Redescriptions and new records of species of *Otobothrium* Linton, 1890 (Cestoda: Trypanorhyncha)

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Abstract Redescriptions are provided for five incompletely described species of *Otobothrium* Linton, 1890: *Otobothrium alexanderi* Palm, 2004 from two species of carcharhinid sharks, *Carcharhinus cautus* (Whitley) and *C. melanopterus* (Quoy & Gaimard) at three localities off northern Australia; *O. australe* Palm, 2004 based on material collected from the type-host and type-locality and from six additional myliobatid and carcharhinid host species off Western Australia, the Northern Territory and northern Queensland; *O. insigne* Linton, 1905 from *Rhizoprionodon terraenovae* (Richardson) and *Sphyrna tudes* (Valenciennes) in the Atlantic Ocean off Senegal and the Democratic Republic of the Congo; *O. mugilis* Hiscock, 1954, previously known only from larval stages, based on adults from five sphyrnid and carcharhinid definitive host species off northern Australia and Malaysian Borneo; and *O. penetrans* Linton, 1907 from material collected from two species of hammerhead sharks (Sphyrnidae) in the Red Sea off Jordan and the Indian Ocean off Western Australia. Additional host and locality records are added for the type-species, *O. crenacolle* Linton, 1890 and for *O. carcharidis* (Shipley & Hornell, 1906). Two descriptions are provided for *Otobothrium* spp. treated here as *Otobothrium* sp. 1 from *C. melanopterus* off northern Australia and *Otobothrium* sp. 2 from *Sphyrna zygaena* (Linnaeus) in the Gulf of California, Mexico.

Introduction

Otobothrium Linton, 1890 was erected (Linton, 1890) to accommodate *O. crenacolle* Linton, 1890. Linton (1890) distinguished the then monotypic genus from species of '*Rhynchobothrium*' by the presence of four otosacs or ciliated pits (i.e. bothridial pits, *sensu* Palm & Overstreet, 2000; Jones, 2000) (now bothrial pits), which he considered 'rudimentary sense organs' (see Linton, 1890, p. 852). This morphological character was used by Dollfus (1942) to erect a new family, the Otobothriidae Dollfus, 1942, to include the atypical heteroacanthous trypanorhynch genera *Otobothrium* and *Poecilancistrum* Dollfus, 1929. Since Linton's (1890) description of *O. crenacolle*, ten additional species have been described within the genus. Dollfus (1942) designated two subgenera, *Otobothrium* (*Otobothrium*) Linton, 1890 for species with short bulbs, retractor muscles inserting in the anteriormost part of the bulbs and a tentacular armature with more than one transverse row of smaller hooks per row of larger hooks (see Dollfus, 1942) and *Otobothrium* (*Pseudotobothrium*) Dollfus, 1942, incorporating species with elongate bulbs, retractor muscles inserting in the anterior quarter of the bulbs and a tentacular armature with the same number of rows of smaller and larger hooks (see Dollfus, 1942). This separation of species into two subgenera was maintained by Campbell & Beveridge (1994). Palm (1995) elevated the subgenus to genus (i.e. *Pseudotobothrium* Dollfus, 1942) and family level (i.e. Pseudotobothriidae Palm, 1995). In his monograph on trypanorhynch cestodes, Palm (2004) recognised nine valid species of *Otobothrium*. The type-species, *O. crenacolle*, together with *O. curtum* (Linton, 1909) Dollfus, 1942, was treated as a synonym of *O. cysticum* (Mayer, 1842) Dollfus, 1942, while *O. dinoi* (Mendez, 1944) Palm, 2004 and *O. karachiense* Bilquees & Muslehuddin, 1975 (orthography corrected) were regarded as *species inquirendae*. Beveridge & Justine (2007a) described a new species, *O. parvum* Beveridge & Justine, 2007, and also provided redescriptions and additional information on four species of *Otobothrium*. These authors (2007a) re-established *O. crenacolle* and *O. curtum* as valid species, but considered *O. cysticum* a *species inquirenda* because the oncotaxy and segment morphology was unknown for this species. At present 11 species of *Otobothrium* are considered valid, namely: *O. alexanderi* Palm, 2004; *O. australe* Palm, 2004; *O. carcharidis* (Shipley & Hornell, 1906) Pintner, 1913; *O. crenacolle*; *O. curtum*; *O. insigne* Linton, 1905; *O. minutum* Subhapradha, 1955; *O. mugilis* Hiscock, 1954; *O. parvum*; *O. penetrans* Linton, 1907; and *O. propecysticum* Dollfus, 1969. Some of these species have been described and reported only from intermediate hosts, whereas, for other species, information on the adult worms and segment morphology is sparse. The current study provides redescriptions and additional information on five species of *Otobothrium* with a particular emphasis on the segment morphology. Novel information on geographical and

host records are provided for *O. carcharidis* and *O. crenacolle*. Two species could only be partly described, due to the small number of worms obtained and limited information available on their ontogeny. Even though distinct from congeners and unique based on morphological characters and in their morphometric data, both species are insufficiently known and are thus referred to as *Otobothrium* sp. 1 and sp. 2.

Materials and methods

Adult and larval cestodes were collected from several sampling localities: Australia: Arafura Sea off Nhulunbuy, Northern Territory (12°11'S, 136°41'E); off Weipa, Queensland (12°35'S, 141°42'E); off the Wessel Islands (eastern part), Northern Territory (11°17'S, 136°59'E); the Brisbane River (lower reaches), Brisbane, Queensland (27°25'S, 153°08'E); the Coral Sea off Heron Island, Queensland (23°26'S, 151°54'E); off Lizard Island, Queensland (14°40'S, 145°28'E); off Mackay, Queensland (21°08'S, 149°14'E); the Great Australian Bight off Esperance, Western Australia (33°51'S, 121°54'E); the Southern Ocean off Goolwa, South Australia (35°31'S, 138°46'E); the Indian Ocean off Bunbury, Western Australia (33°19'S, 115°37'E); off Fremantle, Western Australia (32°03'S, 115°44'E); the Timor Sea off Darwin, Northern Territory (12°27'S, 130°49'E); Fog Bay, Northern Territory (12°45'S, 130°21'E); Mary River (Sampan mouth), Northern Territory (12°16'S, 131°46'E); Nickol Bay, Western Australia (20°42'S, 116°51'E); Africa: Atlantic Ocean off Dakar, Senegal (14°35'N, 17°21'W); South Atlantic Ocean off the Democratic Republic of the Congo; Jordan: Red Sea (Gulf of Aqaba) off Aqaba (29°31'N, 34°58'E); Indonesia: Makassar Strait off Kota Baru, South Kalimantan, Indonesia (03°14'S, 116°13'E); Malaysia: South China Sea off Mukah, Sarawak, Malaysian Borneo (02°53'N, 112°05'E); Mexico: Gulf of California off San José del Cabo, Baja California Sur (23°02'N, 109°41'W); and USA: Atlantic Ocean off Grand Isle, Louisiana (29°12'N, 89°57'W).

Cestodes were fixed in 10% formalin for morphological observations and later transferred to 70% ethanol. Some specimens were provided by colleagues and the precise fixation methods used are not known. Specimens were stained with Celestine Blue, dehydrated in a graded ethanol series, cleared in clove oil and mounted in Canada balsam. Tentacles of selected specimens were detached from scoleces and mounted in glycerine jelly. Serial longitudinal histological sections of mature segments were prepared following embedding in paraffin and were stained with haematoxylin and eosin. Line drawings of specimens and histological sections 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), allowed to air dry, 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). 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 United States National Parasite Collection, Beltsville, Maryland, USA (USNPC), the Muséum National d'Histoire Naturelle, Paris, France (MNHN), the South Australian Museum, Adelaide, Australia (SAM), and the Queensland Museum, Brisbane, Australia (QM). Comparative material has been observed in the Natural History Museum, London, UK (BMNH) and the MNHN. Host nomenclature follows Naylor et al. (2012). If individual host specimens were found to belong to a species complex (e.g. *Rhizoprionodon acutus* (Rüppell)), numerals were added to refer to distinct clusters. These host species (e.g. *Rhizoprionodon* cf. *acutus* 2, *sensu* Naylor et al., 2012) are morphologically similar to the designated taxon, but were shown to be distinct based on their molecular phylogeny (data from Naylor et al., 2012). Abbreviations used for host- and locality records in the form of collection codes are as follows: AU, CM03 and NT, specimens from northern Australia; BO, specimens from Malaysian Borneo; KA, specimens from Indonesian Borneo; and BJ, specimens from Mexico. Additional information on these host specimens, searchable by collection code and accession number, is available from the Global Cestode Database (GCD; <http://elasmobranchs.tapewormdb.uconn.edu/>).

***Otobothrium alexanderi* Palm, 2004**

Type-host: *Tylosurus crocodilus crocodilus* (Péron & Lesueur) (Beloniformes: Belonidae; *intermediate host*).

Additional hosts: *Carcharhinus melanopterus* (Quoy & Gaimard) (Carcharhiniformes: Carcharhinidae).

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

Additional localities: North Pacific Ocean off Enewetak Atoll, Marshall Islands (11°27'N, 162°11'E).

Material examined: 6 voucher specimens from *Carcharhinus cautus* (Whitley)

(Carcharhiniformes: Carcharhinidae) off Darwin Harbour, Northern Territory, coll. B. G.

Robertson, 3.vii.1985 and 28.viii.1986 (SAM AHC 35583–84); 6 voucher specimens from *C.*

melanopterus (CM03-71) off Weipa, Queensland, Australia, coll. J. N. Caira and K. Jensen,

16.v.2004 (SAM AHC 35580; serial sections in SAM AHC 35581); off Darwin Harbour,

Northern Territory, coll. B. G. Robertson, 3.vii.1985 (SAM AHC 35582); and off Lizard Island,

coll. I. Beveridge, 6.ix.2010 (QM G233884).

Site of infection: Spiral intestine (for adults).

Redescription (Figs. 1–3)

[Based on 11 whole-mounts, 1 specimen used for SEM and longitudinal sections; tentacles detached from 2 specimens.] Small cestodes, 17.5–25.9 (21.1 ± 4.3 ; $n = 3$) mm long, with 50–57 (54 ± 4 ; $n = 3$) segments in mature strobilae; first mature segments appear posterior to segment 38–47 (42 ± 5 ; $n = 3$); gravid segments not present. Scolex craspedote (Fig. 1A), 1,920–2,390 ($2,128 \pm 205$; $n = 4$) long; maximum width at level of pars bulbosa, 865–1,050 (975 ± 97 ; $n = 3$) wide; pars bothriialis 270–470 (359 ± 88 ; $n = 4$) long. Bothria 2 in number, patelliform (Figs. 1A; 3A), 325–490 (415 ± 74 ; $n = 5$) $\times$ 410–510 (455 ± 36 ; $n = 8$), with free posterior margins; distal bothrial surface covered with aristate, trifid spinitriches (Fig. 3E); proximal bothrial surface covered with trifid spinitriches (Fig. 3B); paired bothrial pits present on posterior margin of bothria (Figs. 1A; 3A,G), 25–30 (28 ± 3 ; $n = 5$) $\times$ 20–25 (23 ± 2 ; $n = 5$) in dorsoventral view; area surrounding bothrial pit covered with trifid spinitriches (Fig. 3F) and acicular filitriches. Pars vaginalis longer than pars bothriialis, 1,260–1,760 ($1,520 \pm 252$; $n = 4$) long, covered with acicular filitriches (Fig. 3D); tentacle sheaths sinuous, 60–75 (68 ± 8 ; $n = 3$) in diameter. Pars bulbosa 420–680 (608 ± 125 ; $n = 4$) long; prebulbar organs and gland-cells within bulbs absent; bulbs elongate, fabiform (Fig. 1A,D), 615–700 (662 ± 30 ; $n = 9$) $\times$ 200–240 (218 ± 14 ; $n = 9$), surround anterior part of pars proliferans scolecis; bulb width : length ratio 1.0 : 2.6–3.5 (3.1 ± 0.3 ; $n = 9$); retractor muscle originates in anterior region of bulb; pars post-bulbosa absent; velum present. Scolex ratio (pars bothriialis : pars vaginalis : pars bulbosa) 1.0 : 3.7–4.8 : 0.9–2.4 ($1.0 : 4.3 \pm 0.5 : 1.8 \pm 0.7$; $n = 4$).

Fully everted tentacles 540–635 (578 ± 40 ; $n = 6$) long; diameter 44–90 (65 ± 23 ; $n = 5$) at base, 64–110 (87 ± 15 ; $n = 10$) in metabasal region, 58–70 (64 ± 9 ; $n = 2$) in distal region. Metabasal armature heteroacanthous, heteromorphous; hooks hollow, in ascending half spiral

rows. Hook files begin on internal surface of tentacle (Fig. 2C), terminate on external surface (Figs. 2A; 3C); 7 hooks per principle row (Fig. 2D); prominent space between hook files 1 and 1' (Fig. 2C). Hooks 1(1') uncinat, 48–70 (57 ± 10 ; $n = 4$) long, base 40–54 (47 ± 6 ; $n = 4$) long; hooks 2(2') uncinat, smaller, 38–57 (45 ± 7 ; $n = 10$) long, base narrower, 34–43 (37 ± 3 ; $n = 10$) long; hooks 3(3') uncinat, smaller, 33–52 (41 ± 8 ; $n = 6$) long, base narrower, 28–35 (30 ± 3 ; $n = 3$) long; hooks 4(4') uncinat, smaller, 30–40 (34 ± 5 ; $n = 5$) long, base narrower, 20–25 (22 ± 2 ; $n = 5$) long; hooks 5(5') uncinat, smaller, 22–33 (25 ± 5 ; $n = 5$) long, base narrower, 13–17 (15 ± 2 ; $n = 5$) long; hooks 6(6') rosethorn-shaped, 19–25 (21 ± 2 ; $n = 7$) long, base 15–22 (19 ± 3 ; $n = 7$) long, separated from hooks 5(5'); hooks 7(7') spiniform, 16–23 (19 ± 2 ; $n = 14$) long, base 2–4 (4 ; $n = 14$) long; intercalary hook row present (Fig. 2B), with 2 hooks a(a')–b(b') (Fig. 2D); hooks a(a') falcate, with angled tip, posterior to hooks 5(5'), 25–33 (28 ± 3 ; $n = 8$) long, base 4–7 (5 ± 1 ; $n = 8$) long; hooks b(b') falcate, with angled tip, posterior to hooks 5(5') and 6(6'), 25–35 (29 ± 3 ; $n = 9$) long, base 4–7 (6 ± 1 ; $n = 10$) long; first intercalary hooks appear posterior to hook row 7.

