermaphroditic sac, runs posteriorly towards Mehlis' gland, 8–10 (9 ± 1 ; $n = 4$) wide. Seminal receptacle absent. Ovary in posterior half of segment, distant from posterior margin of segment (Fig. 4C); ovarian lobes 130–185 (157 ± 24 ; $n = 5$) $\times$ 125–195 (160 ± 31 ; $n = 5$); Mehlis' gland 100–135 (120 ± 16 ; $n = 5$) in diameter. Vitelline follicles small, circumcortical, 15–25 (18 ± 3 ; $n = 20$) in diameter. Uterus median, tubular; uterine pore absent. Ventral osmoregulatory canals 15–30 (20 ± 5 ; $n = 8$) in diameter.

Remarks

Symbothriorhynchus tigaminacantha is characterised by a craspedote scolex bearing two small, patelliform bothria, a characteristic basal tentacular armature with a basal swelling with two greatly enlarged macrohooks on the internal surface, a group of billhooks on the external surface and a heteroacanthous metabasal tentacular armature with five principle hooks, a single intercalary hook and similar uncinuate hooks forming three longitudinal files on the external surface. Palm (2004) described this species based on larval stages collected in Indonesian waters. He also provided SEM micrographs of the scolex, tentacular armature and surface ultrastructure. The small bothrial pits illustrated in the original description (see Palm, 2004; fig. 186g) are not visible with light microscopy and are apparently in such a reduced state, that only the few bifurcate microtriches indicate the presence of this structure. This caused confusion in previous classification schemes; both Yamaguti (1959) and Schmidt (1986) listed *Symbothriorhynchus* as insufficiently known. Campbell & Beveridge (1994) treated the then monotypic genus as a synonym of *Otobothrium*. Palm (2004) re-established the genus within the Otobothriidae and

considered the reduced bothrial pits a characteristic generic feature. However, the type-species of the genus, *S. uranoscopi*, has not been examined with the aid of scanning electron microscopy, and the assumption of Palm (2004, p. 395), that reduced bothrial pits are present, has not been verified. Although, reduced bothrial pits were not observed in the present specimens of *S. tigaminacantha* using light microscopy and could therefore not be included in the redescription, we assume their existence based on the evidence provided by Palm (2004).

Palm (2004) provided three line-drawings of the tentacular armature of *S. tigaminacantha*. The sole illustration of the basal armature (Palm, 2004; fig. 183g) shows only part of this region of the tentacle, and the interpretation of the basal oncotaxy is difficult, due to the absence of basal hooks. This absence of hooks becomes obvious when compared with the SEM micrographs provided (Palm, 2004; figs. 184e,f). Furthermore, only a single enlarged macrohook was illustrated (Palm, 2004; fig. 183g), which represents one of the most characteristic features of the species. The two greatly enlarged hooks on the basal swelling of each tentacle were reported to be situated on the bothrial surface (Palm, 2004), which is different to the situation seen in the present specimens, in which the macrohooks are located on the internal surface, although slightly displaced towards the bothrial surface. The adult specimens examined in the present study are larger than the plerocerci described by Palm (2004), with a larger scolex, individual scolex regions and bulbs. The hook measurements, oncotaxy and other morphological features are, however, identical.

Symbothriorhynchus tigaminacantha differs from its congener *S. uranoscopi* in the number of longitudinal files of similar hooks on the external tentacular surface of the metabasal armature (i.e. three files in *S. tigaminacantha* versus four in *S. uranoscopi*; see Fig. 6A and 6B, respectively). The specimen of *S. uranoscopi* from off Mozambique illustrated by Palm (2004; fig. 182d-i), however, differs in the arrangement and numbers of hooks on the external metabasal surface (Palm, 2004; fig. 182g) to the type-specimen from off Japan (Palm, 2004; fig. 183b). This difference between specimens becomes apparent in a two-dimensional schematic illustration showing the hook arrangements (Fig. 6B,C). The specimens of *S. uranoscopi* from off Mozambique appear to have an asymmetrical arrangement (Fig. 6C) compared to the type-specimens from Japanese waters, in which all hooks on the external tentacular surface form a symmetrical pattern of four anteriorly displaced hooks in four longitudinal files (Fig. 6B). Due to the obvious differences between these specimens, we assume that the Mozambican specimens might in fact represent a different, but closely related species. Additionally, a two-dimensional schematic illustration of the hook arrangement of the external surface is provided for *S.*

tigaminacantha (Fig. 6A) as a direct comparison. The latter species possesses three anteriorly displaced hooks between the principle hook rows, forming three longitudinal files (Fig. 6A).

Both species within *Symbothrionchus* Yamaguti, 1952 possess similar features in their morphology and ontotaxy as compared to those features in *Otobothrium mugilis* Hiscock, 1954, such as the craspedote scolex, and the two greatly enlarged macrohooks and a group of billhooks on the basal swelling of each tentacle. However, *O. mugilis* differs from both species of *Symbothrionchus* in the presence of visible bothrial pits on the posterior margin of each bothrium, a much smaller scolex and tentacular bulbs, an orientation of the principle hook rows from the bothrial towards the antibothrial surface, the absence of longitudinal hook files on the antibothrial surface of the tentacle and the presence of three heteromorphous intercalary hooks in the metabasal armature.

The present material consisted of both larval and adult specimens. The adults of *S. tigaminacantha* have not been described previously and were obtained from two species of hammerhead sharks (Sphyrnidae). This might reflect a relatively high host-specificity for this species. Furthermore, new locality records were added from off Australia and New Caledonia, which expands the geographical distribution of this species in the Australasian realm.

***Parotobothrium balli* (Southwell, 1929) Palm, 2004**

Syns *Otobothrium balli* Southwell, 1929; *O. ballium* (Southwell, 1929); *O. karachii* (Southwell, 1929) Bilqees & Khurshid, 1987 (*lapsus calami*); *Nybelinia karachii* Khurshid & Bilqees, 1988; *Paranybelinia balli* (Southwell, 1929) Beveridge & Campbell, 1998

Type-host: *Pristipomoides argyrogrammicus* (Valenciennes) (Perciformes: Lutjanidae)

(*intermediate host*) [as *Aprion pristipoma* in Southwell (1929)].

