***Dollfusiella* Campbell & Beveridge, 1994 (Trypanorhyncha: Eutetrarhynchidae) from elasmobranchs off Borneo, including descriptions of five new species**

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Abstract Sampling of a large number of elasmobranchs from coastal waters off Borneo revealed the presence of five new species of *Dollfusiella* Campbell & Beveridge, 1994 (Trypanorhyncha: Eutetrarhynchidae), namely *D. angustiformis* n. sp., *D. hemispinosa* n. sp., *D. spinosa* n. sp., *D. imparispinis* n. sp. and *D. parva* n. sp. *Dollfusiella angustiformis* n. sp. is described from the spiral intestines of four species of the dasyatid stingray genus *Himantura* Müller & Henle from both the Indonesian and Malaysian parts of Borneo. All the other species were obtained from Malaysian Borneo. *Dollfusiella hemispinosa* n. sp. is described from the spiral intestines of three species of *Himantura*, whereas *D. spinosa* n. sp. was obtained from several specimens of *Pastinachus solocirostris* Last, Manjaji & Yearsley (Dasyatidae) as well as from *Taeniura lymma* 1 (*sensu* Naylor et al., 2012) (Dasyatidae), *Neotrygon kuhlii* 2 (*sensu* Naylor et al., 2012) (Dasyatidae), and *Glaucostegus* cf. *typus* (*sensu* Naylor et al., 2012) (Rhinobatidae). *Dollfusiella imparispinis* n. sp. is described from the spiral intestine of a single specimen of *Chiloscyllium punctatum* Müller & Henle (Hemiscyllidae) from the South China Sea off Sarawak, whereas *D. parva* n. sp. was obtained from several species of *Himantura*. Specimens of the five novel taxa possess scoleces covered with enlarged microtriches, a morphological characteristic exhibited by several other congeners. However, the new species differ from all congeners by possessing unique patterns of oncotaxy as well as combinations of additional morphological features. The number of valid species within *Dollfusiella* is increased

to 26. For this reason, a key for the species of *Dollfusiella* is provided. Furthermore, novel information on hosts and geographic distribution is provided for two previously described species of *Dollfusiella*, *D. michiae* (Southwell, 1929) and *D. spinulifera* (Beveridge & Jones, 2000). The latter species differs slightly from the original description and shows a much higher variability with regard to the lengths of the scolex and muscular bulbs and the number of testes. These variable characters subdivided specimens of *D. spinulifera* into relatively distinct groups. However, the specimens did not differ in their oncotaxy and are considered to represent a single variable species.

Introduction

Dollfusiella Campbell & Beveridge, 1994 is one of the most species-rich genera of trypanorhynch cestodes. It currently comprises 21 valid species, namely *Dollfusiella australis* (Prudhoe, 1969) Campbell & Beveridge, 1994 (type-species); *D. aculeata* Beveridge, Neifar & Euzet, 2004; *D. aetobati* (Beveridge, 1990) Beveridge, Neifar & Euzet, 2004; *D. bareldsi* (Beveridge, 1990) Beveridge, Neifar & Euzet, 2004; *D. carayoni* (Dollfus, 1942) Campbell & Beveridge, 1994; *D. elongata* Beveridge, Neifar & Euzet, 2004; *D. geraschmidtii* (Dollfus, 1974) Beveridge & Jones, 2000; *D. lineata* (Linton, 1909) Beveridge, Neifar & Euzet, 2004; *D. litocephala* (Heinz & Dailey, 1974) Beveridge, Neifar & Euzet, 2004 (orthography corrected); *D. macrotrachela* (Heinz & Dailey, 1974) Beveridge, Neifar & Euzet, 2004 (orthography corrected); *D. martini* (Beveridge, 1990) Beveridge & Jones, 2000; *D. michiae* (Southwell, 1929) Beveridge, Neifar & Euzet, 2004; *D. micracantha* (Carvajal, Campbell & Cornford, 1976) Beveridge & Jones, 2000; *D. musteli* (Carvajal, 1974) Beveridge, Neifar & Euzet, 2004; *D. ocallaghani* (Beveridge, 1990) Beveridge & Jones, 2000; *D. owensi* (Beveridge, 1990) Beveridge & Jones, 2000; *D. schmidtii* (Heinz & Dailey, 1974) Beveridge, Neifar & Euzet, 2004; *D. spinifer* (Dollfus, 1969) Beveridge & Jones, 2000; *D. spinulifera* (Beveridge & Jones, 2000) Beveridge, Neifar & Euzet, 2004; *D. tenuispinis* (Linton, 1890) Beveridge, Neifar & Euzet, 2004; and *D. vooremi* (São Clemente & Gomes, 1989) Beveridge, Neifar & Euzet, 2004.