Distinctive basal armature present; initial 3 rows terminate in cluster of falcate hooks on external surface (Fig. 2A,B); falcate hooks erect, 26–35 (29 ± 3 ; $n = 5$) long, base narrow in lateral view, 3–4 (3 ± 1 ; $n = 5$) long, broad in dorso-ventral view; 3 characteristic, enlarged hooks on external surface (Figs. 2A,B; 3C), uncinat, with interdigitating bases, anterior to cluster of falcate hooks, increasing in size towards antithoracic surface, largest hook 49–50 (50 ± 1 ; $n = 2$) long, base 39–43 (41 ± 3 ; $n = 2$) long; medium-sized hook median, 40–41 (40 ± 1 ; $n = 2$) long, base 35–37 (36 ± 1 ; $n = 2$) long; smallest hook 28–33 (31 ± 4 ; $n = 2$) long, base 30–33 (32 ± 2 ; $n = 2$) long.

Segments acraspedote; first segments immediately posterior to velum immature, 15–20 (18 ± 3 ; $n = 3$) $\times$ 440–1,020 (760 ± 295 ; $n = 3$); first mature segments 500–515 (508 ± 11 ; $n = 2$) $\times$ 1,090–1,210 ($1,150 \pm 85$; $n = 2$); terminal mature segments 1,825–2,540 ($2,183 \pm 506$; $n = 2$) $\times$ 580–890 (735 ± 219 ; $n = 2$) (Fig. 1C). Genital pores alternate irregularly, in posterior third of segment (Fig. 1C); pore inconspicuous; regions anterior and posterior to pore thickened. Hermaphroditic sac oval (Fig. 1B,C), 145–175 (164 ± 13 ; $n = 4$) $\times$ 225–255 (241 ± 16 ; $n = 4$); internal seminal vesicle present, at proximal pole of hermaphroditic sac, 80 ($n = 3$) $\times$ 25 ($n = 3$); cirrus joins vagina at distal pole of hermaphroditic sac, unarmed; external seminal vesicle absent. Vas deferens coils posteriorly to ovarian isthmus. Testes numerous, 70–85 (78 ± 5 ; $n = 16$) $\times$ 50–60 (54 ± 3 ; $n = 16$), occupy entire intervascular space, in several layers (Fig. 1C); testes $c.375$ ($n = 1$) in number, $c.270$ ($n = 1$) pre-ovarian, $c.105$ ($n = 1$) postovarian. Vagina 15–20 (18 ± 4 ; $n = 2$) wide inside hermaphroditic sac, penetrates proximal pole of hermaphroditic sac (Fig. 1B), runs posteriorly towards Mehlis' gland, $c.13$ ($n = 1$) wide. Seminal receptacle absent. Ovary in

posterior third of segment (Fig. 1C), distant from posterior margin of segment; ovarian lobes 240–345 (292 ± 38 ; $n = 8$) $\times$ 230–255 (239 ± 11 ; $n = 8$); Mehlis' gland 95–110 (105 ± 9 ; $n = 3$) in diameter. Vitelline follicles small, circumcortical, 30–40 (35 ± 3 ; $n = 16$) $\times$ 20–25 (25 ± 1 ; $n = 16$). Uterus median, tubular (Fig. 1C); uterine pore absent. Ventral osmoregulatory canal 20–25 (23 ± 2 ; $n = 8$) in diameter.

Remarks

Otobothrium alexanderi differs from its congeners in possessing a very wide pars bulbosa and a distinctive basal tentacular armature with three characteristic, uncinata macrohooks on the external surface. Palm (2004) described the species based on plerocerci from the extraocular musculature of the hound needlefish *Tylosurus crocodilus crocodilus* off Pelabuhan Ratu, Indonesia and adult worms from the spiral intestine of the blacktip reef shark *Carcharhinus melanopterus*, from off Enewetak Atoll, Marshall Islands. Although the plerocerci and adult specimens possessed an identical ontotaxy and similar bulb measurements, the adult worms had a much smaller scolex compared to the plerocerci (i.e. 2.9–3.4 vs 1.5–2.0 mm in length, respectively; see Palm, 2004). The present specimens were obtained from the spiral intestine of *C. melanopterus* and *C. cautus* from three different localities off northern Australia. This increases the geographical distribution of this parasite in South-East Asia and, furthermore, represents the first record of *O. alexanderi* from Australian waters.

The Australian specimens possess a scolex which is slightly larger than those described by Palm (2004) from adult cestodes (i.e. 1.9–2.4 vs 1.5–2.0 mm, respectively), but much smaller than those of the plerocerci from Indonesia (i.e. 2.9–3.4 mm). Possible explanations for the differences in morphometric data between these plerocerci and adults from Australia could be regional disparities or species-specific adaptations to different intermediate hosts. New material of *O. alexanderi* is needed to clarify the size differences. At present, we follow the decision made by Palm (2004) and tentatively consider both adults and plerocerci conspecific.

Although, Palm (2004), in the original description, stated that the vagina runs parallel to the cirrus-sac and that a seminal receptacle is present in specimens of *O. alexanderi* (see Palm, 2004), the present specimens lacked a seminal receptacle and possessed a hermaphroditic sac (Fig. 1B,C), which is in accordance with every other species of *Otobothrium* examined within the present study. Scanning electron micrographs of the northern Australian specimens provided novel information about the microthrix pattern of *O. alexanderi*, which was not given in the original description by Palm (2004).

***Otobothrium australe* Palm, 2004**

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

Type-locality: Nickol Bay, Western Australia, Australia.

Material examined: 111 specimens from *C. limbatus*, Nickol Bay, Western Australia, coll. B. G. Robertson, 11.xi.1986 (paralectotypes: SAM AHC 35502–53; serial sections in SAM AHC 35561); Mary River (Sampan mouth), Northern Territory, coll. B. G. Robertson, 12.ix.1986 (voucher specimens: SAM AHC 35558); 12 voucher specimens from *C. amboinensis* (Müller & Henle) (Carcharhiniformes: Carcharhinidae), Nickol Bay, Western Australia, coll. B. G. Robertson, 11.xi.1986 (SAM AHC 35559); 1 voucher specimen from *C. melanopterus*, Mackay, Queensland, coll. B. G. Robertson, 21.viii.1985 (SAM AHC 35554); 28 voucher specimens from *C. sorrah* (Müller & Henle) (Carcharhiniformes: Carcharhinidae), Nickol Bay, Western Australia, coll. B. G. Robertson, 11.xi.1986 (SAM AHC 35560); 16 voucher specimens from *Myliobatis australis* Macleay (Rajiformes: Myliobatidae) from off Esperance, Western Australia, coll. B. G. Robertson, 20.xii.1986 (SAM AHC 35555); off Fremantle, Western Australia, coll. B. G. Robertson, 4.xii.1986 (SAM AHC 35557); and 1 voucher specimen from *Rhizoprionodon acutus* (Rüppell) (Carcharhiniformes: Carcharhinidae), Nickol Bay, Western Australia, coll. B. G. Robertson, 11.xi.1986 (SAM AHC 35556).

Site of infection: Spiral intestine.

Redescription (Figs. 4–6)

[Based on 165 whole-mounts, 4 specimens used for SEM, segments of 2 worms used for longitudinal sections.] Small cestodes, 12.4–29.7 (18.9 ± 4.8 ; $n = 14$) mm long, with 27–40 (35 ± 4 ; $n = 15$) segments in mature strobilae; first mature segments appear posterior to segments 22–31 (26 ± 3 ; $n = 15$); gravid segments not present. Scolex craspedote (Figs. 4A,B; 6A,B), 700–980 (851 ± 95 ; $n = 15$) long; maximum width at mid-level of pars bulbosa, 400–510 (458 ± 36 ; $n = 14$) wide; pars bothrialis 250–330 (283 ± 21 ; $n = 15$) $\times$ 320–435 (366 ± 57 ; $n = 4$). Bothria 2 in number, patelliform (Figs. 4A,B; 6A,B), 235–310 (284 ± 19 ; $n = 16$) $\times$ 300–440 (372 ± 43 ; $n = 16$); proximal bothrial surface covered with trifid spinitriches and acicular filitriches; paired bothrial pits present on posterior margin of bothria (Figs. 4A,B; 6A–C); bothrial pit lined with bifid spinitriches (Fig. 6C). Pars vaginalis longer than pars bothrialis, 360–740 (589 ± 114 ; $n = 15$) long, covered with acicular filitriches; tentacle sheaths sinuous. Pars bulbosa 230–360 (259 ± 34 ; $n = 15$) long; prebulbar organs and gland-cells absent; bulbs ovoid (Fig. 4A,B,E), 205–260

(233 ± 15 ; $n = 25$) $\times$ 90–160 (123 ± 15 ; $n = 25$), surrounding pars proliferans scolecis; bulb width : length ratio 1.0 : 1.5–2.3 (1.9 ± 0.2 ; $n = 25$); retractor muscle originates in anterior region of bulb, describes internal loop inside bulb in some specimens; pars post-bulbosa absent; velum present. Scolex ratio (pars bothriialis : pars vaginalis : pars bulbosa) 1.0 : 1.3–2.8 : 0.7–1.3 ($1.0 : 2.1 \pm 0.4 : 0.9 \pm 0.2$; $n = 15$).

Fully everted tentacles 340–500 (389 ± 54 ; $n = 8$) long; diameter 25–29 (27 ± 3 ; $n = 2$) at base, 38–44 (41 ± 4 ; $n = 2$) at basal swelling, 22–33 (27 ± 4 ; $n = 8$) in metabasal region.

Metabasalar armature heteroacanthous, heteromorphous; hooks hollow, in ascending half spiral rows. Hook files begin on internal surface of tentacle (Figs. 5A; 6F), terminate on external surface (Figs. 5D; 6E); 7 hooks per principle row; prominent space between hook files 1 and 1' (Figs. 5A; 6F). Hooks 1(1') uncinat, 15–18 (17 ± 1 ; $n = 8$) long, base 11–14 (12 ± 1 ; $n = 8$) long; hooks 2(2') uncinat, smaller, 11–17 (14 ± 2 ; $n = 12$) long, base 10–11 (10 ± 1 ; $n = 11$) long; hooks 3(3') uncinat, 12–16 (14 ± 1 ; $n = 7$) long, base 7–10 (9 ± 1 ; $n = 7$) long; hooks 4(4') uncinat, smaller, 8–13 (11 ± 2 ; $n = 6$) long, base 4–7 (6 ± 1 ; $n = 6$) long; hooks 5(5') uncinat, smaller, 7–11 (9 ± 2 ; $n = 6$) long, base 3–6 (4 ± 1 ; $n = 6$) long; hooks 6(6') falcate, smaller, 2–5 (4 ± 1 ; $n = 10$) long, base 1–3 (2; $n = 13$) long; hooks 7(7') falcate, smaller, 2–4 (3 ± 1 ; $n = 6$) long, base 1–2 (2; $n = 7$) long; intercalary hook row present (Figs. 5D; 6E), with 2 hooks a(a')–b(b'); hooks a(a') falcate, 4–7 (6 ± 1 ; $n = 13$) long, base 1–3 (2; $n = 13$) long; hooks b(b') falcate, smaller, 2–5 (3 ± 1 ; $n = 10$) long, base 1–2 (2; $n = 10$) long.

Distinctive basal armature present; initial 4 rows of hooks falcate (Fig. 5B,C), 18–27 (22 ± 2 ; $n = 12$) long, base 7–12 (9 ± 2 ; $n = 12$) long; basal swelling present, with greatly enlarged hook on internal surface (Figs. 5B,C,E; 6D,G), 30–39 (35 ± 5 ; $n = 3$) long, base 25–30 (27 ± 2 ; $n = 3$) long; largest hook on tentacle; adjacent hooks smaller, decreasing in size towards external surface; 2 characteristic billhooks on external surface (Figs. 5C,E; 6D), on apical region of basal swelling; billhooks b1–b2 (Figs. 5C,E; 6D) of characteristic shape; b1 18–26 (22 ± 5 ; $n = 2$) long, base 10–12 (11 ± 1 ; $n = 2$) long; b2 displaced posteriorly, c.20 ($n = 1$) long, base c.3 ($n = 1$) long.

Segments acraspedote; first segments posterior to velum immature, much wider than long, 15–40 (25 ± 8 ; $n = 13$) $\times$ 190–375 (280 ± 55 ; $n = 13$); first mature segments 470–1,070 (732 ± 225 ; $n = 15$) $\times$ 225–485 (391 ± 70 ; $n = 15$); mature segments become longer than wide posteriorly; terminal mature segments 1,530–2,820 ($2,163 \pm 352$; $n = 13$) $\times$ 390–690 (555 ± 91 ; $n = 13$) (Fig. 4C). Genital pores alternate irregularly, in posterior third of segment (Fig. 4C); pore inconspicuous; regions anterior and posterior to pore thickened. Hermaphroditic sac oval (Fig. 4C,D), 210–285 (243 ± 21 ; $n = 10$) $\times$ 150–195 (176 ± 14 ; $n = 10$); internal seminal vesicle present, at proximal pole of hermaphroditic sac, 60–100 (80 ± 28 ; $n = 2$) $\times$ 20–25 (23 ± 4 ; $n = 2$);

cirrus joins vagina at distal pole of hermaphroditic sac (Fig. 4D), unarmed; external seminal vesicle absent. Vas deferens coils posteriorly to ovarian isthmus. Testes numerous, occupy complete intervascular space, in several layers (Fig. 4C), 75–100 (83 ± 7 ; $n = 15$) $\times$ 60–70 (65 ± 4 ; $n = 15$); testes 184–263 (225 ± 26 ; $n = 10$) in number, 112–159 (133 ± 17 ; $n = 10$) preporal, 72–112 (93 ± 12 ; $n = 10$) postporal, 57–91 (74 ± 10 ; $n = 10$) postovarian. Vagina penetrates antero-proximal pole of hermaphroditic sac, runs posteriorly towards Mehlis' gland, 10–15 (13 ± 3 ; $n = 4$) wide, increases in width inside hermaphroditic sac, 20–45 (34 ± 9 ; $n = 7$) wide. Seminal receptacle absent. Ovary in posterior third of segment, distant from posterior margin of segment (Fig. 4C); ovarian lobes 175–280 (219 ± 35 ; $n = 10$) $\times$ 120–240 (160 ± 34 ; $n = 10$); Mehlis' gland 90–110 (98 ± 9 ; $n = 4$) in diameter. Vitelline follicles small, circumcortical, 20–35 (28 ± 4 ; $n = 17$) $\times$ 15–25 (19 ± 3 ; $n = 17$). Uterus median, tubular (Fig. 4C); uterine pore absent.

Remarks

Campbell & Beveridge (1994) provided drawings of the scolex, a mature segment and two tentacular surfaces of an undescribed species of *Otobothrium* (see Campbell & Beveridge, 1994, figs. 7.250, 7.252–7.254). This species remained undescribed until Palm (2004) provided a species description, including the drawings of Campbell & Beveridge (1994). Although the tentacular armature of *O. australe* was sufficiently well described by Palm (2004), only a few measurements were provided for morphological features (i.e. the length of the adult worms, scolex and individual body regions and proportions, and the number of segments and testes), indicating that only a single specimen was measured. The type-material is deposited in the BMNH and had been collected by B. G. Robertson in 1986 from a blacktip shark *C. limbatus* at Nickol Bay, Western Australia. The present material includes specimens from the same collection as the types and from five additional host species from the type-locality and four additional localities from off Australia. This increases the host spectrum to six definitive host species (i.e. mostly carcharhinid sharks) and the geographical distribution of this species within Australian waters. *O. australe* is here redescribed with particular emphasis on the segment morphology.