Additional hosts: *Abalistes stellatus* (Anon. in Lacépède) (Tetraodontiformes: Balistidae)

(*intermediate host*); *Chaetodon lunula* (Lacépède) (Perciformes: Chaetodontidae) (*intermediate*

host); *Gymnura australis* (Ramsay & Ogilby) (Rajiformes: Gymnuridae) (*intermediate host*);

Lates calcarifer (Bloch) (Perciformes: Latidae) (*intermediate host*); *Lethrinus ornatus*

Valenciennes (Perciformes: Lethrinidae) (*intermediate host*); *Scomberomorus guttatus* (Bloch & Schneider) (Perciformes: Scombridae) (*intermediate host*).

Type-locality: Laccadive Sea off Kollam, India [Quilon in Southwell (1929)] (08°50'N, 76°36'E).

Additional localities: Bay of Bengal off Nagapattinam, India (10°45'N, 79°51'E); Arabian Sea off Karachi, Pakistan (24°45'N, 66°57'E); Indian Ocean off Pelabuhan Ratu, Indonesia (07°01'S, 106°28'E); Indian Ocean off Ningaloo Reef, Western Australia, Australia (22°50'S, 113°44'E).

Material examined: Specimens from *Sc. guttatus* (BMNH 1989.5.18.11; types of “*O. karachii*”) and *La. calcarifer* off Karachi, Pakistan (BMNH 1989.5.18.15); specimens from *Cha. lunula* from Ningaloo Reef, Western Australia (BMNH 2008.5.21.5); 2 voucher specimens from *Carcharhinus amblyrhynchoides* (Whitley) (Carcharhiniformes: Carcharhinidae) (BO-31) from the South China Sea off Sematan, Sarawak, Malaysia, coll. J. N. Caira and K. Jensen, 4.vi.2002 (LRP 7892; USNPC 105634).

Site of infection: Spiral intestine (for adults).

Redescription (Fig. 7)

[Based on 2 whole-mounts, segments of 1 specimen sectioned longitudinally.] Small cestodes; mature specimen 12.5 (n = 1) mm long, with 38–43 (n = 2) segments; first mature segments appear posterior to segments 31–37 (n = 2); gravid segments not present. Scolex craspedote (Fig. 7A), 1,055 (n = 1) long; maximum width at level of pars bothriialis, 820 (n = 1) wide; pars bothriialis 690 (n = 1) long, extending into anterior pars bulbosa (Fig. 7A). Bothria 2 in number, oval, 510 (n = 1) × 640–660 (n = 2), with prominent median ridge, free margins, rims thickened; paired bothrial pits present on lateral margin of bothria. Pars vaginalis 620 (n = 1) long; tentacle sheaths sinuous, 25–30 (27 ± 2; n = 4) wide. Pars bulbosa 255 (n = 1) × 265 (n = 1); prebulbar organs and gland-cells absent; bulbs ovoid (Fig. 7A), 245–310 (268 ± 29; n = 6) × 85–120 (98 ± 17; n = 6); bulb width/length ratio 1.0 : 2.5–2.9 (2.7 ± 0.2; n = 6); retractor muscle originates in anterior third of bulb (Fig. 7A); velum surrounds anterior 60 (n = 1) of pars proliferans scolecis (Fig. 7A), 155 (n = 1) × 265 (n = 1); bulbs not reaching posterior part of velum, with prominent space 100 (n = 1) posteriorly. Scolex ratio (pars bothriialis/pars vaginalis/pars bulbosa) 1.0 : 0.9 : 0.4 (n = 1).

Everted tentacles c.320 (n = 2) long; diameter at base 28 (n = 2), 33 (n = 2) wide in metabasal region, 30 (n = 2) wide in distal tentacular region. Armature homeoacanthous, heteromorphous; hooks solid, quincuncial; largest hooks on bothrial surface uncinata; hooks gradually decrease in size towards antibothrial surface of tentacle; hooks on antibothrial surface falcate. Distinctive basal armature and basal swelling absent.

Segments acraspedote; immature segments posterior to velum much wider than long (Fig. 7A), 30 ($n = 2$) $\times$ 215–370 ($n = 2$); first mature segments 530–650 ($n = 2$) $\times$ 440–470 ($n = 2$); more mature segments become longer than wide; late mature segments 830–1,090 (928 ± 124 ; $n = 4$) $\times$ 460–530 (510 ± 34 ; $n = 4$) (Fig. 7B). Genital pores alternate irregularly, in posterior third of segment (Fig. 7B); pore inconspicuous; regions anterior and posterior to pore thickened. Hermaphroditic sac elongate (Fig. 7B,C), 55–68 (51 ± 6 ; $n = 4$) $\times$ 125–145 (134 ± 11 ; $n = 4$); internal seminal vesicle present, at proximal pole of hermaphroditic sac; external vesicle absent; cirrus joins vagina at distal pole of hermaphroditic sac, unarmed. Vas deferens coils posteriorly to ovarian isthmus. Testes numerous, in several layers (Fig. 7B), occupy complete intervascular space, 48–53 (51 ± 2 ; $n = 15$) $\times$ 28–33 (30 ± 2 ; $n = 15$); testes 219–251 (237 ± 13 ; $n = 4$) in number, 159–200 (184 ± 18 ; $n = 4$) pre-ovarian, 47–60 (53 ± 5 ; $n = 4$) postovarian. Vagina thin-walled, 5–8 ($n = 2$) wide, penetrates proximal pole of hermaphroditic sac (Fig. 7C), runs posteriorly towards Mehlis' gland. Seminal receptacle absent. Ovary distant from posterior margin of segment (Fig. 7B); ovarian lobes elongate, 55–75 (63 ± 7 ; $n = 6$) $\times$ 133–148 (143 ± 6 ; $n = 6$). Mehlis' gland 90–113 (98 ± 9 ; $n = 5$) in diameter. Vitelline follicles small, circumcortical, 18–20 (19 ± 1 ; $n = 15$) $\times$ 8–10 (9 ± 1 ; $n = 15$). Uterus median, tubular (Fig. 7B); uterine pore absent. Ventral osmoregulatory canals 18–20 (19 ± 1 ; $n = 6$) in diameter.