Campbell & Beveridge (1994) erected the genus to accommodate species possessing a characteristic basal armature, a basal swelling and apposed hook files 1 and 1' in the metabasal tentacular armature. These morphological characteristics separated *Dollfusiella* from the two closely related genera *Eutetrarhynchus* Pintner, 1913 and *Prochristianella* Dollfus, 1946. However, apart from transferring two species of *Eutetrarhynchus* into *Dollfusiella* and designating the type-species, the authors (Campbell & Beveridge, 1994) did not provide new

combinations for additional taxa, which formally remained in either of the two other genera. Beveridge & Jones (2000) described *Prochristianella spinulifera* Beveridge & Jones, 2000, which represented an intermediate form between *Dollfusiella* and *Prochristianella*, with a minimal gradation in hook sizes along the principle rows and slightly separated hooks 1 and 1'. Moreover, five species of *Eutetrarhynchus* and one species of *Prochristianella* were assigned to *Dollfusiella* by Beveridge & Jones (2000) without further explanation. In a survey of eutetrarhynchids from Western Europe and Africa, Beveridge et al. (2004) described two new species of *Dollfusiella*. These authors also proposed 11 new combinations for taxa transferred into *Dollfusiella* and provided the most recent generic diagnosis (Beveridge et al., 2004).

At present, species of *Dollfusiella* are characterised by an acraspedote scolex with two oval bothria, a typical heteroacanthous armature with hook rows commencing on the antbothrial surface of the tentacle and terminating on the bothrial surface, a metabasal armature with hooks 1 and 1' abutting or only slightly separated, a characteristic basal armature with a basal swelling, the presence of prebulbar organs, elongate bulbs including gland-cells, a retractor muscle inserting at the base of the bulb, elongate segments with two or four parallel columns of testes and an ovary situated at the posteriormost margin. Palm (2004) described the possible existence of two distinct groups within *Dollfusiella*: one group possessing a scolex with enlarged microtriches and a second group lacking this microtrich cover. However, this hypothesis cannot be verified at present.

Recent examinations of a large number of trypanorhynch specimens from Borneo revealed five new species of *Dollfusiella*, all of which possess microscopically visible microtriches on the scolex peduncle. In the species descriptions below we compare the new species only with already described species exhibiting prominent microtriches. Moreover, we provide new host and locality records for *D. spinulifera* and *D. michiae* and a key for all valid species of *Dollfusiella*.

Materials and Methods

Specimens were obtained from the spiral intestines of a wide array of elasmobranch hosts from several sampling localities: Indonesian Borneo:[the Java Sea off Singkawang (00°55'N, 108°58'E), Sungai Jawi (01°54'S, 110°00'E), Jungkat (00°03'N, 109°12'E) and Pagarantimum, West Kalimantan (02°14'S, 110°05'E)]; the Makassar Strait off Manggar, East Kalimantan (01°12'S, 116°58'E) and Pagatan, South Kalimantan (03°36'S, 115°54'E); and the Sulawesi Sea off Pulau Rabu Rabu, East Kalimantan (02°19'N, 118°07'E); Malaysian Borneo: the Celebes