This species is readily distinguished from congeners by two characteristically shaped billhooks on the external surface of the basal tentacular swelling (Figs. 5C,E; 6D). Palm (2004) stated that there were two enlarged hooks on the internal surface of the basal swelling. The present specimens possess several enlarged hooks on the basal swelling. However, only one hook is greatly enlarged and represents the largest hook of the tentacle (Figs. 5B,C,E; 6G). Although, *O. australe* is allegedly closely related to *O. mugilis* (see Palm, 2004), the presence of

this single enlarged hook and two characteristic billhooks on the basal swelling clearly separate both species. The present specimens possessed a craspedote scolex and a hermaphroditic sac incorporating both vagina and cirrus, unlike the original description in which specimens were characterised by an acraspedote scolex and a cirrus-sac (see Palm, 2004). Furthermore, a different numbering system for the metabasal armature was applied. We recognised seven principle and two intercalary hooks in the metabasal armature (Fig. 5D). The final hooks of the intercalary hook row, hooks c(c') of Palm (2004), now become hooks 7(7'), because they are in line with the principle hook row (Fig. 5D), which has priority over the intercalary hook row.

Palm (2004) did not designate a holotype for *O. australe*. We here take the opportunity to designate a lectotype and paralectotypes (designated on the slides). Furthermore, we here include the remaining specimens from the type-host and type-locality (SAM AHC 35502–53) as part of the type-series.

***Otobothrium insigne* Linton, 1905**

Type-host: *Carcharhinus obscurus* (Lesueur) (Carcharhiniformes: Carcharhinidae).

Additional hosts: *C. leucas* (Müller & Henle) (Carcharhiniformes: Carcharhinidae); *Ariopsis felis* (Linnaeus) (Siluriformes: Ariidae; *intermediate host*); *Balistes polylepis* Steindachner (Tetraodontiformes: Balistidae; *intermediate host*).

Type-locality: North Atlantic Ocean off Beaufort, North Carolina, USA (34°40'N, 76°40'W).

Additional localities: Gulf of Mexico off Grand Isle, Louisiana, USA; North Pacific Ocean off Puerto Angel, Mexico (15°39'N, 96°29'W).

Material examined: 5 plerocerci from *A. felis* off Grand Isle, Louisiana, USA, coll. M. Hildreth (USNPC 78166, USNPC 105630); 8 voucher specimens from *Rhizoprionodon terraenovae* (Richardson) (Carcharhiniformes: Carcharhinidae) in the South Atlantic Ocean off the Democratic Republic of the Congo (formerly Zaire), Africa, coll. E. Dartevelle, 1.xii.1947 (MNHN HEL280–292; serial sections in MNHN HEL293–299); 1 voucher specimen from *Sphyrna tudes* (Valenciennes) (Carcharhiniformes: Sphyrnidae) in the Atlantic Ocean off Dakar, Senegal, Africa, coll. E. Dartevelle, 14.vii.1946 (MNHN HEL300).

Site of infection: Spiral intestine (for adults).

Redescription (Figs. 7–10)

[Based on 12 whole-mounts, 2 specimens used for SEM, segments of 1 specimen used for longitudinal sections, tentacles removed from 2 specimens.] Mature cestodes 14.7–25.2 (19.9 ± 0.4 ; $n = 5$) mm long, with 21–34 (28 ± 4 ; $n = 7$) segments; gravid segments not present. Scolex craspedote (Fig. 7A), 4,450–5,175 ($4,842 \pm 307$; $n = 6$) long; maximum width at mid-level of pars bothrialis 3,050–3,425 ($3,270 \pm 158$; $n = 5$); pars bothrialis 1,550–2,200 ($1,850 \pm 268$; $n = 6$) long. Bothria 2 in number, oval (Fig. 7A), with thick, fleshy margins (Fig. 9A,B), 1,800–2,125 ($1,963 \pm 230$; $n = 2$) $\times$ 1,275–1,525 ($1,400 \pm 177$; $n = 2$); paired bothrial pits present on posterior margins of bothria (Figs. 7A; 9B,C), 140–220 (184 ± 24 ; $n = 9$) $\times$ 90–210 (132 ± 39 ; $n = 9$) in lateral view. Pars vaginalis longer than pars bothrialis, 2,675–3,075 ($2,875 \pm 157$; $n = 6$) long; tentacle sheaths almost straight in pars bothrialis, strongly coiled to sinuous anterior to bulbs, 100–113 (101 ± 4 ; $n = 10$) wide. Pars bulbosa 1,150–1,475 ($1,279 \pm 113$; $n = 6$) $\times$ 1,775–2,150 ($1,958 \pm 142$; $n = 6$); prebulbar organs and gland-cells within bulbs absent; bulbs ovoid (Fig. 7A,C), 1,025–1,325 ($1,203 \pm 87$; $n = 16$) $\times$ 300–500 (422 ± 47 ; $n = 16$), surround pars proliferans scolecis (Fig. 7A); bulb width : length ratio 1.0 : 2.4–3.8 (2.9 ± 0.4 ; $n = 16$); retractor muscle originates in anterior region of bulb; velum 1,225–1,700 ($1,450 \pm 171$; $n = 8$) $\times$ c.1,450 ($n = 1$) posteriorly, surrounds anterior 950 ($n = 1$) of pars proliferans scolecis; bulbs not reaching posterior region of velum (Fig. 7A), prominent space 475–950 (656 ± 165 ; $n = 8$) between bulbs and posterior extremity of velum. Scolex ratio (pars bothrialis : pars vaginalis : pars bulbosa) 1.0 : 1.3–1.9 : 0.6–0.8 ($1.0 : 1.6 \pm 0.3 : 0.7 \pm 0.1$; $n = 6$).

Fully everted tentacles 2,375–3,175 ($2,775 \pm 566$; $n = 2$) long, slightly wider at base; diameter 89–150 (127 ± 23 ; $n = 10$) at base, 94–114 (106 ± 11 ; $n = 3$) at level of billhooks, 86–140 (109 ± 16 ; $n = 14$) in metabasal region, 84–120 (104 ± 12 ; $n = 9$) in distal region.

Metabasal armature heteroacanthous, heteromorphous; hooks hollow, in ascending half spiral rows (Figs. 8C; 9D,G,I). Hook files begin on bothrial surface of tentacle (Figs. 8A; 9D,H), terminate on antibothrial surface (Figs. 8B,C; 9E,F); 7 hooks per principle row; prominent space between hook files 1 and 1'; hooks 5(5') and 6(6') separated. Hooks 1(1') uncinata, 43–63 (49 ± 6 ; $n = 18$) long, base 35–53 (43 ± 6 ; $n = 17$) long; hooks 2(2') uncinata, 46–60 (52 ± 5 ; $n = 30$) long, base narrower, 28–43 (37 ± 3 ; $n = 30$) long; hooks 3(3') falcate, 41–60 (50 ± 5 ; $n = 18$) long, base 21–30 (26 ± 4 ; $n = 18$) long; hooks 4(4') falcate, smaller, 31–53 (44 ± 9 ; $n = 12$) long, base 15–25 (21 ± 4 ; $n = 12$) long; hooks 5(5') falcate, smaller, 21–40 (31 ± 9 ; $n = 14$) long, base 7–20 (14 ± 4 ; $n = 14$) long; hooks 6(6') rosethorn-shaped, 20–28 (24 ± 2 ; $n = 20$) long, base 18–30 (23 ± 3 ; $n = 20$) long; hooks 7(7') falcate, smaller, displaced anteriorly; 5–18 (10 ± 5 ; $n = 16$) long, base 3–5 (4 ± 1 ; $n = 16$) long; intercalary hook row present (Figs. 8B,C; 9E,F), with 2

hooks a(a')–b(b'); hooks a(a') falcate, posterior to hooks 5(5') and 6(6'), 15–28 (21 ± 4 ; $n = 21$) long, base 4–10 (7 ± 2 ; $n = 21$) long; hooks b(b') falcate, posterior to hooks 6(6'), smaller, 10–25 (18 ± 5 ; $n = 12$) long, base 3–10 (6 ± 2 ; $n = 12$) long.

Distinctive basal armature present; hooks 1(1') of first principle row much smaller than those of remaining metabasal armature (Fig. 8C), 40–50 (45 ± 5 ; $n = 3$) long, base 25–30 (27 ± 3 ; $n = 3$) long. Initial 2 rows terminate in group of spiniform hooks on antiothrial surface (Fig. 8B–D); spiniform hooks erect, 18–40 (27 ± 6 ; $n = 22$) long, base 3–15 (6 ± 4 ; $n = 22$) long; group of billhooks anterior to spiniform hooks on antiothrial surface (Fig. 8B–D); billhooks 15–35 (23 ± 5 ; $n = 37$) long, base 3–20 (8 ± 4 ; $n = 37$) long; first intercalary hooks appear posterior to hook row 4.

Segments acraspedote; immature segments posterior to velum much wider than long (Fig. 7A), 125–225 (175 ± 46 ; $n = 4$) $\times$ 1,775–2,650 ($2,256 \pm 366$; $n = 4$); first mature segments 425–700 (550 ± 117 ; $n = 4$) $\times$ 1,400–2,300 ($1,938 \pm 386$; $n = 4$); mature segments becoming longer than wide posteriorly; terminal mature segments 1,300–1,675 ($1,542 \pm 210$; $n = 3$) $\times$ 1,000–1,375 ($1,158 \pm 194$; $n = 3$). Genital pores alternate irregularly, in mid-line of segment or slightly posterior to mid-line (Fig. 7B); pore inconspicuous; regions anterior and posterior to pore thickened. Hermaphroditic sac oval (Fig. 7B,D), 115–165 (148 ± 29 ; $n = 3$) $\times$ 230–260 (247 ± 15 ; $n = 3$); internal seminal vesicle present, at proximal pole of hermaphroditic sac, 40–90 (61 ± 17 ; $n = 6$) $\times$ 55–105 (78 ± 21 ; $n = 6$); cirrus joins vagina at distal pole of hermaphroditic sac (Fig. 7D), unarmed; external seminal vesicle absent. Vas deferens coils posteriorly to ovarian isthmus. Testes numerous, occupy complete intervacular space (Fig. 7B), in several layers, 45–85 (66 ± 11 ; $n = 21$) $\times$ 35–60 (48 ± 8 ; $n = 21$); testes 429–597 (499 ± 87 ; $n = 3$) in number, 311–388 (342 ± 41 ; $n = 3$) preporal, 128–209 (161 ± 43 ; $n = 3$) postporal. Vagina penetrates proximal pole of hermaphroditic sac (Fig. 7B,D), runs posteriorly towards Mehlis' gland, 18–25 (22 ± 3 ; $n = 9$) wide. Seminal receptacle absent. Ovary not fully developed; ovarian lobes 100–115 (108 ± 11 ; $n = 2$) $\times$ 185–235 (210 ± 35 ; $n = 2$); Mehlis' gland 125–165 (137 ± 17 ; $n = 5$) in diameter. Vitelline follicles inconspicuous, circumcortical, 8–13 (9 ± 2 ; $n = 15$) in diameter. Uterus median, tubular (Fig. 7B); uterine pore absent. Ventral osmoregulatory canals 50–100 (83 ± 19 ; $n = 8$) in diameter.

Remarks

Otobothrium insigne was described by Linton (1905) from the spiral intestine of a dusky shark *Carcharhinus obscurus* off the coast of Beaufort, North Carolina, USA. Linton (1905) provided line drawings of one complete specimen, the anterior part of the scolex of two specimens and

two tentacular surfaces (i.e. bothrial and antibothrial surface) of the metabasal armature. Yamaguti (1959) treated this species as a synonym of *Pseudotobothrium dipsacum* (Linton, 1897). Hildreth & Lumsden (1985) described the plerocercus of this species from catfishes collected from the Gulf of Mexico. These authors (1985) recovered 3,656 plerocerci and were the first to describe the ontotaxy of this species in great detail and to provide SEM micrographs of the scolex and the tentacular armature. Additional studies on the plerocerci focused on the microanatomy (Hildreth & Lumsden, 1987), excystment (Hildreth & Lazzara, 1987) and carbohydrate metabolism (Hildreth & Lumsden, 1988; Hildreth, 1989). Campbell & Beveridge (1994) redrew the scolex of *O. insigne* after Hildreth & Lumsden (1985) and applied a different numbering system for the tentacular hooks (see Campbell & Beveridge, 1994, figs. 7.251, 7.255). Palm (1995) added a second definitive host, *C. leucas*, and provided SEM micrographs of the tentacular armature and microthrix morphology. The present specimens were obtained from the spiral intestines of two species of sphyrid and carcharhinid sharks, representing two additional definitive hosts. *O. insigne* has thus far been reported only from the western North Atlantic Ocean (i.e. off North Carolina) and the Gulf of Mexico (i.e. off Louisiana). This study expands the geographical range of this species in the Atlantic Ocean to the western coastline of Africa, where specimens have been obtained from off Senegal (i.e. North Atlantic Ocean) and the Democratic Republic of the Congo (i.e. South Atlantic Ocean).

Hildreth & Lumsden (1985) described five hooks per principle row in the metabasal armature and smaller hooks on the external tentacular surface, which allegedly formed a longitudinal band (Fig. 10A). This numbering system was amended by Campbell & Beveridge (1994), who considered the smaller hooks of the 'longitudinal band' to be part of either the principle or intercalary hook rows. However, their numbering system is inconsistent, with opposing rows having six and seven principle hooks and two and three intercalary hooks (labelled a-e). The metabasal hooks labelled 5', 6', c, d and e in fact represent hooks a', b', 7', 6' and 5', respectively (see Campbell & Beveridge, 1994, fig. 7.255). Palm (1995) amended the numbering system of Campbell & Beveridge (1994) and described the metabasal armature as being composed of seven hooks per principle row and two intercalary hooks (Fig. 10B).

The origin and termination of the principle rows in the metabasal tentacular armature was described as commencing on the internal tentacular surface (see Hildreth & Lumsden, 1985). The principle hook rows were not considered to extend to the external surface, while smaller hooks formed a 'longitudinal band' of arrays of four hooks a(a')-d(d') (Hildreth & Lumsden, 1985). The internal to external orientation of the principle hook rows was accepted by Campbell & Beveridge (1994) and Palm (2004). The present study reveals a different orientation of the principle hook rows from the bothrial to antibothrial tentacular surfaces and was consistent in all

specimens observed. However, tentacles frequently twisted along their lengths towards the apical region (Fig. 8B), which could have caused earlier misinterpretations. This, however, can be avoided by a careful observation of the basal armature.