Remarks

Parotobothrium balli is characterised by a small, craspedote scolex with two large, oval bothria with paired bothrial pits on the lateral margins, a pars bothrialis reaching posterior to the mid-level of the the pars bulbosa and a tentacular armature with solid hooks. Southwell (1929) described this species on the basis of five plerocerci and placed it within *Otobothrium* (as *O. balli* Southwell, 1929), since paired bothrial pits were present on each bothrial margin. This species remained within *Otobothrium* until Beveridge & Campbell (1998) re-examined the type-material and allocated the species to *Paranybelinia* Dollfus, 1946, as *Paranybelinia balli* (Southwell, 1929), based on the presence of a solid tentacular armature in a homeomorphous arrangement. However, at that time these authors also admitted that the allocation at the generic level was somewhat problematical. The tentacular armature exhibited a 'heteroacanthous nature', with an axis of symmetry commencing from the bothrial to the antibothrial tentacular surface (Beveridge & Campbell, 1998). This is in contrast to the original definition of a heteroacanthous armature by Dollfus (1942), in which the axis of symmetry runs from the internal to the external surface. However, several otobothrioid species are now recognised as having a heteroacanthous

armature with principle hook rows originating either on the bothrial surface and terminating on the antibothrial surface [e.g. *O. propecysticum* Dollfus, 1969; *O. carcharidis* (Shipley & Hornell, 1906); *O. parvum* Beveridge & Justine, 2007; and *Pseudotobothrium arii*; see Beveridge et al. (2000); Beveridge & Justine (2007)] or with rows commencing from the antibothrial to the bothrial surface [e.g. *Ps. dipsacum* (Linton, 1897); see Beveridge et al. (2000)]. Palm (2004) erected a new genus, *Parotobothrium* Palm, 2004, within the Pseudotobothriidae, to accommodate two species, *Pa. balli* and *Pa. dollfusi* (Chandra & Hanumantha Rao, 1985) Palm, 2004. Both previously belonged to the Paranybeliniidae. However, *Pa. balli* was differentiated from species within the Paranybeliniidae by its possession of a blastocyst and a similar surface ultrastructure (i.e. microthrix patterns), as seen in other otobothriid and pseudotobothriid species (Palm, 2004). Palm (2004) described plerocerci from the stomach wall of *Gymnura australis*, collected off Pelabuhan Ratu, Indonesia, and furthermore provided SEM micrographs of the scolex, the tentacular armature and the surface ultrastructure. Adult specimens of *Pa. balli* have not, until now, been described and thus information about the segment morphology and morphometric data of adult worms has been entirely lacking. Although only two specimens were available for the present study, both are well preserved. The specimens were obtained from the spiral intestine of a single specimen of the graceful shark *Carcharhinus amblyrhynchoides* in the South China Sea off Sematan (Malaysian Borneo). This represents the first record of a definitive host for this species and a new geographical record. The present redescription of *Pa. balli* focuses particularly on the morphology of the adult stage and little effort was devoted to its oncotaxy, which has been described in detail by Beveridge & Campbell (1998). The adult specimens described herein are consistent with that description.

***Pseudotobothrium arii* (Bilqees & Shaukat, 1976) Beveridge, Campbell & Jones, 2000**

Syns *Otobothrium arii* Bilqees & Shaukat, 1976; *O. megatentaculum* Bilqees & Khurshid, 1987

Type-host: *Netuma thalassina* (Rüppell) (Siluriformes: Ariidae) (*intermediate host*) [as *Arius serratus* Day].

Additional hosts: *Lamiopsis tephrodes* (Fowler) (Carcharhiniformes: Carcharhinidae);

Scomberomorus guttatus (Bloch & Schneider) (*intermediate host*); *Neoarius graeffei* (Kner & Steindachner) (Siluriformes: Ariidae) (*intermediate host*).

Type-locality: Arabian Sea off Karachi, Pakistan (24°45'N, 66°57'E).

Additional localities: Brisbane River (lower reaches), Brisbane, Queensland, Australia; South China Sea off Mukah, Sarawak, Malaysia.

Material examined: Plerocerci from *Ne. thalassina* (BMNH 1989.5.18.14; labelled as “*O. arii*”) and from *Sc. guttatus* off Karachi, Pakistan (BMNH 1989.5.18.12; labelled as “*O. megatentaculum*”); 11 voucher specimens from *L. tephrodes* (BO-74, BO-441, BO-488) from Mukah, Sarawak, Malaysia, coll. J. N. Caira and K. Jensen, 14.vi.2002, 28.iv. 2004 and 30.iv.2004 (LRP 7893–95; USNPC 105635–37).

Site of infection: Spiral intestine (for adults).

Redescription (Figs. 8A,B, 9A–E)

[Based on 9 whole-mounts, 2 slides with individual segments, 1 specimen used for SEM, 2 specimens longitudinally sectioned.] Small cestodes; specimens 8.6–16.3 (12.4 ± 3.8 ; $n = 3$) mm long, with 34–41 (36 ± 4 ; $n = 3$) segments in mature strobilae; first mature segments appear posterior to segments 23–27 (25 ± 2 ; $n = 3$); gravid segments not present. Scolex elongate, craspedote (Fig. 9A), 1,590–1,940 ($1,750 \pm 138$; $n = 9$) long; maximum width of scolex at level of pars bulbosa, 435–875 (515 ± 147 ; $n = 8$) wide; pars bothrials 280–450 (340 ± 47 ; $n = 9$) $\times$ 390–600 (454 ± 73 ; $n = 8$). Bothria 2 in number, elongate (Fig. 9A), 340–350 (345 ± 7 ; $n = 2$) $\times$ 200–230 (215 ± 21 ; $n = 2$), with free margins, rims thickened; distal bothrial surface (Fig. 9B) and proximal bothrial surface (Fig. 9D) covered with trifid spinitriches; paired bothrial pits present, small, prominent, on posterior margins of each bothrium. Pars vaginalis very long, slender, 1,120–1,520 ($1,257 \pm 132$; $n = 9$) long, of variable size depending on state of contraction, covered with papilliform to acicular filitriches (Fig. 9E); tentacle sheaths sinuous or coiled. Pars bulbosa 430–610 (501 ± 50 ; $n = 9$) long; prebulbar organs and gland-cells absent; bulbs elongate, 410–590 (499 ± 43 ; $n = 20$) $\times$ 120–190 (153 ± 23 ; $n = 20$); bulb width/length ratio 1.0 : 2.6–4.9 (3.3 ± 0.7 ; $n = 20$); retractor muscle originates in anterior third of bulb; pars post-bulbosa absent; velum surrounds anterior 160–350 (260 ± 63 ; $n = 9$) of pars proliferans scolecis. Scolex ratio (pars bothrials/pars vaginalis/pars bulbosa) 1.0 : 3.3–4.2 : 1.0–2.2 ($1.0 : 3.7 \pm 0.4 : 1.5 \pm 0.3$; $n = 9$).