Sea off Pulau Mabul (04°14'N, 118°37'E), Semporna (04°28'N, 118°37'E) and Tawau, Sabah (04°14'N, 117°53'E); the mouth of the Kinabatangan River, Sabah (05°47'N, 118°20'E); the South China Sea off Mukah (02°53'N, 112°05'E), Santubong (01°43'N, 110°19'E), Sematan, Sarawak (01°48'N, 109°46'E) and Pulau Balambangan, Sabah (07°16'N, 116°56'E); the Sulu Sea off Kampung Tetabuan (06°01'N, 117°42'E) and Sandakan, Sabah (05°50'N, 118°07'E). They were processed for morphological study as described by Schaeffner et al. (2011). Drawings were made with the aid of an Olympus BH2 microscope with a drawing attachment tube and Nomarski interference contrast. Measurements were made with an ocular micrometer and are presented in micrometres as the range followed by the mean, standard deviation and the number of specimens measured in parentheses. Individual measurements are presented, if the number of measurements available for this character was less than three. Due to the small size of the tentacles and tentacular hooks, the measurements of the oncotaxy were obtained directly from line drawings. Vitelline follicles which encircle the medulla are shown on the lateral margins of segments only. Enlarged microtriches on the scolex peduncle of specimens were visible with light microscopy (referred to as 'microscopically visible microtriches' in the text). Specimens used for scanning electron microscopy (SEM) were processed as described by Schaeffner et al. (2011). Representative segments were embedded in paraffin and serial sections were cut at a thickness of 5 µm. Sections were stained with haematoxylin and eosin. Morphological characteristics in the species descriptions follow the terminology of Pintner (1913), Dollfus (1942) and Campbell & Beveridge (1994). Microthrix morphology follows the terminology of Chervy (2009).

Specimens have been deposited in the Muzium Zoologi, University of Malaya, Institute of Biological Sciences, Kuala Lumpur, Malaysia (MZUM); the Museum Zoologicum Bogoriense, Zoological Division, Research Center for Biology, Indonesian Institute of Science, Cibinong, Indonesia (MZB); 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) and the South Australian Museum, Adelaide, Australia (SAM).

Host nomenclature follows Last et al. (2010). Host specimens belonging to a species complex [e.g. *Himantura uarnak* (Gmelin)] are characterised with a numeral to indicate the provisional identification (e.g. *Himantura uarnak* 3, *sensu* Naylor et al., 2012). Although these specimens possess a similar morphology to the designated taxon, they were shown to be distinct based on their molecular phylogeny (see data from Naylor et al., 2012). Abbreviations used for host and locality records are as follows: BO, specimens from Malaysian Borneo; KA, specimens

from Indonesian Borneo. Information on individual host records and sampling localities is available from the Global Cestode Database (<http://tapewormdb.uconn.edu/>).

Family Eutetrarhynchidae Guiart, 1927

Genus *Dollfusiella* Campbell & Beveridge, 1994

***Dollfusiella angustiformis* n. sp.**

Type-host: *Himantura uarnacoides* (Bleeker) (Myliobatiformes: Dasyatidae) (KA-146, KA-143, KA-206, KA-433, BO-118).

Additional hosts: *Himantura pastinacoides* (Bleeker) (Myliobatiformes: Dasyatidae) (KA-203); *Himantura* cf. *oxyrhyncha* (*sensu* Naylor et al., 2012) (Myliobatiformes: Dasyatidae) (KA-189); *Himantura* cf. *uarnacoides* (*sensu* Naylor et al., 2012) (Myliobatiformes: Dasyatidae) (BO-95).

Type-locality: Java Sea off Singkawang, West Kalimantan, Indonesia.

Additional localities: Java Sea off Sungai Jawi, Jungkat and Pagarantimum, West Kalimantan, Indonesia; Makassar Strait off Manggar, East Kalimantan, Indonesia; Sulu Sea off Kampung Tetabuan, Sabah, Malaysia.