The microtrix morphology for the distal and bothrial surfaces and the pars vaginalis was described and illustrated by Palm (1995). Specimens included in the present study had been mounted on microscope slides for some years prior to their removal from the mounting medium and utilisation for SEM. The microtriches had been lost and it was not possible to describe their morphology.

Although Linton (1905) described *O. insigne* from a carcharhinid definitive host, the specimens obtained were immature and, thus, information about the segment morphology could not be provided. The present study illustrates and describes adult specimens with mature strobilae. The segment morphology, described for the first time, is consistent with other species within *Otobothrium*, with pre- and postovarian testes, a hermaphroditic sac with an internal seminal vesicle and ovarian lobes being separated from the posterior margin of the segment.

***Otobothrium mugilis* Hiscock, 1954**

Syn. *Otobothrium hexacanthus* Bilqees & Kurshid, 1987

Type-host: *Mugil cephalus* Linnaeus (Mugiliformes: Mugilidae; *intermediate host*).

Additional hosts: *Neoarius graeffei* (Kner & Steindachner) (Siluriformes: Ariidae; *intermediate host*); *Otolithes ruber* (Bloch & Schneider) (Perciformes: Sciaenidae; *intermediate host*).

Type-locality: Brisbane River (lower reaches), Brisbane, Queensland, Australia.

Additional localities: Off Heron Island, Queensland; Arabian Sea off Karachi, Pakistan (24°45'N, 66°57'E).

Material examined: Plerocerci from *Ne. graeffei* from the Brisbane River (QM 233878–83), and from *M. cephalus* in the Coral Sea off Heron Island (QM 233877), Queensland, Australia, coll. M. K. Jones; 1 specimen from *C. cautus* (AU-45) off Darwin, Northern Territory, coll. J. N. Caira and K. Jensen, 6.viii.1997 (used for SEM); 3 voucher specimens from *C. limbatus* in the Mary River (Sampan mouth), Northern Territory, coll. B. G. Robertson, 12.ix.1986 (SAM AHC 35564–65); 5 voucher specimens from *Eusphyra blochii* (Cuvier) (Carcharhiniformes: Sphyrnidae) (AU-70; AU-90), Fog Bay, Northern Territory, coll. J. N. Caira and K. Jensen, 9. and 10.viii.1997 (SAM AHC 35563, 35566); 2 voucher specimens from *Lamiopsis tephrodes* (Fowler) (Carcharhiniformes: Carcharhinidae) (BO-488) off Mukah, Sarawak, Malaysia, coll. J. N. Caira and K. Jensen, 30.iv.2004 (LRP 7890); 33 voucher specimens from *Sphyrna mokarran*

2 (*sensu* Naylor et al., 2012) (Carcharhiniformes: Sphyrnidae) (NT-99) off the Wessel Islands, Northern Territory, coll. J. N. Caira and K. Jensen, 18.xi.1999 (SAM AHC 35567; serial sections in SAM AHC 35568).

Site of infection: Spiral intestine (for adults).

Redescription (Figs. 11–13)

[Based on 46 whole-mounts, 2 specimens used for SEM, 1 specimen used for longitudinal sections.] Mature cestodes 3.8–8.9 (6.1 ± 1.9 ; $n = 11$) mm long, with 16–29 (22 ± 4 ; $n = 10$) segments in mature strobilae; first mature segments appear posterior to segment 12–22 (17 ± 3 ; $n = 10$); gravid segments not present. Scolex craspedote, very variable in size (Figs. 11A,B; 13A,B), 250–880 (484 ± 178 ; $n = 19$) long; pars bothrials 120–230 (173 ± 31 ; $n = 19$) $\times$ 190–410 (269 ± 64 ; $n = 19$). Bothria 2 in number, oval (Fig. 13B), 165–290 (213 ± 52 ; $n = 8$) $\times$ 180–280 (214 ± 40 ; $n = 8$), with free margins, rims thickened; distal bothrial surface covered with aristate trifid spinitriches (Fig. 13E); proximal bothrial surface covered with penta- and hexadigitate spinitriches (Fig. 13G) and acicular filitriches (Fig. 13F); paired bothrial pits present (Fig. 11B), small, on posterior margins of each bothrium; bothrial pits lined with bifid spinitriches (Fig. 13C). Pars vaginalis slender, 160–630 (329 ± 130 ; $n = 19$) long, covered with acicular filitriches (Fig. 13H); tentacle sheaths sinuous or coiled. Pars bulbosa 85–250 (146 ± 42 ; $n = 19$) $\times$ 100–425 (264 ± 90 ; $n = 19$); prebulbar organs and gland-cells within bulbs absent; bulbs variable in size, elongate or stout (Fig. 11D), 70–250 (143 ± 44 ; $n = 52$) $\times$ 40–130 (76 ± 21 ; $n = 52$); bulb width : length ratio 1.0 : 1.3–2.4 (1.9 ± 0.3 ; $n = 52$); retractor muscle originates in anteriormost region of bulb; pars post-bulbosa absent; velum surrounds anterior 50–220 (98 ± 48 ; $n = 10$) of pars proliferans scolecis. Scolex ratio (pars bothrials : pars vaginalis : pars bulbosa) 1.0 : 1.3–3.5 : 0.6–1.4 ($1.0 : 1.9 \pm 0.6 : 0.9 \pm 0.2$; $n = 19$).

Everted tentacles 750–810 (768 ± 29 ; $n = 4$) long; diameter 18–25 (21 ± 2 ; $n = 7$) at base, 40–48 (44 ± 3 ; $n = 9$) at basal swelling, 20–25 (21 ± 2 ; $n = 7$) in metabasal region, 18–20 (18 ± 1 ; $n = 6$) in apical region. Metabasal armature heteroacanthous, heteromorphous; hooks hollow, in ascending half spiral rows. Hook files commence on bothrial surface of tentacle (Fig. 12F), terminate on antibothrial surface (Fig. 12G); 5 hooks per principle row (Fig. 12D,E); prominent space between hook files 1 and 1' (Fig. 12F). Hooks 1(1') uncinata, 7–11 (9 ± 1 ; $n = 13$) long, base 7–9 (8 ; $n = 13$) long; hooks 2(2') uncinata, with erect tip, larger, 9–12 (11 ± 1 ; $n = 16$) long, base 8–9 (8 ± 1 ; $n = 16$) long; hooks 3(3') uncinata, with erect tip, slightly smaller, 9–12 (10 ± 1 ; $n = 18$) long, base narrower, 6–8 (7 ; $n = 19$) long; hooks 4(4') uncinata, smaller, 5–9 (7 ± 1 ; $n = 20$) long, base narrower, 4–7 (5 ± 1 ; $n = 20$) long; hooks 5(5') uncinata, smaller, 3–5 (4 ± 1 ; $n =$

15) long, base narrower, 2–4 (3 ± 1 ; $n = 15$) long; intercalary hook row present (Fig. 12G), with three intercalary hooks a(a')–c(c') (Fig. 12E,G), on antiothrial surface; hooks a(a') falcate, posterior to and between hooks 4(4') and 5(5'), 5–7 (6 ± 1 ; $n = 19$) long, base 1–3 (2; $n = 16$) long; hooks b(b') falcate, smaller, 4–6 (4 ± 1 ; $n = 16$) long, base narrower, 1–2 (1; $n = 12$) long; hooks c(c') falcate, 3–5 (4 ± 1 ; $n = 17$) long, base narrower, 1 ($n = 8$) long.

Distinctive basal armature present; basal hooks on antiothrial surface uncinat, with area devoid of hooks on antiothrial surface (Fig. 12A,C); hooks on bothrial surface falcate (Fig. 12B,C,E), with prominent space between hooks 1 and 1', 15–18 (17 ± 1 ; $n = 13$) long, base 6–7 (7 ± 1 ; $n = 12$) long, becoming spiniform, slender towards antiothrial surface (Fig. 12A,C,E), with broad base in dorso-ventral view (Fig. 12E), 7–9 (8 ± 1 ; $n = 11$) long, base 2–3 (2 ± 1 ; $n = 12$) long. Basal swelling present (Fig. 12A–C), with group of billhooks on antiothrial surface (Figs. 12A,C,E; 13D), 5–7 (6 ± 1 ; $n = 5$) long, base 3–4 (3 ± 1 ; $n = 5$) long; 2 greatly enlarged hooks on bothrial surface (Fig. 12B,C,E), uncinat, with tips apposed (Fig. 12B); larger hook 28–30 (29 ± 1 ; $n = 3$) long, base 20–22 (21 ± 1 ; $n = 3$) long; second enlarged hook slightly smaller, 20–22 (21 ± 1 ; $n = 3$) long, base 18–21 (19 ± 2 ; $n = 2$) long.

Segments acraspedote; first segments posterior to velum immature, much wider than long, 10–20 (14 ± 5 ; $n = 7$) $\times$ 85–250 (168 ± 55 ; $n = 7$); first mature segments 240–470 (353 ± 66 ; $n = 8$) $\times$ 120–330 (234 ± 68 ; $n = 8$); mature segments become longer than wide posteriorly; terminal mature segments 680–1,360 ($1,143 \pm 249$; $n = 10$) $\times$ 160–400 (287 ± 65 ; $n = 10$) Genital pores alternate irregularly, in mid-line of segment or slightly posterior to mid-line (Fig. 11C); pore inconspicuous; regions anterior and posterior to pore thickened (Fig. 11C,E). Hermaphroditic sac oval (Fig. 11C,E), 130–183 (153 ± 18 ; $n = 7$) $\times$ 83–125 (108 ± 14 ; $n = 7$); internal seminal vesicle present, at proximal pole of hermaphroditic sac (Fig. 11C,E); cirrus joins vagina in distal region of hermaphroditic sac, unarmed; external seminal vesicle absent. Vas deferens coils posteriorly to ovarian isthmus. Testes numerous, occupy complete intervacular space (Fig. 11C), in several layers, 55–65 (61 ± 3 ; $n = 20$) $\times$ 30–40 (36 ± 2 ; $n = 20$); testes 108–144 (123 ± 11 ; $n = 8$) in number, 62–78 (69 ± 6 ; $n = 8$) preovarian, 37–68 (54 ± 11 ; $n = 8$) postovarian. Vagina thin-walled, 3–8 (5 ± 2 ; $n = 10$) wide, penetrates proximal pole of hermaphroditic sac (Fig. 11E), runs posteriorly towards Mehlis' gland. Seminal receptacle absent. Ovary in posterior half of segment, distant from posterior margin of segment (Fig. 11C); ovarian lobes 75–103 (89 ± 10 ; $n = 9$) $\times$ 88–138 (109 ± 16 ; $n = 9$). Mehlis' gland 50–75 (61 ± 8 ; $n = 10$) in diameter. Vitelline follicles small, circumcortical, 6–13 (10 ± 2 ; $n = 20$) in diameter. Uterus median, tubular (Fig. 11C); uterine pore absent.

Remarks

Otobothrium mugilis was described by Hiscock (1954) from the mesenteries, peritonea and body walls of the flathead grey mullet *Mugil cephalus* and the blue salmon catfish *Neoarius graeffei* (as *Netuma australis*) from the lower reaches of the Brisbane River, Brisbane, Queensland, Australia. Although Hiscock (1954) provided detailed descriptions of the plerocerci, cysts and the musculature of the scolex, the description of the oncotaxy lacked detail, with two rather superficially illustrated tentacular surfaces. Jones (2000) studied the ultrastructure of *O. mugilis*, with particular emphasis on the scolex, bothrial pits and rhyncheal system. Specimens examined for this study were obtained from both previously reported hosts from the Brisbane River and from off Heron Island, Queensland, Australia. Palm (2004) provided a description based on the plerocerci, because the whereabouts of the types is not known. Thus far, neither adult worms nor potential definitive host were known for this species. The present study reveals five new definitive hosts from five different localities off the Northern Territory, Australia and an additional locality from off Malaysian Borneo. This increases the distribution of *O. mugilis* in Australian waters.

For the first time, adult worms are described, with particular emphasis on the segment morphology. Specimens observed in the present study showed a high variability in their morphometric data, most obvious in the size of the scolex and muscular bulbs. The plerocerci reported by Palm (2004) ranged from 775 to 1,025 μm in scolex length and 190 to 225 μm in bulb length. The adult specimens from the present study were much smaller, with the scolex ranging from 250 to 880 (mean: 484) μm in length (Fig. 11A,B) and bulb lengths of 70 to 250 (mean: 143) μm (Fig. 11D). Although the oncotaxy of adults and plerocerci was identical, no plausible explanation can be provided for the size difference between the developmental stages. Another difference to the previously described material is the orientation of principle hook rows in the metabasal armature. Hiscock (1954) described the principle hook rows as commencing on the internal and terminating on the external tentacular surface. Our material revealed a different orientation, with the principle hook rows beginning on the bothrial surface and terminating on the antibothrial surface.

Otobothrium mugilis shows a striking similarity to both representatives of another otobothrioid genus, *Symbothriorhynchus* Yamaguti, 1952, in terms of its oncotaxy, with two greatly enlarged macrohooks and a group of billhooks on the basal swelling of each tentacle. However, *O. mugilis* differs from both *S. uranoscopi* Yamaguti, 1952 and *S. tigaminacantha* Palm, 2004 in the length of the scolex (484 vs 1,027–1,267 and 975–1,025 μm , respectively), the length of the bulbs (143 vs 323–376 and 233–260 μm , respectively), the presence of bothrial pits (vs absence or a reduced state of pits), the orientation of the principle hook rows

(bothrial/antibothrial vs internal/external orientation) and in the general size of the hooks (small vs large hooks). *O. mugilis* also differs in its number of hooks in the metabasal tentacular armature, with five principle hooks and an intercalary hook row of three hooks; both species of *Symbothriorhynchus* possess five principle hooks, a single intercalary hook and three (*S. tigaminacantha*) or four (*S. uranoscopi*) longitudinal files of analogous hooks. There also appear to be differences in the basal armature. *Otobothrium mugilis* has enlarged, falcate hooks posterior to the two macrohooks on the bothrial surface, whereas the hooks posterior to the greatly enlarged hooks of *S. uranoscopi* and *S. tigaminacantha* are of a smaller size and are falcate to uncinata in shape. Nonetheless, these species appear very similar.

***Otobothrium penetrans* Linton, 1907**

Syns *Otobothrium* sp. of Linton (1905); *Otobothrium pephrikos* Dollfus, 1969; *Otobothrium kurisi* Shields, 1985

Type-host: *Tylosurus acus acus* (Lacépède) (Beloniformes: Belonidae; *intermediate host*).

Additional hosts: *Carcharhinus leucas*; *C. limbatus*; *C. longimanus* (Poey) (Carcharhiniformes: Carcharhinidae); *Rhizoprionodon terraenovae*; *Sphyrna lewini* (Griffith & Smith) (Carcharhiniformes: Sphyrnidae); *Sp. zygaena* (Linnaeus) (Carcharhiniformes: Sphyrnidae); *Hyporhamphus dussumieri* (Valenciennes) (Beloniformes: Hemirhamphidae; *intermediate host*); *Platybelone* sp. (Beloniformes: Belonidae; *intermediate host*); *Ty. crocodilus crocodilus* (*intermediate host*).