Tentacles only partly everted, 210–260 (235 ± 35 ; $n = 2$) long, diameter at base 43–53 (48 ± 7 ; $n = 2$). Metabasal armature heteroacanthous, heteromorphous; hooks hollow, in ascending half spiral rows. Hook files commence on bothrial surface of tentacle, terminate on antibothrial surface; 6 hooks per principle row; prominent space between hooks 6(6') and central

hook files on antiothrial surface; antiothrial surface with 6 longitudinal files of hooks, spiniform; outer files displaced from four inner files, in close arrangement.

Basal armature distinct; basal swelling present, *c.* 70 (*n* = 1) in diameter, with characteristic group of billhooks on antiothrial surface (Fig. 9C); hooks on bothrial surface falcate, enlarged, in tight arrangement, with interdigitated bases (Fig. 9C); internal and external surface on apical part of basal swelling devoid of hooks.

Segments acraspedote; first segments posterior to velum immature, much wider than long, 20 (*n* = 3) $\times$ 225–360 (308 ± 73 ; *n* = 3); first mature segments 195–340 (274 ± 72 ; *n* = 4) $\times$ 315–600 (441 ± 141 ; *n* = 4); most mature segments longer than wide (Fig. 8A), 1,210–2,875 ($1,966 \pm 567$; *n* = 7) $\times$ 460–650 (532 ± 65 ; *n* = 6). Genital pores alternate irregularly, in posterior third of segment (Fig. 8A); pore inconspicuous; regions anterior and posterior to pore thickened (Fig. 8A,B). Hermaphroditic sac oval, 85–110 (97 ± 10 ; *n* = 6) $\times$ 123–165 (133 ± 16 ; *n* = 6), 130–138 (133 ± 4 ; *n* = 3) $\times$ 188–213 (202 ± 13 ; *n* = 3) in late mature segments; internal seminal vesicle present, at proximal pole of hermaphroditic sac (Fig. 8A,B); cirrus joins vagina at distal pole of hermaphroditic sac, unarmed; external seminal vesicle absent. Vas deferens coils posteriorly to ovarian isthmus. Testes numerous, occupy entire intervacular space, in several layers (Fig. 8A), 45–63 (52 ± 6 ; *n* = 10) $\times$ 30–38 (34 ± 3 ; *n* = 10) in mature segments, 68–75 (70 ± 2 ; *n* = 10) $\times$ 45–50 (46 ± 2 ; *n* = 10) in late mature segments; testes 243–297 (273 ± 26 ; *n* = 4) in number, 186–234 (210 ± 22 ; *n* = 4) pre-ovarian, 57–69 (63 ± 5 ; *n* = 4) postovarian. Vagina thin-walled, *c.* 5 (*n* = 1) wide, penetrates proximal pole of hermaphroditic sac (Fig. 8B), runs posteriorly towards Mehlis' gland. Seminal receptacle absent. Ovary in posterior third of segment, distant from posterior margin of segment (Fig. 8A); ovarian lobes 63–123 (107 ± 20 ; *n* = 8) $\times$ 155–195 (174 ± 13 ; *n* = 8) in mature segments, 158–283 (205 ± 51 ; *n* = 6) $\times$ 180–233 (208 ± 21 ; *n* = 6) in late mature segments. Mehlis' gland 55–93 (77 ± 16 ; *n* = 4) in diameter, 93–115 (107 ± 12 ; *n* = 3) wide in late mature segments. Vitelline follicles small, circumcortical, 18–23 (19 ± 2 ; *n* = 10) $\times$ 10–15 (13 ± 2 ; *n* = 10) in mature segments, 30–35 (32 ± 2 ; *n* = 10) $\times$ 18–20 (19 ± 1 ; *n* = 10) in terminal mature segments. Uterus median, tubular (Fig. 8A); uterine pore absent.

Remarks

Bilqees & Shaukat (1976) described the plerocercus of *Ps. arii* (as *Otobothrium arii* Bilqees & Shaukat, 1976) from *Ne. thalassina* (as *Arius serratus* Day) from the Arabian Sea off Karachi, Pakistan. The description of the tentacular armature, however, was inadequate and the specimens

were only differentiated from other species of '*Otobothrium*' recorded from Indian waters by the shape and position of the tentacular bulbs, the number of longitudinal rows of hooks and the infected host species. Beveridge et al. (2000) redescribed the species based on three plerocerci from *Neo. graeffei* (as *Arius graeffei*) off Brisbane, Queensland, Australia, and compared this material with a specimen deposited in the BMNH. These authors provisionally assigned the species to *Pseudotobothrium* Ward, 1954, based on an equal number of hooks on the external and internal tentacular surfaces of *Ps. dipsacum* (Linton, 1897) (type-species) and in *Ps. arii*. However, they admitted that their decision was a 'conservative approach' to avoid the erection of another monotypic genus within the Otobothriidae. Morphological differences between *Ps. dipsacum* and *Ps. arii* were demonstrated, e.g. the presence of a basal armature and origin of the principle hook rows on the bothrial surface in *Ps. arii* compared with the absence of a basal armature and origin of the principle hook rows on the antibothrial surfaces in *Ps. dipsacum* (see Beveridge et al., 2000). Beveridge et al. (2000) also synonymised the Pseudotobothriidae with the Otobothriidae, since each longitudinal file of hooks (i.e. 'band') on the bothrial surface of the tentacle corresponded to a principle row (in *Ps. dipsacum* and *Ps. arii*), as it is seen in the otobothriid genus *Poecilancistrum* Dollfus, 1929. This decision, however, was rejected by Palm (2004), who re-established the family Pseudotobothriidae.

The basal tentacular armature of *Ps. arii* is highly characteristic, with a group of billhooks on the antibothrial surface of the basal swelling and falcate hooks on the bothrial surface which are greatly enlarged and in a tight arrangement. The basal armature, thus, closely resembles that seen in *Poeciloacanthum oweni* Palm, 1995. The latter species, however, has a poeciloacanthous typical metabasal armature, with triangular chainette elements on the external tentacular surface and an orientation of the principle hook rows from the internal to the external surface (Palm, 1995), whereas *Ps. arii* possesses a heteroacanthous armature with six longitudinal files of hooks on the antibothrial surface and hook rows commencing on the bothrial surface (Beveridge et al., 2000). Following the definitions of a chainette given by Pintner (1913) and Dollfus (1942), as described in detail in Schaeffner et al. (2011), we do not consider the six longitudinal files of hooks on the antibothrial surface in *Ps. arii* to represent chainette elements. Therefore, the tentacular armature is of a heteroacanthous rather than a poeciloacanthous type, which clearly differentiates these species from one another.

The present material was collected from three specimens of the Borneo broadfin shark *Lamiopsis tephrodes*, which occurs around the coast of Borneo. The occurrence of *Ps. arii* from off Malaysian Borneo represents a new geographical record and expands the geographical range from Pakistan to the Indo-Malayan Archipelago and south to the eastern coast of Australia. The

presence of *Ps. arii* in three host individuals of a single species suggests a high degree of host-specificity.

In the redescription provided above, little effort has been made to describe the oncotaxy of this species, which was described in detail by Beveridge et al. (2000). The oncotaxy of the worms studied herein is consistent with that described previously.

Additional new host and locality records

***Fossobothrium perplexum* Beveridge & Campbell, 2005**

(Fig. 9F–H)

Type-host: *Anoxypristis cuspidata* (Latham) (Rajiformes: Pristidae).

Additional hosts: *Pristis zijsron* Bleeker (Rajiformes: Pristidae).

Type-locality: Arafura Sea off the Wessel Islands (eastern part), Northern Territory, Australia.

Additional localities: Coral Sea off Balgal, Queensland, Australia.

Material examined: 5 voucher specimens from *An. cuspidata* (NT-58) off the Wessel Islands (eastern part), Northern Territory, Australia, coll. J. N. Caira and K. Jensen, 13.xi.1999 (SAM AHC 35605); 1 voucher specimen from *Carcharhinus tilstoni* (Whitley) (Carcharhiniformes: Carcharhinidae) (AU-29) from Darwin (Buffalo Creek), Northern Territory, Australia, coll. J. N. Caira and K. Jensen, 5.viii.1997 (SAM AHC 35606).

Site of infection: Spiral intestine.

Remarks

Fossobothrium perplexum was recently described by Beveridge & Campbell (2005) from material collected from two species of sawfishes (Pristidae) off the Wessel Islands, Northern Territory and off Balgal, Queensland, Australia. Although, this species was described from a limited number of specimens, it is readily distinguishable from other otobothriid species by the presence of a ‘velum’, which combines both bothrial pits on the posterior margin of each bothrium (Beveridge & Campbell, 2005). The description of this species provided detailed information (including figures) of the scolex and segment morphology, and on the tentacular armature on every surface. The current specimens were obtained from the type-host (i.e. *An. cuspidata*) from the type-locality (i.e. the Wessel Islands, Northern Territory). An additional

specimen was obtained from the spiral intestine of *C. tilstoni* collected near Darwin (Northern Territory), which provides a new definitive host record, as well as a slight expansion of the geographical distribution of the species. One specimen was prepared for examination with SEM (Fig. 9F–H), which revealed novel information on the velum (*sensu* Beveridge & Campbell, 2005) connecting the paired bothrial pits (Fig. 9G). This bothrial area is covered with trifid spinitriches (Fig. 9H). The microthrix morphology of other areas of the scolex could not, however, be observed, because the entire specimen was covered with mucus.

***Proemotobothrium linstowi* (Southwell, 1912) Beveridge & Campbell, 2001**

Syns *Otobothrium linstowi* Southwell, 1912; *O. magnum* Southwell, 1924; *Rhynchobothrius aetobati* MacCallum, 1921
(Figs. 8C, 10, 12A,B)

Type-host: *Anoxypristis cuspidata* (Latham) (Rajiformes: Pristidae).

Additional hosts: *Rhynchobatus* cf. *laevis* (Rajiformes: Rhinobatidae); *Rhy. djiddensis* (Forsskal) (Rajiformes: Rhinobatidae); *Aetobatus narinari* (Euphrasen) (Rajiformes: Myliobatidae); *Carcharhinus* sp. (Carcharhiniformes: Carcharhinidae).

Type-locality: Gulf of Manaar, Sri Lanka ('Ceylon Pearl Banks') (08°52'N, 79°50'E).

Additional localities: Bay of Bengal off Nagapattinam (10°45'N, 79°51'E) and off Chennai ('Madras Coast'), India (13°03'N, 80°18'E); Strait off Singapore, Republic of Singapore (01°15'N, 103°51'E); Arafura Sea off the Wessel Islands, Northern Territory; Coral Sea off Mackay (21°08'S, 149°14'E); Flat Top Island (21°09'S, 149°14'E) and Heron Island, Queensland; Indian Ocean off Broome, Western Australia (17°58'S, 122°15'E); Timor Sea off Cape Van Diemen (11°10'S, 130°22'E) and Fog Bay, Northern Territory (12°45'S, 130°21'E).

Material examined: 5 voucher specimens from *Neotrygon picta* Last & White (Rajiformes: Dasyatidae) (NT-61) from the Arafura Sea off the Wessel Islands (eastern part), Northern Territory, coll. J. N. Caira and K. Jensen, 13.xi.1999 (SAM AHC 35610); 1 specimen from *N. leylandi* (Last) (Rajiformes: Dasyatidae) (NT-64) off Wessel Islands (eastern part), Northern Territory, coll. J. N. Caira and K. Jensen, 13.xi.1999 (used for SEM); 3 voucher specimens from *Rhynchobatus* sp. (Rajiformes: Rhinobatidae) (CM03-28) off Weipa, Queensland, Australia, coll. J. N. Caira and K. Jensen, 7.vi.2003 (SAM AHC 35608; serial sections in SAM AHC 35609).

Site of infection: Spiral intestine.