Type-locality: North Atlantic Ocean off Flatts Village, Bermuda (32°19'N, 64°44'W).

Additional localities: Mediterranean Sea off Sète, France (43°23'N, 03°42'E); Gulf of Mexico off the Dry Tortugas, Florida, USA (24°37'N, 82°55'W); North Atlantic Ocean off Woods Hole, Massachusetts, USA (41°30'N, 70°39'W); Pacific Ocean off Santa Barbara, California, USA (34°24'N, 119°41'W); Río Colorado off Barra del Colorado, Costa Rica (10°46'N, 83°35'W); Visayan Sea off Cebu Island (10°19'N, 123°55'E); off Mactan Island (10°17'N, 123°59'E); off Leyte Island, Philippines (10°35'N, 124°36'E); and Indian Ocean off Pelabuhan Ratu, Indonesia (07°01'S, 106°28'E).

Material examined: Type-material from *Ty. acus acus* off Flatts Village, Bermuda (USNPC 7608, 7609); from *Sp. zygaena* from the Mediterranean Sea off Sète, France (MNHN BD 16, coll. L. Euzet, 27.ix.1951; types of *O. pephrikos*); from *Sp. lewini* in the Northern Pacific Ocean off Santa Barbara, USA (USNPC 78243; types of *O. kurisi*); 2 voucher specimens from *Sphyrna* sp. (Carcharhiniformes: Sphyrnidae) in the Red Sea (Gulf of Aqaba), Aqaba, Jordan, coll. A.

Lipschitz, 2003 (SAM AHC 35570; serial sections in SAM AHC 35571); 1 voucher specimen from *Sp. lewini* in the Indian Ocean off Bunbury, Western Australia, Australia, coll. B. G. Robertson, 11.xii.1986 (SAM AHC 35569).
Site of infection: Spiral intestine (for adults).

Redescription (Figs. 14–15)

[Based on 3 whole-mounts, 2 specimens used for longitudinal sections.] Small cestodes, *c.* 80.9 (n = 1) mm long, with *c.* 70 (n = 1) segments in mature strobila; first mature segments appear posterior to segment 46 (n = 1); gravid segments not present. Scolex craspedote (Fig. 14A), 2,700–3,900 (3,108 ± 686; n = 3) long; maximum width at level of pars bulbosa, 2,250–2,525 (2,433 ± 159; n = 3) wide; pars bothriialis 625–725 (683 ± 52; n = 3) × 1,250–1,500 (1,367 ± 126; n = 3). Bothria 2 in number, patelliform to oval (Fig. 14A), 625–700 (663 ± 53; n = 2) × 675–1,000 (838 ± 230; n = 2), with thick, fleshy rims and free margins; paired bothrial pits present on posterior margin of bothria. Pars vaginalis longer than pars bothriialis, 1,975–3,150 (2,367 ± 678; n = 3) long; tentacle sheaths sinuous, increasing in width anteriorly. Pars bulbosa 725–750 (742 ± 14; n = 3) long; prebulbar organs and gland-cells within bulbs absent; bulbs fabiform (Fig. 14B), 1,075–1,275 (1,175 ± 81; n = 6) × 450–625 (550 ± 71; n = 6), directed laterally (Fig. 14A); bulb width : length ratio 1.0 : 2.0–2.4 (2.2 ± 0.2; n = 6); retractor muscle originates in anterior region of bulb; pars post-bulbosa absent. Scolex ratio (pars bothriialis : pars vaginalis : pars bulbosa) 1.0 : 2.7–4.5 : 1.0–1.2 (1.0 : 3.5 ± 0.9 : 1.1 ± 0.1; n = 3).

Fully everted tentacles *c.* 1,440 (n = 1) long; diameter at base 130–150 (138 ± 10; n = 4), 110 (n = 2) in metabasal region, *c.* 70 (n = 1) in apical region, *c.* 50 (n = 1) at most distal tip. Metabasal armature heteroacanthous, heteromorphous; hooks hollow, in ascending half spiral rows (Fig. 15C). Hook files begin on internal surface of tentacle (Fig. 15B), terminate on external surface (Fig. 15A); 7 hooks per principle row (Fig. 15D); prominent space between hook files 1 and 1' (Fig. 15B); hooks 1(1') enlarged, uncinata (Fig. 15 B–D), 91–104 (97 ± 7; n = 3) long, base 71–75 (73 ± 2; n = 3) long; hooks 2(2') smaller, uncinata, 66–82 (74 ± 5; n = 6) long, base 43–66 (54 ± 7; n = 6) long; hooks 3(3') smaller, uncinata, 45–54 (49 ± 3; n = 10) long, base 41–54 (47 ± 4; n = 10) long; hooks 4(4') smaller, initially uncinata (Fig. 15D), becoming slender, falcate anteriorly (Fig. 15C), 30–37 (35 ± 2; n = 8) long, base 25–30 (27 ± 2; n = 7) long; hooks 5(5')–7(7') undergo transition in size and shape along tentacle (Fig. 15D); hooks 5(5') initially billhook-shaped (Fig. 15D), 27–32 (29 ± 3; n = 4) long, base 14–21 (17 ± 3; n = 4) long, becoming more slender, falcate anteriorly (Fig. 15D), 35–39 (37 ± 2; n = 7) long, base 9–12 (10 ± 2; n = 7) long; hooks 6(6') greatly enlarged in basal region (Fig. 15D), *c.* 83 (n = 1)

long, base $c.43$ ($n = 1$) long, diminishing in size to 46–66 (56 ± 14 ; $n = 2$) long, base 34–37 (35 ± 3 ; $n = 2$) long, undergoing transition to billhook-shape (Fig. 15D), 29–32 (30 ± 3 ; $n = 2$) long, base 14–16 (15 ± 1 ; $n = 2$) long, more slender, falcate anteriorly (Fig. 15D), 39–45 (41 ± 2 ; $n = 7$) long, base 9–14 (11 ± 2 ; $n = 7$) long; hooks 7(7') initially small, falcate (Fig. 15D), 23–30 (27 ± 5 ; $n = 2$) long, base 7–9 (8 ± 1 ; $n = 2$) long, becoming more elongate anteriorly (Fig. 15D), 50–59 (55 ± 3 ; $n = 8$) long, base 11–18 (13 ± 2 ; $n = 7$) long; intercalary hook row present (Fig. 15A, C, D), with two intercalary hooks a(a') and b(b') (Fig. 15A); hooks a(a') elongate, falcate (Fig. 15D), 52–59 (55 ± 3 ; $n = 7$) long, base 11–14 (13 ± 2 ; $n = 7$) long; hooks b(b') larger, falcate (Fig. 15D), 64–71 (67 ± 3 ; $n = 6$) long, base 13–18 (15 ± 2 ; $n = 6$) long.

Distinctive basal armature present; falcate hooks present on internal surface (Fig. 15B), 65–75 (72 ± 3 ; $n = 7$) long, base 20–26 (22 ± 3 ; $n = 5$) long; hooks on external surface smaller, falcate to spiniform (Fig. 15A); 2 greatly enlarged hooks present on external surface (Fig. 15A); first principle rows appear anterior to hook row 4.

Segments acraspedote; first segments immature, much wider than long, $c.100$ ($n = 1$) $\times$ $c.1,275$ ($n = 1$); first mature segments $c.1,000$ ($n = 1$) $\times$ $c.1,700$ ($n = 1$); terminal mature segments 3,150–3,175 ($3,163 \pm 18$; $n = 2$) $\times$ 1,875–1,900 ($1,888 \pm 18$; $n = 2$). Genital pores alternate irregularly, in posterior third of segment; pore inconspicuous; regions anterior and posterior to pore thickened. Hermaphroditic sac oval (Fig. 14C), 240–360 (279 ± 38 ; $n = 8$) $\times$ 370–570 (468 ± 71 ; $n = 8$); internal seminal vesicle present, at proximal pole of hermaphroditic sac (Fig. 14C), 110–150 (130 ± 28 ; $n = 2$) $\times$ 90 ($n = 2$); cirrus unarmed, joins vagina in distal pole of hermaphroditic sac (Fig. 14C); external seminal vesicle absent. Vas deferens coils posteriorly to ovarian isthmus. Testes 90–140 (110 ± 18 ; $n = 15$) $\times$ 60–100 (77 ± 14 ; $n = 15$), occupy complete intervascular space, in single layer, partially overlapping; number of testes not possible to estimate. Vagina $c.40$ ($n = 1$) wide, penetrates proximal pole of hermaphroditic sac, runs posteriorly towards Mehlis' gland. Seminal receptacle absent. Ovary in posterior third of segment, distant from posterior margin of segment; ovarian lobes 290–480 (354 ± 70 ; $n = 7$) $\times$ 250–380 (329 ± 41 ; $n = 7$); Mehlis' gland 160–200 (180 ± 28 ; $n = 2$) in diameter. Vitelline follicles small, circumcortical, 25–30 (27 ± 3 ; $n = 15$) in diameter. Uterus median, tubular; uterine pore absent. Ventral osmoregulatory canal 40–80 (52 ± 16 ; $n = 6$) in diameter.

Remarks

Otobothrium penetrans was described by Linton (1907a) based on plerocerci from the musculature of the Agujon needlefish, *Ty. acus acus*, collected off Bermuda. Linton (1924) described adult worms of this species, which he obtained from two elasmobranch definitive

hosts, *Sp. zygaena* (= '*Cestracion zygaena*' in Linton, 1924) off the Dry Tortugas and *C. longimanus* (= '*C. commersonii*' in Linton, 1924; '*C. lamia*' in Dollfus, 1942) off Woods Hole, USA. Moreover, this author (1924) amended the record for plerocerci of an unidentified species of *Otobothrium* of his earlier publication (= *Otobothrium* sp. in Linton, 1905), which was obtained from a hound needlefish *Ty. crocodilus crocodilus* (= '*Ty. raphidoma*' in Linton, 1905), and identified it as *O. penetrans*. Additional material from *O. penetrans* was reported by Shuler (1938) from *Rhizoprionodon terraenovae* (= '*Scoliodon terryae-novae*' in Shuler, 1938) and *C. limbatus* (= '*Carcharias limbatus*' in Shuler, 1938) collected off the Dry Tortugas, and Watson & Thorson (1976) reported it from *C. leucas* off Costa Rica. *O. pephrikos* Dollfus, 1969 was described by Dollfus (1969) as a species similar to *O. penetrans*. The type-specimens were obtained from *Sp. zygaena* from the Mediterranean Sea off Sète, France. Dollfus (1969) considered both *O. pephrikos* and *O. penetrans* distinct, due to allegedly different tegumental structures on the scolex (i.e. 'roughly papillate' surface in *O. penetrans*; see Linton, 1924 vs enlarged tegumental papillae in *O. pephrikos*; see Dollfus, 1969). However, Palm (2000) considered *O. pephrikos* a junior synonym of *O. penetrans*. Shields (1985) described *O. kurisi* Shields, 1985 from a scalloped hammerhead shark *Sp. lewini* collected off Santa Barbara, California. This author provided SEM micrographs of the scolex, bothrial pits, tentacular armature and surface ultrastructure. *O. kurisi* was differentiated from *O. penetrans* only by a smaller size of the scolex and tentacular bulbs. The oncotaxy, however, was not taken into consideration (see Shields, 1985). In a study of the flesh parasites of needle fishes (Beloniformes) from the Visayan Sea (central Philippines), Palm et al. (1993) and Petersen et al. (1993) reported plerocerci of *O. penetrans* from four different intermediate host species, namely *Ty. acus acus*, *Ty. crocodilus crocodilus*, *Platybelone* sp. and *Hy. dussumieri*. This represented the first record of *O. penetrans* from the Pacific Ocean. Due to the variable size of the scoleces of their specimens and apparent similarities in morphological characters and oncotaxy, Palm et al. (1993) synonymised *O. kurisi* with *O. penetrans*. In more recent studies, Palm (1995, 2000) focused on the morphology, oncotaxy and surface ultrastructure of larval stages of *O. penetrans*. This author (2000) also reported this species for the first time from the eastern Indian Ocean off Indonesia, further increasing the geographical distribution of this parasite.

The present study adds two geographical records for this parasite. The records from the Red Sea (Jordan) and the eastern Indian Ocean (Western Australia) support Palm's (2000) hypothesis of a worldwide distribution of this parasite in tropical and subtropical waters and also includes the first record from Australian waters. One additional species of hammerhead shark increases the definitive host spectrum of *O. penetrans* and also suggests a close affiliation of this parasite with sharks of the family Sphyrnidae, as suggested by Palm et al. (1993). Although only

one of three worms possessed fully mature segments, we have emphasised the segment morphology, to provide additional information to the relatively few descriptions which have focused on mature specimens of this species (see Linton, 1924; Shields, 1985).

Otobothrium penetrans shows considerable variability in its morphometric data for the scolex and tentacular bulbs (Palm et al., 1993). Linton (1907a, 1924) described specimens from the western North Atlantic possessing a scolex ranging from 4 to 5 mm and a bulb length of 1.35 to 1.40 mm (the latter only stated for plerocerci; Linton, 1907a; Shields, 1985). Specimens described by Dollfus (1969) from the Mediterranean Sea had a larger scolex and larger tentacular bulbs (i.e. 7.5 and 1.75 mm, respectively), whereas Shield's (1985) specimens were smaller (i.e. 1.9 to 2.7 mm for the scolex and 0.9 to 1.2 mm for the bulbs; Shields, 1985). The greatest differences in morphometric data were observed by Palm et al. (1993) and Palm (2000) in plerocerci collected off Indonesia and the Philippines. Plerocerci from the Philippines possessed a much smaller scolex than those from Indonesia (1.9–3.9 vs 6.4 mm, respectively) but slightly higher bulb ratios (2.8–3.9 vs 2.4–2.8, respectively). The specimens from Jordan and Western Australia were similar to the specimens from the Philippines, with scoleces ranging from 2.7 to 3.9 mm in length, bulb lengths of 1.1 to 1.3 mm and bulb ratios of 2.0 to 2.4. There appear no obvious correlations between the morphometric data of *O. penetrans* to either the infected definitive/intermediate host species or its geographical distribution. The scolex length can range from 1.9 to 7.5 mm, which makes this species one of the most variable of all trypanorhynchs.

Previous publications are inconsistent in the origin of principle hook rows in the metabasal armature. Shields (1985) reported a commencement of the principle rows on the external tentacular surface, whereas Dollfus (1969) and Palm et al. (1993) identified an internal to external orientation. The specimens of the present study are consistent with the descriptions of Dollfus (1969) and Palm et al. (1993) and the drawings of the specimens of Dollfus (1969) (Fig. 15C) and Linton (1924) (Fig. 15A,B). The transition of hook files 5(5') to 7(7') in shape and size along the tentacle is a novel feature not explicitly reported for this species. Shields (1985) reported the presence of an external seminal vesicle and a seminal receptacle (Shields, 1985, fig. 2). The present specimens of *O. penetrans* did not show either of these features, but possessed an internal seminal vesicle and a hermaphroditic sac (Fig. 14C), which is in accordance with all specimens of other species of *Otobothrium* observed for this study.