Remarks

Proemotobothrium was erected by Beveridge & Campbell (2001) to accommodate two species, *Pr. linstowi* (type-species) and *Pr. southwelli* Beveridge & Campbell, 2001. The genus is characterised by an acraspedote scolex, two bothria with prominent, paired bothrial pits on the posterior margins, elongate bulbs and a heteroacanthous, heteromorphous tentacular armature with hollow hooks, four distinctive hooks per principle row, a single intercalary hook and two or three hooks in a tandem position at the termination of each principle row. *Pr. linstowi* was described by Southwell (1912) as *Otobothrium linstowi* Southwell, 1912. The same author (1929) synonymised *O. magnum* Southwell, 1924 with *Pr. linstowi*. This decision, however, was not justified, and Dollfus (1942) noted that both species represented congeners rather than the same species. The type-specimens of *Pr. linstowi* were re-examined by Beveridge & Campbell (2001) and a direct comparison with new material collected from northern Australia revealed the congruence of these with Southwell's (1924) description of *O. magnum*, rather than the earlier description of *Pr. linstowi* by Southwell (1912). The types of *O. magnum* are not extant. Accordingly, Beveridge & Campbell (2001) synonymised *O. magnum* with *Pr. linstowi*, described *Pr. southwelli* for the specimens originally described by Southwell (1912), and transferred both species in a newly erected genus, *Proemotobothrium*. Both species show remarkable similarities in, for instance, the acraspedote scolex with long bulbs and an oncotaxy with a metabasal armature with four principle hooks and a single intercalary hook. However, Beveridge & Campbell (2001) clearly demonstrated the conspecificity of both species. *Pr. linstowi* possesses a larger scolex, larger tentacular hooks and bulbs of almost twice the size compared to the ones in *Pr. southwelli*. Although the tentacular armature appears similar in both species and distinct from other otobothriid taxa, they differ in the number of hooks in a tandem position associated with each principle row (i.e. two tandem hooks in *Pr. linstowi* versus three in *Pr. southwelli*) (see Fig. 12B and 12D, respectively). Palm (2004) applied a different numbering system for the metabasal hooks, to match the pattern in the oncotaxy of the Otobothriidae (i.e. with an intercalary hook row), thus the hooks in the tandem position a(a') and b(b') (in *Pr. linstowi*) or a(a') to c(c') (in *Pr. southwelli*) were regarded as part of either the principle hook row or part of the intercalary hook row (Fig. 12A and 12C). However, in Palm's (2004) numbering system, the hooks on the external tentacular surface are arranged asymmetrically (Fig. 12C). Furthermore, this system disregarded the presence of an intercalary hook row consisting of a single intercalary hook of the previous system by Beveridge & Campbell (2001).

Proemotobothrium linstowi was originally reported from the giant guitarfish *Rhynchobatus djiddensis*, from the ‘Ceylon Pearl Banks’ (off Sri Lanka) by Southwell (1924; as *O. magnum*). Beveridge & Campbell (2001) reported this species from the same host species from six different localities off northern Australia. These authors (2001) also listed two specimens of *Pr. linstowi* (deposited in the BMNH), which were obtained from an unidentified shark species (*Carcharhinus* sp.) off Sri Lanka. Palm (2004) listed *Aetobatus narinari* as another definitive host and off Singapore as a new locality record for this species, after re-examining material labelled as *Rhynchobothrium aetobati* McCallum, 1921 in the USNPC.

The present specimens are consistent with *Pr. linstowi* in their morphometric data and ontotaxy (Fig. 10B–D,F). A redescription of the species was not considered necessary, since it has already been described by Beveridge & Campbell (2001). However, longitudinal sections of a mature segment of one specimen revealed the presence of a hermaphroditic sac (Fig. 8C). Scanning electron micrographs show the tentacular armature (Fig. 10B–D,F), different views of the anterior part of the scolex (Fig. 10A,E) and tri- and tetra-radiate spinitriches on the distal bothrial surface (Fig. 10G). Additionally, three new host records are provided, which highlights a much wider host range for *Pr. linstowi*.

***Proemotobothrium southwelli* Beveridge & Campbell, 2001**

Syn. *Otobothrium linstowi* Southwell, 1912 (in part)

(Figs. 11, 12C,D)

Type-host: *Carcharhinus limbatus* (Müller & Henle) (Carcharhiniformes: Carcharhinidae).

Additional hosts: *Carcharhinus* cf. *dussumieri* (Carcharhiniformes: Carcharhinidae); *Gymnura* cf. *poecilura* (Rajiformes: Gymnuridae); *Rhizoprionodon acutus* (Rüppell) (Carcharhiniformes: Carcharhinidae); *Istiophorus platypterus* (Shaw) (Perciformes: Istiophoridae) (*intermediate host*); *Johnius borneensis* (Bleeker) (Perciformes: Sciaenidae) (*intermediate host*).

Type-locality: Fog Bay, Northern Territory, Australia (12°45’S, 130°21’E).

Additional localities: Coral Sea off Whitsunday Islands (20°15’S, 148°58’E), and off Heron Island, Queensland, Australia; Persian Gulf off Bandar Abbas, Iran (27°11’N, 56°16’E).

Material examined: 1 voucher specimen from *Anoxypristis cuspidata* (Latham) (Rajiformes: Pristidae) in Nickol Bay, Western Australia, coll. B. G. Robertson, 11.xi.1986 (SAM AHC 35607); 1 specimen from *C. limbatus* in Nickol Bay, Western Australia, coll. B. G. Robertson, 11.xi.1986 (used for SEM); 1 specimen from *C. fitzroyensis* (Whitley) (Carcharhiniformes:

Carcharhinidae) from Tommy Cut Creek, Northern Territory, Australia, coll. B. G. Robertson, 13.ix.1986 (used for SEM).

Site of infection: Spiral intestine (for adults).

Remarks

Beveridge & Campbell (2001) redescribed *Pr. southwelli* to solve the confusion over two species described by Southwell (1912, 1924) (see above). This species was reported from *C. limbatus* (type-host) from Fog Bay, Northern Territory, Australia (Beveridge & Campbell, 2001) and from *An. cuspidata* off Sri Lanka (Southwell, 1912). Haseli et al. (2010) recently reported it from three species of elasmobranchs in the Persian Gulf. The present study records *Pr. southwelli* from the type-host and two additional definitive hosts, as well as from additional localities off northern Australia.

The three new Australian specimens are consistent with *Pr. southwelli* in their morphometric data and oncotaxy. Two specimens were used for SEM microscopy (Fig. 11A–G). The SEM micrographs show two everted bothrial pits in close proximity on the posterior bothrial margin (Fig. 11C) and the external tentacular surface with tandem arrays of three hooks (Fig. 11G). Observations on the surface ultrastructure revealed additional information on the microthrix morphology. The bothrial pits are lined with enlarged bifid spinitriches (Fig. 11B,C), whereas other areas of the scolex are covered with trifid spinitriches on the distal bothrial surface (Fig. 11D), bifid spinitriches on the proximal bothrial surface (Fig. 11E) and both short and long acicular filitriches on the pars vaginalis (Fig. 11F).

Discussion

Apart from describing a new genus in the Otophthriidae, this study presents data on the adults of *Symbothriorhynchus tigaminacantha*, *Pseudotobothrium arii* and *Parotobothrium balli* for the first time. In addition, the first description of the terminal genitalia of *Proemotobothrium linstowi* provides additional useful information relating to segment morphology in species of this genus. Consequently, it is now possible to include data from the adults of these genera in an evaluation of generic and family characteristics.

Dollfus (1942) erected the Otophthriidae for two genera, *Otophthrium* and *Poecilancistrum*. Taxa in this family were defined by an atypical heteroacanthous armature and

a scolex with two bothria and paired bothrial pits on the bothrial margins ('fossettes ciliées' or 'organes rétractile', *sensu* Dollfus, 1942). The orders/suborders ('Homéacanthes', 'Hétéracanthes typia/atypica' and 'Pécilacanthes', *sensu* Dollfus, 1942) used to classify trypanorhynch cestodes (see Dollfus, 1942) were later rejected by Campbell & Beveridge (1994). These authors (1994) adapted Dollfus' (1942) system, but recognised four superfamilies (Homeoacanthoidea Dollfus, 1942; Heteracanthoidea Dollfus, 1942; Otophthorioidea Dollfus, 1942; and Poeciloacanthoidea Dollfus, 1942). In their new classification scheme (Campbell & Beveridge, 1994), the position of trypanorhynchs with an atypical heteroacanthous armature was amended, and the Poeciloacanthoidea was restricted to trypanorhynch families possessing chainette elements. Families with characteristics of once separate groups were thus placed within the Otophthorioidea, which then combined five families (i.e. Grillotiidae Dollfus, 1969; Molicolidae Beveridge & Campbell, 1989; Otophthoriidae; Pterophthoriidae Pintner, 1931; and Rhinoptericolidae Carvajal & Campbell, 1975) on the basis of the presence of 'bands of hooks' (i.e. heteroacanthous atypical armature; see Campbell & Beveridge, 1994). The reorganisation of trypanorhynchs based on their oncotaxy also separated species possessing bothrial pits ('sensory fossettes' or 'ciliated pits', *sensu* Campbell & Beveridge, 1994) into different superfamilies; for instance, the Paranybeliniidae were placed within the Homeoacanthoidea, whereas the Otophthoriidae remained in the Otophthorioidea (see Campbell & Beveridge, 1994). In a subsequent attempt to classify trypanorhynchs, Palm (1995) re-established the Pseudotophthoriidae and defined the Otophthorioidea by the possession of bothrial pits. As a result, members of the Paranybeliniidae were placed together with otophthoriid and pseudotophthoriid species, although differences in the oncotaxy were apparent. Beveridge et al. (2000) synonymised the Pseudotophthoriidae with the Otophthoriidae, since each longitudinal file of hooks (i.e. 'band') in the metabasal tentacular armature corresponded with a principle hook row. In his monograph, Palm (2004) rejected the decision made by Beveridge et al. (2000) and re-established the Pseudotophthoriidae, which then included *Parotophthrium*, *Pseudotophthrium* and *Poeciloacanthum* Palm, 1995. The Pseudotophthoriidae thereby incorporated genera with a homeoacanthous (i.e. *Parotophthrium*), heteroacanthous typical (i.e. *Pseudotophthrium*) and poeciloacanthous typical (i.e. *Poeciloacanthum*) tentacular armature. However, the main argument differentiating the three genera from taxa of the Otophthoriidae was the absence of intercalary hooks in the Pseudotophthoriidae, whereas all otophthoriid species possess a heteroacanthous atypical armature (i.e. with intercalary hooks) (Palm, 2004). Observations on the surface ultrastructure of one representative of the Paranybeliniidae by Palm (2008) revealed a microthrix pattern of the scolex

which resembled that of the Tentacularioidea. This author (Palm, 2008) subsequently transferred the Paranybeliniidae from the Obothrioidea to the Tentacularioidea.

The adults of *Pristiorhynchus*, *Symbothriorhynchus*, *Pseudotobothrium* and *Parotobothrium*, described here for the first time, possess a number of characters in common with other obothrioids, namely testes posterior to the female genitalia, the presence of a hermaphroditic sac, an internal seminal vesicle and the absence of a uterine pore. Although these features suggest a degree of uniformity in the segment morphology of the Obothrioidea, they do not allow these taxa to be distinguished from those in the sister group, the Lacistorhynchoidea (see Palm et al., 2009, and Olson et al., 2010). As a consequence, the sole feature currently differentiating these two superfamilies is the presence or absence of bothrial pits. However, some species within the Obothrioidea either lack bothrial pits (i.e. *Ancipirhynchus afossalis* or *Otobothrium curtum*), or possess reduced bothrial pits (i.e. *S. tigaminacantha*). The present redescriptions provide no ready solution to this dilemma, but reaffirm that the Obothrioidea, while a valid phylogenetic entity based on molecular data, is not identifiable on a morphological basis solely by the presence or absence of bothrial pits. Furthermore, the morphology of the segments does not provide any distinguishing features for these two related superfamilies.

On basis of the tentacular armature, both the Obothrioidea and the Lacistorhynchoidea exhibit a combination of distinct hook patterns. The Lacistorhynchoidea possess either a heteroacanthous atypical/multiatypical or poeciloacanthous atypical tentacular armature. The Obothrioidea show a combination of three different armature types within the Pseudotobothriidae (i.e. homeoacanthous armature, heteroacanthous typical and poeciloacanthous typical), whereas the Otobothriidae possess a heteroacanthous atypical tentacular armature. With respect to the surface ultrastructure, Palm (2008) observed that both the Obothrioidea and the Lacistorhynchoidea possess spinitriches with digitiform projections on the bothria or the entire scolex peduncle. Although related phylogenetically (Olson et al., 2010), no obvious differences can be observed in the oncotaxy, segment morphology or microthrix morphology of both superfamilies. Additional characters are therefore needed to allow the separation of these two taxa.

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Captions to figures

Fig. 1 *Pristiorhynchus palmi* n. g., n. sp. from *Anoxypristis cuspidata* in the Arafura Sea (A, C, D) and from *Pristis zijsron* in the Coral Sea (B). A, scolex, lateral view; B, scolex, dorso-ventral view; C, mature segment; D, bulb. *Abbreviations*: c, cirrus; ov, ovary; rm, retractor muscle; t, testis.