***Otobothrium* sp. 1**

Material examined: 3 specimens from *Carcharhinus melanopterus* (CM03-71) from the Arafura Sea off Weipa, Queensland, Australia, coll. J. N. Caira and K. Jensen, 16.v.2004 (SAM AHC 35585; serial sections in SAM AHC 35586).

Site of infection: Spiral intestine.

Description (Figs. 16A,B,D; 17; 18A–E)

[Based on 3 whole-mounts; 1 specimen used for both SEM and longitudinal sections.] Mature cestodes 5.9–10.8 (7.8 ± 2.7 ; $n = 3$) mm long; with 22–25 (24 ± 2 ; $n = 3$) segments; first mature segments appear posterior to segment 17–20 (18 ± 2 ; $n = 3$); gravid segments not present. Scolex craspedote (Figs. 16A; 18A), 590–690 (637 ± 50 ; $n = 3$) long; maximum width at level of pars bothriialis, 300–510 (407 ± 105 ; $n = 3$) wide; pars bothriialis 230–300 (270 ± 36 ; $n = 3$) long. Bothria 2 in number, oval (Fig. 18A), 295–310 (300 ± 7 ; $n = 4$) long; bothrial pits present (Figs. 16A; 18C), small, on lateral margins of bothria (Fig. 16A); bothrial pit lined by bifid spinitriches (Fig. 18C,E); bothrial groove present (Fig. 18B); distal bothrial surface covered with trifid spinitriches and papillate filitriches (Fig. 18D). Pars vaginalis longer than pars bothriialis, 420–515 (458 ± 50 ; $n = 3$) long; tentacle sheaths irregularly coiled to almost straight anteriorly (Fig. 16A). Pars bulbosa 170–190 (178 ± 10 ; $n = 3$) $\times$ 230–285 (265 ± 30 ; $n = 3$); prebulbar organs and gland-cells within bulbs absent; bulbs ovoid (Fig. 16A,D), 140–165 (153 ± 9 ; $n = 9$) $\times$ 70–105 (89 ± 12 ; $n = 9$), surround pars proliferans scolecis; bulb width : length ratio 1.0 : 1.5–2.1 (1.8 ± 0.2 ; $n = 9$); retractor muscle originates in anterior region of bulb; pars post-bulbosa absent; velum present. Scolex ratio (pars bothriialis : pars vaginalis : pars bulbosa) 1.0 : 1.6–1.8 : 0.6–0.7 ($1.0 : 1.7 \pm 0.1 : 0.7 \pm 0.1$; $n = 3$).

Tentacles only partly everted, 93–118 (105 ± 12 ; $n = 2$) long; diameter 15–19 (16 ± 2 ; $n = 5$) at base, *c.*18 ($n = 1$) in metabasal region. Armature heteroacanthous; hooks heteromorphous, hollow, in ascending half spiral rows (Fig. 17B,C); hook files begin on bothrial surface, terminate on antibothrial surface (Fig. 17D); 5 hooks per principle row; prominent space between hook files 1 and 1'; hooks 1(1') uncinata, largest hooks on tentacle; hooks 2(2') smaller, uncinata, 9–11 (10 ± 1 ; $n = 3$) long, base 7–8 (8 ± 1 ; $n = 3$) long; hooks 3(3') uncinata, 9–11 (10 ± 1 ; $n = 5$) long, base narrower, 5–7 (6 ; $n = 5$) long; hooks 4(4') slightly larger, uncinata, 10–13 (12 ± 1 ; $n = 3$) long, base 5–6 (6 ± 1 ; $n = 4$) long; hooks 5(5') slightly smaller, falcate, 9–12 (10 ± 1 ; $n = 5$) long, base 2–5 (3 ± 1 ; $n = 5$) long; single intercalary hooks a(a') falcate, 8–9 (9 ± 1 ; $n = 2$) long, base 3 ($n = 2$) long.

Characteristic basal armature present; falcate to uncinata hooks on bothrial surface (Fig. 17B); small, falcate hooks on antibothrial surface (Fig. 17D), 2–3 (2 ; $n = 7$) long, base 1 ($n = 3$)

long; basal swelling present, with distinctive group of billhooks on antibothrial surface (Fig. 17C,D); billhooks 3–6 (4 ± 1 ; $n = 12$) long, base 1–2 (2 ; $n = 12$) long; first principle rows appear anterior to hook row 6.

Segments acraspedote; first segments posterior to velum wider than long (Fig. 16A), 15 ($n = 3$) $\times$ 150–190 (168 ± 20 ; $n = 3$); first mature segments 260–345 (303 ± 60 ; $n = 2$) $\times$ 320–325 (323 ± 3 ; $n = 2$); terminal mature segments elongate, 1,190–2,005 ($1,626 \pm 394$; $n = 4$) $\times$ 380–465 (424 ± 37 ; $n = 4$) (Fig. 17A). Genital pores alternate irregularly, in posterior third of segment (Fig. 17A); pore inconspicuous; regions anterior and posterior to pore thickened (Figs. 16B; 17A). Hermaphroditic sac oval (Figs. 16B; 17A), 88–178 (126 ± 42 ; $n = 5$) $\times$ 105–150 (128 ± 20 ; $n = 5$); internal seminal vesicle present, at proximal pole of hermaphroditic sac (Figs. 16B; 17A), 58–63 (60 ± 3 ; $n = 2$) $\times$ 15–20 (18 ± 3 ; $n = 2$); cirrus joins vagina in distal pole of hermaphroditic sac, unarmed; external seminal vesicle absent. Vas deferens coils posteriorly to ovarian isthmus. Testes occupy complete intervacular space, in 1–2 layers (Fig. 17A), partly overlapping each other, 55–63 (59 ± 3 ; $n = 10$) $\times$ 35–43 (38 ± 2 ; $n = 10$); testes 123–143 (130 ± 9 ; $n = 4$) in number, 87–110 (97 ± 10 ; $n = 4$) preporal, 28–37 (33 ± 4 ; $n = 4$) postporal, 23–27 (26 ± 2 ; $n = 4$) postovarian. Vagina $c.10$ ($n = 1$) wide, thin-walled, runs posteriorly to cirrus within hermaphroditic sac, penetrates proximal pole of hermaphroditic sac (Fig. 16B), runs posteriorly towards Mehlis' gland. Seminal receptacle absent. Ovary in posterior third of segment, distant from posterior margin of segment (Fig. 17A); ovarian lobes 73–178 (118 ± 42 ; $n = 8$) $\times$ 75–125 (112 ± 17 ; $n = 8$). Mehlis' gland 53–80 (65 ± 15 ; $n = 4$) in diameter. Vitelline follicles small, circumcortical, 20–28 (24 ± 2 ; $n = 10$) $\times$ 13–18 (15 ± 1 ; $n = 10$). Uterus median, tubular (Fig. 17A); uterine pore absent.

Remarks

The specimens from off northern Australia are characterised by a craspedote scolex, two oval bothria with bothrial pits situated on the lateral margins, a hermaphroditic sac, a heteroacanthous, heteromorphous tentacular armature with five hooks per ascending half spiral row, and a single intercalary hook and a basal armature with a weakly developed basal swelling bearing a group of billhooks on the antibothrial tentacular surface. The only other species which possesses a group of billhooks on the basal armature of each tentacle are *O. insigne* and *O. mugilis* (see above). However, the present specimens have a much smaller strobila and morphometric data than *O. insigne* and, furthermore, differ in their metabasal armature. The specimens only possess five hooks per principle row and a single intercalary hook, whereas specimens of *O. insigne* have six principle and three intercalary hooks. The most obvious

characteristic differentiating *O. mugilis* from these specimens is the presence of two greatly enlarged macrohooks on the bothrial surface of the basal swelling, which are absent in the species described here. In addition, *O. mugilis* possesses two additional intercalary hooks in its metabasal tentacular armature.

Given the unique combination of morphological characters, we consider the present specimens to represent a new species of *Otobothrium*. However, since only very few specimens were obtained and only a partial description of the oncotaxy could be provided, the specimens are referred to as *Otobothrium* sp. 1. Additional specimens with fully everted tentacles are needed from the blacktip shark *C. melanopterus* off the Northern Territory to complement the present knowledge of this species and to verify the decision made herein.

***Otobothrium* sp. 2**

Material examined: 2 specimens from *Sphyrna zygaena* (BJ-414) from the Gulf of California off San José del Cabo, Baja California Sur, Mexico, coll. J. N. Caira, 15.ix.1993 (LRP 7891).

Site of infection: Spiral intestine.

Description (Figs. 16C,E,F; 18F,G)

[Based on 2 whole-mounts; 1 specimen used for SEM.] Small cestodes, 3.9–4.9 (4.4 ± 0.7 ; $n = 2$) mm long, with $c.23$ ($n = 1$) segments in mature strobilae; first mature segments appear posterior to segment 20 ($n = 1$); gravid segments not present. Scolex craspedote (Figs. 16F; 18F), elongate, 525–615 (570 ± 64 ; $n = 2$) long, with thick tegument (Fig. 16F); pars bothrialis 175–180 (178 ± 4 ; $n = 2$) $\times$ 210–250 (230 ± 28 ; $n = 2$). Bothria 2 in number, oval (Fig. 18F), 180–190 (187 ± 6 ; $n = 3$) $\times$ $c.120$ ($n = 1$), with free margins and thickened rims; proximal bothrial surface covered with trifold spiniriches; paired bothrial pits present, small, on posterior margins of each bothrium. Pars vaginalis 395–475 (435 ± 57 ; $n = 2$) long; tentacle sheaths irregularly coiled. Pars bulbosa 130–140 (135 ± 7 ; $n = 2$) $\times$ 230–240 (235 ± 7 ; $n = 2$), of almost similar width to pars bothrialis; prebulbar organs and gland-cells absent; bulbs elongate (Figs. 16E,F), 115–140 (129 ± 7 ; $n = 7$) $\times$ 50–70 (59 ± 11 ; $n = 7$); 2 larger and 2 smaller bulbs; bulb width : length ratio 1.0 : 1.9–2.6 (2.2 ± 0.3 ; $n = 7$); retractor muscle originates in anterior region of bulb; pars post-bulbosa absent; velum present. Scolex ratio (pars bothrialis : pars vaginalis : pars bulbosa) 1.0 : 2.3–2.6 : 0.7–0.8 ($1.0 : 2.5 \pm 0.3 : 0.8$; $n = 2$).

Tentacles only partly everted. Metabasal armature heteroacanthous, heteromorphous; hooks hollow, in ascending half spiral rows. Hook files commence on bothrial surface of tentacle, terminate on antibothrial surface. Basal armature distinct; basal swelling present; group of billhooks on antibothrial surface of basal armature (Fig. 18G); billhooks variable in size (Fig. 18G), 6–11 (8 ± 3 ; $n = 3$) long, base $c.2$ ($n = 4$) long; single, enlarged macrohook, uncinata, on bothrial surface of basal armature.

Segments acraspedote; first segments posterior to velum immature (Fig. 16F), 10–15 (13 ± 4 ; $n = 2$) $\times$ 140–150 (145 ± 7 ; $n = 2$); first mature segment $c.535$ ($n = 1$) $\times$ $c.170$ ($n = 1$); posteriormost mature segment $c.965$ ($n = 1$) $\times$ $c.160$ ($n = 1$) (Fig. 16C). Genital pores alternate irregularly, in posterior third of segment (Fig. 16C); pore inconspicuous; regions anterior and posterior to pore thickened (Fig. 16C). Hermaphroditic sac oval (Fig. 16C). Testes numerous, occupy complete intervascular space (Fig. 16C), pre- and postovarian; testes $c.130$ ($n = 1$) in number, $c.95$ ($n = 1$) preporal, $c.30$ ($n = 1$) postporal; few testes postovarian, $c.25$ ($n = 1$). Vitelline follicles small, circumcortical. Uterus median, tubular; uterine pore absent.

Remarks

The two specimens from Mexico possess a basal tentacular armature with a group of billhooks on the antibothrial surface and a single enlarged macrohook on the bothrial surface of the basal swelling. Several other species of *Otobothrium* possess a group of billhooks on the basal swelling, e.g. *O. insigne*, *O. mugilis* or *Otobothrium* sp. 1 (see above). However, the present specimens clearly differ from these species in having a single enlarged macrohook on the basal swelling, whereas the other species either lack a characteristically enlarged hook (i.e. *O. insigne* and *Otobothrium* sp. 1) or possess two enlarged hooks on the basal swelling (i.e. *O. mugilis*). The presence of a single macrohook resembles another species, *O. australe*. This species, however, has only two characteristically-shaped billhooks opposite the single macrohook rather than a group of billhooks. The combination of these features in the basal tentacular armature is unique and does not correspond to any other species of *Otobothrium*. However, since only a few specimens were obtained and information on many morphological characters were unavailable and could not be observed, only a partial species description is provided and the species is referred to as *Otobothrium* sp. 2.

Additional new host and locality records

***Otobothrium crenacolle* Linton, 1890 (type-species)**

Syns *Tetrarhynchus crenacollis* (Linton, 1890) Vaullegeard, 1899; *Otobothrium cysticum* (Linton, 1890) *sensu* Palm & Overstreet (2000)

Type-host: *Sphyrna zygaena*.