Fig. 2 *Pristiorhynchus palmi* n. g., n. sp. from *Anoxypristis cuspidata* in the Arafura Sea (A, D, E) and from *Pristis zijsron* in the Coral Sea (B, C). A, basal and metabasal tentacular armature, external surface; B, basal and metabasal tentacular armature, bothrial surface; C, basal and metabasal tentacular armature, antibothrial surface - note opposing surface to (B); D, profiles of tentacular hooks; E, apical tentacular armature, antibothrial surface. *Abbreviation*: bih, billhook.

Fig. 3 Scanning electron micrographs of *Pristiorhynchus palmi* n. g., n. sp. from *Anoxypristis cuspidata* in the Arafura Sea. A, scolex, dorso-ventral view; B, basal tentacular armature, antibothrial surface showing characteristic erect billhooks; C, pars bothrialis, oblique dorso-ventral view; D, distal bothrial surface showing trifid spinitriches; E, basal tentacular armature, external surface showing billhooks; F, proximal bothrial surface showing trifid spinitriches; G, pars vaginalis covered with papilliform to acicular filitriches.

Fig. 4 *Symbothriorhynchus tigaminacantha* Palm, 2004 from *Sphyrna lewini* in the Coral Sea (A–C) and the Indian Ocean (D). A, scolex, dorso-ventral view; B, detail of terminal genitalia; C, mature segment; D, bulbs showing retractor muscle forming internal loop (left) or directly inserting in anterior region (right). *Abbreviations*: c, cirrus; ex, excretory canal; hs, hermaphroditic sac; mg, Mehlis' gland; ov, ovary; rm, retractor muscle; t, testis; va, vagina; vd, vas deferens; vit, vitelline follicle.

Fig. 5 *Symbothriorhynchus tigaminacantha* Palm, 2004 from *Platycephalus bassensis* (A, B, D) and *Sphyrna lewini* (C) in the Coral Sea. A, metabasal tentacular armature, external surface; B, metabasal tentacular armature, internal surface - note opposing surface to (A); C, basal and metabasal tentacular armature, antibothrial surface; D, profiles of tentacular hooks. *Abbreviations*: eh, hooks on external surface of metabasal armature; enh 1 and 2, enlarged hooks on internal surface of basal armature; bh, hook on external surface of basal armature in lateral (left) and dorsal view (right); bih, billhooks.

Fig. 6 Diagrammatic representation of the external surface of the tentacular armature of *Symbothriorhynchus tigaminacantha* Palm, 2004 (A, based on specimens new to this study), *S. uranoscopi* Yamaguti, 1952 from Tosa Bay, Japan (B, based on type-specimen in MPM, SY50-71/22649) and ‘*S. uranoscopi*’ from off Mozambique (C, based on Palm, 2004, fig. 182g).

Fig. 7 *Parotobothrium balli* (Southwell, 1929) from *Carcharhinus amblyrhynchoideus* in the South China Sea. A, scolex, lateral view; B, mature segment; C, detail of terminal genitalia. *Abbreviations:* c, cirrus; ex, excretory canal; mg, Mehlis’ gland; ov, ovary; t, testis; ut, uterus; va, vagina; vd, vas deferens; vit, vitelline follicle.

Fig. 8 *Pseudotobothrium arii* (Bilqees & Shaukat, 1976) from *Lamiopsis tephrodes* in the South China Sea (A, B) and *Proemotobothrium linstowi* (Southwell, 1912) from *Neotrygon leylandi* in the Arafura Sea (C). A, mature segment; B,C, detail of terminal genitalia. *Abbreviations:* c, cirrus; mg, Mehlis’ gland; ov, ovary; t, testis; va, vagina; vd, vas deferens; vit, vitelline follicle.

Fig. 9 Scanning electron micrographs of *Pseudotobothrium arii* (Bilqees & Shaukat, 1976) from *Lamiopsis tephrodes* in the South China Sea (A–E) and *Fossobothrium perplexum* Beveridge & Campbell, 2005 from *Anoxypristis cuspidata* in the Arafura Sea (F–H). A, scolex, dorso-ventral to lateral view; B, distal bothrial surface showing trifold spinitriches; C, basal tentacular armature, external surface; D, proximal bothrial surface showing trifold spinitriches; E, pars vaginalis showing acicular filitriches; F, anterior region of scolex, lateral view; G, posterior bothrial margin showing paired bothrial pit connected by ‘velum’; H, delineated bothrial area between bothrial pits showing trifold spinitriches.

Fig. 10 Scanning electron micrographs of *Proemotobothrium linstowi* (Southwell, 1912) from *Neotrygon leylandi* in the Arafura Sea. A, anterior region of scolex, lateral view; B, basal tentacular armature, external surface showing region devoid of hooks; C, basal and metabasal tentacular armature, external surface; D, row of billhooks on external surface of the basal tentacular armature; E, anterior region of scolex, sub-lateral view; F, metabasal tentacular armature, external surface; G, distal bothrial surface showing tri- and tetra-radiate spinitriches.

Fig. 11 Scanning electron micrographs of *Proemotobothrium southwelli* Beveridge & Campbell, 2001 from *Carcharhinus fitzroyensis* in the Timor Sea (A–F) and from *C. limbatus* in the Indian

Ocean (G). A, scolex, dorso-ventral view; B, enlarged bifid spinitriches lining bothrial pit; C, posterior bothrial margin showing everted, paired bothrial pits; D, distal bothrial surface showing trifold spinitriches; E, proximal bothrial surface showing bifid spinitriches; F, pars vaginalis showing short and long acicular filitriches; G, metabasal tentacular armature, external surface.

Fig. 12 Diagrammatic representation of the external surface of the tentacular armature of *Proemotobothrium linstowi* (Southwell, 1912) (A,B, from Fig. 10F) and *Proemotobothrium southwelli* Beveridge & Campbell, 2001 (C,D, from Fig. 11G). Different numbering systems for the tentacular hooks; A,C, after Palm (2004); B,D, Present study.

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Title:

Pristiorhynchus palmi n. g., n. sp (Cestoda: Trypanorhyncha) from sawfishes (Pristidae) off Australia, with redescrptions and new records of six species of the Otabothrioidea Dollfus, 1942

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