Additional hosts: **definitive hosts**: *Carcharhinus leucas*; *C. limbatus*; *C. melanopterus*; *C. obscurus*; *Lamiopsis temmincki* (Müller & Henle) (Carcharhiniformes: Carcharhinidae); *Rhizoprionodon terraenovae*; **intermediate hosts**: *Acanthurus coeruleus* Bloch & Schneider (Perciformes: Acanthuridae); *Aluterus schoepfii* (Walbaum) (Tetraodontiformes: Monacanthidae); *Ariopsis felis*; *Bairdiella chrysoura* (Lacépède) (Perciformes: Sciaenidae); *Bagre marinus* (Mitchill) (Siluriformes: Ariidae); *Balistes caprisca* Gmelin (Tetraodontiformes: Balistidae); *Caranx crysos* (Mitchill) (Perciformes: Carangidae); *C. melanopterus*; *C. limbatus*; *C. obscurus*; *Coryphaena hippurus* Linnaeus (Perciformes: Coryphaenidae); *Cynoscion nebulosus* (Cuvier) (Perciformes: Sciaenidae); *Cy. regalis* (Bloch & Schneider) (Perciformes: Sciaenidae); *Diplodus sargus sargus* (Linnaeus) (Perciformes: Sparidae); *Dorytheuthis pealeii* (Lesueur) (Teuthida: Loliginidae); *Euthynnus alletteratus* (Rafinesque) (Perciformes: Scombridae); *Fundulus heteroclitus heteroclitus* (Linnaeus) (Cyprinodontiformes: Fundulidae); *Lagodon rhomboides* (Linnaeus) (Perciformes: Sparidae); *Leiostomus xanthurus* Lacépède (Perciformes: Sciaenidae); *Lepidotrigla faurei* Gilchrist & Thompson (Scorpaeniformes: Triglidae); *Lobotes surinamensis* (Bloch) (Perciformes: Lobotidae); *Micropogonias undulatus* (Linnaeus) (Perciformes: Sciaenidae); *Mustelus canis* (Mitchill) (Carcharhiniformes: Triakidae); *Mu. mustelus* (Linnaeus) (Carcharhiniformes: Triakidae); *Neoscombrops cynodon* (Regan) (Perciformes: Acropomatidae); *Ocyurus chrysurus* (Bloch) (Perciformes: Lutjanidae); *Opsanus tau* (Linnaeus) (Batrachoidiformes: Batrachoididae); *Orthopristis chrysoptera* (Linnaeus) (Perciformes: Haemulidae); *Paralichthys albigutta* Jordan & Gilbert (Pleuronectiformes: Paralichthyidae); *Pa. dentatus* (Linnaeus) (Pleuronectiformes: Paralichthyidae); *Peprilus paru* (Linnaeus) (Perciformes: Stromateidae); *Pe. triacanthus* (Peck) (Perciformes: Stromateidae); *Pomatomus saltatrix* (Linnaeus) (Perciformes: Pomatomidae); *Sarda sarda* (Bloch) (Perciformes: Scombridae); *Rh. terraenovae*; *Scomberomorus cavalla* (Cuvier) (Perciformes: Scombridae); *Sc. regalis* (Bloch) (Perciformes: Scombridae); *Squalus acanthias* (Linnaeus) (Squaliformes: Squalidae); *Trichiurus lepturus* Linnaeus (Perciformes: Trichiuridae); *Wallago attu* (Bloch & Schneider) (Siluriformes: Siluridae); *Xiphias gladius* Linnaeus (Perciformes: Xiphiidae).

Type-locality: North Atlantic Ocean off Woods Hole, Massachusetts, USA (41°30'N, 70°39'W).

Additional localities: Gulf of Mexico off the Dry Tortugas, Florida, USA (24°37'N, 82°55'W); Alvarado, Mexico (18°48'N, 95°44'W); North Atlantic Ocean off Beaufort, North Carolina, USA (34°40'N, 76°40'W); off Flatts Village, Bermuda (32°19'N, 64°44'W); Cape Cod Bay, Massachusetts, USA (41°55'N, 70°19'W); Chesapeake Bay off Solomons, Maryland, USA (38°19'N, 76°27'W); Indian Ocean off Mozambique; Andaman Sea off Yangon, Burma (16°44'N, 96°11'E); Timor Sea off Fog Bay; Darwin (Harbour); and Mary River (Sampan mouth), Northern Territory, Australia; South China Sea off Mukah, Sarawak, Malaysia.

Material examined: 4 voucher specimens from *Carcharhinus amboinensis* 1 (*sensu* Naylor et al., 2012) (Carcharhiniformes: Carcharhinidae) (AU-104) from Fog Bay, Northern Territory, Australia, coll. J. N. Caira and K. Jensen, 12.viii.1997 (SAM AHC 35562).

Site of infection: Spiral intestine (for adults).

Remarks

Linton (1890) erected the genus *Otobothrium* to accommodate a single species, *O. crenacolle* Linton, 1890. This species was differentiated from others by the presence of four bothrial pits ['otosacs', 'ciliated pits' or 'supplemental pits' *sensu* Linton (1890)]. Later, this author reported *O. crenacolle* from several definitive and different teleost intermediate hosts (see Linton, 1897, 1900, 1901, 1905, 1907a,b,c, 1908, 1910a,b, 1911, 1912, 1914, 1915, 1924) from the eastern coastline of North America. *O. crenacolle* was considered a synonym of *O. cysticum* (Mayer, 1842) (see Palm, 1995; Palm & Overstreet, 2000) based on examination of plerocerci. The synonymy of both species, however, was rejected by Beveridge & Justine (2007a), because the larval stages of species within this group cannot be confidently identified to species level. Beveridge & Justine (2007a) redescribed the type-species and designated a neotype from the type-host and type-locality, since the holotype was not extant. These authors (2007a) also compared the North American specimens with new material collected from three species of carcharhinid sharks from off Australia and the Malaysian part of Borneo. The specimens from the present study are considered to be conspecific with *O. crenacolle* based on their oncotaxy, scolex morphology and morphometric data (see Beveridge & Justine, 2007a for Australian specimens). Although the current study only provides one additional definitive host species, we emphasise the compilation of intermediate and definitive host records, which illustrate the global distribution of this species in subtropical and tropical waters and provides insights to the extensive host range of this parasite. *O. crenacolle* infects carcharhinid sharks as definitive hosts, whereas a wide array of marine organisms can serve as intermediate hosts: most commonly teleosts, but also carharhinid sharks and cephalopods.

***Otobothrium carcharidis* (Shipley & Hornell, 1906) Pintner, 1913**

Syns *Tetrarhynchus carcharidis* Shipley & Hornell, 1906; *Rhynchobothrius carcharidis* (Shipley & Hornell, 1906) Southwell, 1924; *Tentacularia carcharidis* (Shipley & Hornell, 1906) Southwell, 1929

Type-host: *Carcharhinus melanopterus*.

Additional hosts: *C. amblyrhynchoides* (Whitley) (Carcharhiniformes: Carcharhinidae); *C. limbatus*; *C. sorrah*; *Carcharhinus* cf. *dussumieri* (Carcharhiniformes: Carcharhinidae); *Carcharhinus* cf. *sealei* (Carcharhiniformes: Carcharhinidae); *Carcharhinus* cf. *sorrah* (Carcharhiniformes: Carcharhinidae); *Himantura walga* (Müller & Henle) (Rajiformes: Dasyatidae); *Lamiopsis temmincki*; *Rhizoprionodon acutus*; *Scoliodon laticaudus* Müller & Henle (Carcharhiniformes: Carcharhinidae); *Sphyrna lewini*.

Type-locality: Gulf of Manaar off Dutch Bay, Sri Lanka (08°20'N, 79°47'E).

Additional localities: Gulf of Manaar, Sri Lanka ('Ceylon Pearl Banks') (08°52'N, 79°50'E); Arafura Sea off the Wessel Islands; Darwin (Harbour), Northern Territory, and Nickol Bay, Western Australia; Coral Sea off Balgal, Queensland; off Snapper Island, Queensland, Australia (16°17'S, 145°29'E); off Nouméa, New Caledonia (22°40'S, 165°58'E); South China Sea off Mukah, Sarawak, Malaysia; Persian Gulf off Bandar Abbas, Iran (27°11'N, 56°16'E).

Material examined: 1 voucher specimen from *Carcharhinus* cf. *sealei* off the Wessel Islands, Northern Territory (LRP 3675); 3 voucher specimens from *Carcharhinus brachyurus* (Günther) (Carcharhiniformes: Carcharhinidae) off Goolwa, South Australia, coll. R. Martin, 28.x.1985 (SAM AHC 35579); 2 voucher specimens from *C. maclovi* (Müller & Henle) (Carcharhiniformes: Carcharhinidae) (NT-5) off Nhulunbuy, Northern Territory, coll. J. N. Caira and K. Jensen, 3.xi.1999 (SAM AHC 35572); 1 voucher specimen from *C. melanopterus* (KA-51) in the Makassar Strait off Kota Baru, South Kalimantan, Indonesia (SAM AHC 35619); 4 voucher specimens from *C. sealei* (Pietschmann) (Carcharhiniformes: Carcharhinidae) (NT-14) off Nhulunbuy, Northern Territory, coll. J. N. Caira and K. Jensen, 7.xi.1999 (SAM AHC 35573); 1 voucher specimen from *C. sorrah* (KA-60) from the Makassar Strait off Kota Baru, South Kalimantan, Indonesia (SAM AHC 35620); 2 voucher specimens from *Carcharhinus* cf. *sorrah* (*sensu* Naylor et al., 2012) (NT-15) off Nhulunbuy, Northern Territory, coll. J. N. Caira and K. Jensen, 7.xi.1999 (SAM AHC 35574); 4 voucher specimens from *Eusphyra blochii* (AU-70, AU-71) in Fog Bay, Northern Territory, coll. J. N. Caira and K. Jensen, 10.viii.1997 (SAM AHC 35575–76); 3 voucher specimens from *Rhizoprionodon taylori* (Ogilby)

(Carcharhiniformes: Carcharhinidae) (CM03-51) off Weipa, Queensland, coll. J. N. Caira and K. Jensen, 10.vi.2003 (SAM AHC 35578); 3 voucher specimens from *Rhizoprionodon* cf. *acutus* 2 (*sensu* Naylor et al., 2012) (Carcharhiniformes: Carcharhinidae) (CM03-84) off Weipa, Queensland, Australia, coll. J. N. Caira and K. Jensen, 18.v.2004 (SAM AHC 35577).
Site of infection: Spiral intestine.

Remarks

Shipley & Hornell (1906) first described this species as *Tetrarhynchus carcharidis* Shipley & Hornell, 1906 on the basis of a single specimen from *Carcharhinus melanopterus* collected in Dutch Bay, Sri Lanka. Although Pintner (1913) allocated this species to *Otobothrium*, the taxonomic change was disregarded by Southwell (1924), who placed it in *Rhynchobothrius* van Beneden, 1849, as *R. carcharidis* (Shipley & Hornell, 1906). Dollfus (1942), however, retained this species in *Otobothrium*, whereas Yamaguti (1959) and Schmidt (1986) considered it a species *incertae sedis* (see Beveridge & Campbell, 1998). Beveridge & Campbell (1998) provided a redescription of the holotype and confirmed Pintner's (1913) allocation of the species to *Otobothrium*. The single specimen from Sri Lanka, however, was poorly preserved and a complete description of the segment morphology and the tentacular armature could not be provided. More recently, Beveridge & Justine (2007a) provided a more precise description based on material from several elasmobranch hosts from off Australia, New Caledonia and Malaysian Borneo. The geographical distribution of this species was extended and seven additional definitive host species were added (Beveridge & Justine, 2007a). Haseli et al. (2010) reported *O. carcharidis* from the Persian Gulf from the spiral intestines of three carcharhinid shark species. The present specimens of *O. carcharidis* were identified by the presence of characteristic billhooks on the basal tentacular armature, which are slender in lateral view (Fig. 18H) but plate-like in dorsal views (Fig. 18H) (see Beveridge & Justine, 2007a). Specimens were obtained from elasmobranchs from five localities in Australia, making it a prevalent species in Australian waters. Furthermore, six new host records are provided (see above), five species of requiem sharks (Carcharhinidae) and one species of hammerhead sharks (Sphyrnidae). The known host spectrum of *O. carcharidis* now includes 18 different species (i.e. 15 carcharhinids, two sphyrnids and one dasyatid).

Discussion

The present series of redescriptions of species of *Otobothrium* considerably expands both their host ranges and geographical distributions, particularly in the Indo-Pacific region. The geographical distribution varies significantly between individual species. Of the 11 currently recognised species, some exhibit a global distribution (i.e. *O. crenacolle* and *O. penetrans*), whereas others are either endemic to a particular region (i.e. *O. australe* is only found off Australia) or a specific ocean (i.e. *O. insigne* only occurs in the Atlantic Ocean). Three species are known from the Indo-Pacific region. Both *O. carcharidis* and *O. mugilis* occur in the western and central Indo-Pacific, whereas *O. alexanderi* is found in central and eastern Indo-Pacific waters. For the remaining four species it is difficult to describe any distributional pattern, because these species are either poorly known (i.e. *O. minutum*), were obtained only once (i.e. *O. parvum*) or are of such a small size that specimens could easily be overlooked (i.e. *O. curtum* and *O. propecysticum*). The latter two species, however, appear to be highly host-specific; *O. propecysticum* only occurs in hammerhead sharks (Sphyrnidae), whereas *O. curtum* occurs exclusively infects the tiger shark *Galeocerdo cuvier* (Péron & Lesueur). The other species of *Otobothrium* are less host-specific, usually infecting several species of carcharhinid and/or sphyrnid sharks. In exceptional cases, rays also can act as definitive hosts; *O. australe* was obtained from eagle rays (Myliobatidae) and *O. carcharidis* was found in whiptail stingrays (Dasyatidae). The present study also indicates the presence of two additional, undescribed species, although the material available was inadequate for full descriptions. Given the number of species in the preferred host groups of *Otobothrium*, i.e. requiem sharks (Carcharhinidae) and hammerhead sharks (Sphyrnidae), with about 62 nominal species (Froese & Pauly, 2012), some additional species of *Otobothrium* are likely to be present and yet to be discovered.

In the present study, the adult of *O. mugilis* is described for the first time, the first adequately detailed description of the segment morphology of *O. insigne* is presented and additional details are provided on the morphology of the adults of *O. australe*, *O. penetrans* and *O. alexanderi*. Descriptions of mature segments of the species included here confirm the initial observations of Beveridge & Justine (2007a) that in the type-species, *O. crenacolle*, as well as in others, a hermaphroditic sac is present. All species of *Otobothrium* examined in detail to date possess a hermaphroditic sac rather than a cirrus-sac. These include *O. crenacolle*, *O. carcharidis*, *O. curtum* and *O. parvum* reported by Beveridge & Justine (2007a), and *O. alexanderi*, *O. australe*, *O. insigne*, *O. mugilis* and *O. penetrans* in the present study. The situation in *O. minutum* and *O. propecysticum* remains to be determined. The presence of a hermaphroditic duct in a trypanorhynch was first illustrated by Dollfus (1942, fig. 261) in *Lacistorhynchus tenuis* (van Beneden, 1858), although it was not referred to as such in the text. The structure was first identified clearly as a hermaphroditic duct in the genera *Lacistorhynchus*

Pintner, 1913 and *Hornelliella* Yamaguti, 1954 by Beveridge & Sakanari (1987) and Campbell & Beveridge (1987a), and was subsequently identified in the following genera: *Floriceps* Cuvier, 1917 by Campbell & Beveridge (1987b) and Richmond & Caira (1991), *Dasyrhynchus* Pintner, 1928 by Beveridge & Campbell (1993), *Diesingium* Pintner, 1929 by Beveridge & Campbell (1994), *Pterobothrium* Diesing, 1850 by Campbell & Beveridge (1996), *Callitetrarhynchus* Pintner, 1931 by Beveridge & Campbell (1996), *Pterobothrioides* Campbell & Beveridge, 1997 by Campbell & Beveridge (1997), *Fossobothrium* Beveridge & Campbell, 2005 by Beveridge & Campbell (2005), *Paragrillotia* Dollfus, 1969 by Beveridge & Justine (2007b) and *Grillotia* Guiart, 1927 by Beveridge & Campbell (2007). Thus the presence of a hermaphroditic duct appears to represent a synapomorphy for the clade uniting the Lacistorhynchoidea and the Otophthorioidea in the molecular phylogeny of Olson et al. (2010, fig. 6). The sole exceptions to this pattern based on the genera examined to date appear to be *Poecilancistrum* Dollfus, 1929 (see Beveridge & Campbell, 1996) and the recently described genus *Ancipirhynchus* Schaeffner, Gasser & Beveridge, 2011 (see Schaeffner et al., 2011). Apart from the site of origin of the retractor muscle, it was the only morphological character which appeared to be synapomorphic for these two superfamilies. The confirmation of the presence of a hermaphroditic duct in additional species of *Otophthorium* further strengthens the case for considering this morphological character as a significant distinguishing feature of the two superfamilies.

Redescriptions of the armature confirm that in each species, there is a single intercalary row of hooks ranging in extent from one to three hooks. A significant finding in this study was that, while the hook rows of several species begin on the internal surfaces of the tentacles (i.e. *O. alexanderi*, *O. australe* and *O. penetrans*), in other species they begin on the bothrial surface (i.e. *O. insigne* and *O. mugilis*). This variation within the genus was first noted by Beveridge & Justine (2007a), who observed that the hook rows in *O. propecysticum*, *O. carcharidis* and *O. parvum* commenced on the bothrial surface, whereas the principle rows of *O. crenacolle* and *O. curtum* originated on the internal surface (Beveridge & Justine, 2007a). The addition of species to both groups confirms these preliminary observations. An origin on the bothrial surface has been noted in the case of the otophthoroid species *Pseudotopothrium arii* (Bilquees & Shaukat, 1976), whereas in *Ps. dipsacum* the rows originate on the antiothrial surface (Beveridge et al., 2000). The generic definition of *Otophthorium* given by Palm (2004) implies that the hook rows begin on the internal surface; however, this is no longer the case. Within the Eutetrarhynchoidea, the origin of the hook rows appears to be a generic character (Beveridge et al., 2004), while this does not appear to be the case in the Otophthorioidea with the character having specific value only.

The surface ultrastructure of trypanorhynchs is diverse and includes a broad range of different microtrich forms and shapes. Over the last two decades many scientists have focused on this morphological feature and various trypanorhynch species have been observed with SEM (Richmond & Caira, 1991; Palm, 1995, 1997, 2000, 2004, 2008; Palm et al., 1993, 1998, 2000; Palm & Overstreet, 2000; Jones & Beveridge, 1998; Campbell et al., 1999; Beveridge & Jones, 2000; Jones, 2000; Beveridge & Campbell, 2001). Recently, Chervy (2009) proposed a unified terminology for the complex morphology of microtriches of cestodes. Richmond & Caira (1991) reported the application of the microtrich morphology to be of systematic value for trypanorhynchs, and Palm (1995) considered it a useful but subordinate character for the differentiation of taxa of the genus and species level (Palm, 1995; p. 197). In a novel classification, Palm (2004) utilised the surface ultrastructure as an additional character to differentiate trypanorhynchs. He (2004) stated that this characteristic “reveals additional structures that characterize some genera or even families” (Palm, 2004, p. 44). The surface ultrastructure of more than half of all currently known species of *Otobothrium* have been observed with SEM, namely *O. insigne* (Shields, 1985; Palm, 1995), *O. mugilis* (Jones, 2000; Present study), *O. penetrans* (Palm et al., 1993, 2000; Palm, 2000; Palm & Overstreet, 2000), *O. alexanderi* (Present study), *O. australe* (Present study) and *O. carcharidis* (Present study, data not shown). SEM data for these species reflect an almost uniform pattern of the microtrich distribution on different parts of the scolex. The pars vaginalis of most species is covered with acicular filitriches (i.e. in *O. alexanderi*, *O. australe*, *O. insigne*, *O. mugilis* and *O. carcharidis*), whereas the scolex peduncle of *O. penetrans* was reported to be covered in “sausage-like villi with short filamentous microtriches” (*sensu* Palm, 2000). The bothrial pits of *O. australe*, *O. mugilis* and *O. penetrans* are lined by bifid spinitriches. Palm (2004) described the bothrial pits of *O. insigne* as being lined with “characteristic microtriches” (*sensu* Palm, 2004), thus we assume those also represent the bifid spinitrich type. The distal and proximal bothrial surfaces are covered with papillate or aciculate filitriches, upon which are superimposed characteristically-shaped spinitriches. The spinitrich morphology of both bothrial surfaces, however, is somewhat variable. Trifid spinitriches dominate the proximal bothrial surface of most species of *Otobothrium* observed to date (i.e. *O. alexanderi*, *O. australe*, *O. penetrans* and *O. carcharidis*). The proximal bothrial surface of *O. insigne* is covered by lineate spinitriches (= acerosate *sensu* Palm, 2004) and *O. mugilis* possesses penta- and hexa-digitate spinitriches (Present study). Jones (2000), not differentiating between the distal and proximal bothrial surfaces, detected trifid to penta-digitate spinitriches on the bothrial surface of *O. mugilis*. The distal bothrial surface is covered with either trifid (in *O. insigne* and *O. penetrans*) or aristate trifid spinitriches (in *O. alexanderi* and *O. mugilis*). Palm (1995, p. 104) also recorded penta-

digitate spiniriches on the distal bothrial surface of *O. insigne*, although this was not shown in the respective SEM micrograph (Palm, 1995, fig. 168), which illustrated exclusively trifid spiniriches. The findings presented here indicate that species of *Otobothrium* have a general pattern in their microthrix morphology on different regions of the scolex, even though minor differences exist. Overall, we consider the observation of microthrix patterns along the scolex of species of *Otobothrium* as a useful morphological characteristic, although the application of this character as a standardised method to describe all species of trypanorhynchs is simply not practicable.

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Captions to figures

Fig. 1 *Otobothrium alexanderi* Palm, 2004 from *Carcharhinus melanopterus* in the Arafura Sea. A, scolex, dorso-ventral view; B, detail of terminal genitalia; C, mature segment; D, bulb.

Abbreviations: c, cirrus; ex, excretory canal; hs, hermaphroditic sac; mg, Mehlis' gland; ov, ovary; t, testis; va, vagina; vd, vas deferens; vit, vitelline follicle.

Fig. 2 *Otobothrium alexanderi* Palm, 2004 from *Carcharhinus cautus* in the Timor Sea (A) and from *C. melanopterus* in the Arafura Sea (B–D). A, basal tentacular armature, external surface; B, basal and metabasal tentacular armature, bothrial surface; C, basal and metabasal tentacular armature, internal surface; D, profiles of tentacular hooks. *Abbreviation:* bh, basal tentacular hooks on external surface in lateral (left) and dorsal view (right).

Fig. 3 Scanning electron micrographs of *Otobothrium alexanderi* Palm, 2004 from *Carcharhinus melanopterus* in the Timor Sea. A, anterior region of scolex, dorso-ventral to lateral view; B, proximal bothrial surface showing trifold spinitriches; C, basal and metabasal tentacular armature, external surface, note: characteristic group of three hooks; D, acicular filitriches covering pars vaginalis; E, distal bothrial surface showing aristate, trifold spinitriches; F, trifold spinitriches surrounding area of bothrial pit; G, posterior bothrial margin showing bothrial pit.

Fig. 4 *Otobothrium australe* Palm, 2004 from *Carcharhinus limbatus* in the Indian Ocean. A, scolex, dorso-ventral view; B, scolex, lateral view; C, mature segment; D, detail of terminal genitalia; E, bulbs showing retractor muscle originating in anterior region (left) and forming internal loop (right) before originating in anterior region. *Abbreviations:* c, cirrus; hs, hermaphroditic sac; mg, Mehlis' gland; ov, ovary; rm, retractor muscle; t, testis; va, vagina; vd, vas deferens.

Fig. 5 *Otobothrium australe* Palm, 2004 from *Carcharhinus limbatus* in the Indian Ocean. A, metabasal tentacular armature, internal surface; B, basal tentacular armature, internal surface; C, basal and metabasal tentacular surface, bothrial surface; D, metabasal tentacular armature, external surface; E, profiles of characteristic tentacular hooks. *Abbreviations:* bh, macrohook on internal surface of basal swelling; bih1 and 2, characteristic billhooks on external surface of basal swelling.

Fig. 6 Scanning electron micrographs of *Otobothrium australe* Palm, 2004 from *Carcharhinus limbatus* in the Indian Ocean. A, scolex, dorso-ventral to lateral view; B, scolex, dorso-ventral view; C, bothrial pit showing elongate bifid spinitriches; D, basal tentacular armature, bothrial surface of basal swelling, note the macrohook (left) and two characteristic billhooks (right); E, metabasal tentacular armature, external surface; F, apical tentacular surface, internal surface; G, basal tentacular armature, internal to antiothrial surface of basal swelling.

Fig. 7 *Otobothrium insigne* Linton, 1905 from *Rhizoprionodon terraenovae* in the South Atlantic Ocean. A, scolex, lateral view; B, mature segment; C, bulb; D, detail of terminal genitalia. *Abbreviations:* c, cirrus; ex, excretory canal; hs, hermaphroditic sac; mg, Mehlis' gland; ov, ovary; rm, retractor muscle; t, testis; va, vagina; vd, vas deferens.

Fig. 8 *Otobothrium insigne* Linton, 1905 from *Rhizoprionodon terraenovae* in the South Atlantic Ocean. A, metabasal and apical tentacular armature, bothrial surface; B, basal to apical tentacular armature, external to antiothrial, note: tendency of tentacle to twist from external (base) to antiothrial (top) surface; C, basal and metabasal tentacular armature, external surface; D, basal tentacular armature, antiothrial surface.

Fig. 9 Scanning electron micrographs of *Otobothrium insigne* Linton, 1905 from *Rhizoprionodon terraenovae* in the South Atlantic Ocean. A, scolex, lateral view; B, scolex, dorso-ventral view; C, posterior bothrial margin showing paired bothrial pits; D, apical tentacular armature, bothrial surface; E, metabasal tentacular armature, antiothrial surface; F, hook arrangement on antiothrial surface; G, apical tentacular armature, oblique view of external surface; H, metabasal tentacular armature, bothrial surface; I, metabasal tentacular surface, external surface.

Fig. 10 Schematic representation of the antiothrial surface of the tentacular armature of *Otobothrium insigne* Linton, 1905. Different numbering systems for the tentacular hooks; A, after Hildreth & Lumsden (1985), note the arrays of four hooks in a grey rectangle; B, after Palm (1995).

Fig. 11 *Otobothrium mugilis* Hiscock, 1954 from *Lamiopsis tephrodes* in the South China Sea (A, D) and from *Sphyrna mokarran* 2 (*sensu* Naylor et al., 2012) in the Arafura Sea (B, C, E). A, scolex of large forms, lateral view; B, scolex of smaller forms, lateral view; C, mature segment; D, bulbs, note: size difference of bulbs from large (left) and small forms (right); E, detail of

terminal genitalia. *Abbreviations:* c, cirrus; hs, hermaphroditic sac; mg, Mehlis' gland; ov, ovary; t, testis; va, vagina; vd, vas deferens; vit, vitelline follicle.

Fig. 12 *Otobothrium mugilis* Hiscock, 1954 from *Mugil cephalus* in the Coral Sea (A, B, D–G) and from *Lamiopsis tephrodes* in the South China Sea (C). A, basal and metabasal tentacular armature, antibothrial surface; B, basal and metabasal tentacular armature, bothrial surface, note the opposing surface to (A); C, basal tentacular armature, external surface; D, metabasal tentacular armature, internal surface; E, profiles of tentacular hooks; F, metabasal tentacular armature, bothrial surface; G, metabasal tentacular armature, antibothrial surface, note the opposing surface to (F). *Abbreviations:* bih, billhook; boh, hook of basal, bothrial surface; bh 1 and 2, different basal hooks in lateral (left) and dorsal aspects (right); enh 1 and 2, enlarged hooks on bothrial surface of basal swelling.

Fig. 13 Scanning electron micrographs of *Otobothrium mugilis* Hiscock, 1954 from *Carcharhinus cautus* in the Timor Sea (A, C–G) and from *Lamiopsis tephrodes* in the South China Sea (B, H). A, scolex, lateral view; B, scolex, oblique view; C, everted bothrial pit showing bifid spinitriches; D, group of billhooks on antibothrial tentacular surface; E, distal bothrial surface showing aristate trifid spinitriches; F, proximal bothrial surface showing penta- and hexa-digitate spinitriches and acicular filitriches; G, detailed view of penta- and hexa-digitate spinitriches on proximal bothrial surface; H, acicular filitriches covering pars vaginalis.

Fig. 14 *Otobothrium penetrans* Linton, 1907 from *Sphyrna lewini* in the Indian Ocean (A, B) and from *Sphyrna* sp. in the Red Sea (C). A, scolex, dorso-ventral view; B, bulb; C, detail of terminal genitalia. *Abbreviations:* c, cirrus; hs, hermaphroditic sac; mg, Mehlis' gland; ov, ovary; t, testis; va, vagina; vd, vas deferens.

Fig. 15 *Otobothrium penetrans* Linton, 1907 from *Sphyrna lewini* in the North Pacific Ocean (A, B) and from *Sp. zygaena* in the Mediterranean Sea (C, D). A, basal and metabasal tentacular armature, external surface; B, basal tentacular armature, internal surface; C, basal and metabasal tentacular armature, bothrial surface; D, profiles of tentacular hooks, note the transition in shape and size of hook files 5(5') to 7(7').

Fig. 16 *Otobothrium* sp. 1 from *Carcharhinus melanopterus* in the Arafura Sea (A, B, D) and *Otobothrium* sp. 2 from *Sphyrna zygaena* in the Gulf of California (C, E, F). A, scolex, lateral view; B, detail of terminal genitalia; C, mature segment; D, E, bulbs; F, scolex, lateral view.

Abbreviations: c, cirrus; ex, excretory canal; mg, Mehlis' gland; ov, ovary; rm, retractor muscle; t, testis; ut, uterus; va, vagina; vd, vas deferens; vit, vitelline follicle.

Fig. 17 *Otobothrium* sp. 1 from *Carcharhinus melanopterus* in the Arafura Sea. A, mature segment; B, basal and metabasal tentacular armature, bothrial and internal surfaces; C, basal tentacular armature, external surface; D, basal tentacular armature, antibothrial surface.

Fig. 18 Scanning electron micrographs of *Otobothrium* sp. 1 from *Carcharhinus melanopterus* in the Arafura Sea (A–E), *Otobothrium* sp. 2 from *Sphyrna zygaena* in the Gulf of California (F, G) and *Otobothrium carcharidis* (Shiple & Hornell, 1906) from *Eusphyra blochii* in the Timor Sea (H). A, scolex, dorso-ventral to lateral view; B, lateral bothrial margin showing bothrial ridge; C, bothrial pit; D, distal bothrial surface showing trifid spinitriches and papillate filitriches; E, enlarged, bifid spinitriches of bothrial pit; F, scolex, lateral view; G, basal tentacular armature, antibothrial surface showing group of billhooks; H, basal tentacular armature, bothrial surface showing slender billhooks in lateral view (left) and plate-like billhooks in dorsal view (right).

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