Site of infection: Spiral intestine.

Type-material: Holotype in MZB (No. Ca 183); paratypes in MZB (No. Ca 184), MZUM (No. 2013.18), SAM (Nos. AHC 35705–07), USNPC (Nos. 106914–16) and LRP (Nos. 8191–97).

Etymology: The specific name *angustiformis* relates to the narrow, elongate body of this species.

Description (Figs. 1–3)

[Based on 16 whole-mounts, 5 specimens used for SEM and serial sections.] Mature cestodes 2.3–3.3 (2.8 ± 0.3 ; $n = 7$) mm long (Fig. 3A), with 3–5 (4 ± 1 ; $n = 10$) segments (Fig. 1D); single gravid specimen 3.4 mm long, with 5 segments. Scolex acraspedote, 1,265–1,430 ($1,374 \pm 51$; $n = 7$) long (Fig. 1A, B); surface covered with enlarged microtriches extending from between bothria to anterior part or mid-level of pars bulbosa (Fig. 3H); maximum width at level of pars bothrialis, 150–180 (163 ± 11 ; $n = 6$) wide; pars bothrialis 150–170 (160 ± 8 ; $n = 7$) long. Bothria two in number, oval (Figs. 1B, 3B), 150–160 (152 ± 4 ; $n = 4$) long, 105–110 (109 ± 2 ; $n = 5$) wide, with free posterior margins (Figs. 1A, 3I); distal bothrial surface covered with capilliform filitriches; capilliform filitriches enlarged at border to proximal bothrial surface (Fig.

3B); proximal bothrial surface covered with palmate spinitriches and acicular filitriches (Fig. 3G); bothrial pits absent; pars vaginalis longer than pars bothrialis, 730–910 (859 ± 62 ; $n = 7$) long, covered with palmate spinitriches and acicular filitriches (Fig. 3H). Tentacle sheaths sinuous to irregularly coiled; pars bulbosa 470–555 (516 ± 32 ; $n = 7$) long, 120–150 (138 ± 10 ; $n = 7$) wide; prebulbar organs present; bulbs elongate (Fig. 1A–C), thick-walled, 480–550 (523 ± 26 ; $n = 12$) long, 60–70 (65 ± 4 ; $n = 12$) wide, reach into pars proliferans scolecis in some specimens (Fig. 1A); bulb width : length ratio 1.0 : 6.9–9.2 (8.0 ± 0.9 ; $n = 12$); retractor muscle originates at base of bulb (Fig. 1C); gland-cells present, surround retractor muscle to middle or anterior third of bulb (Fig. 1C); scolex ratio (pars bothrialis : pars vaginalis : pars bulbosa) 1.0 : 4.3–5.9 : 2.9–3.5 ($1.0 : 5.4 \pm 0.5 : 3.2 \pm 0.2$; $n = 7$).

Fully everted tentacle 700–850 (757 ± 81 ; $n = 3$) long; tentacle diameter 15–16 (15 ± 1 ; $n = 7$) at base, 18–20 (19 ± 1 ; $n = 7$) at basal swelling, 15–18 (16 ± 1 ; $n = 7$) in metabasal region, 13–15 (14 ± 1 ; $n = 7$) in distal region.

Armature heteroacanthous, homeomorphous; hooks hollow, falcate, in ascending half spiral rows (Figs. 2A, B, 3E, F, J). Hook files begin on antibothrial surface of tentacle (Figs. 2A, 3F), terminate on bothrial surface (Figs. 2B, 3E); 7 hooks per principle row (Fig. 2B); hook files 1 and 1' not separated (Fig. 2A). Hooks 1(1') 3–4 (3; $n = 10$) long, base 1 ($n = 10$) long; hooks 2(2') similarly sized, 3–4 (4; $n = 10$) long, base 1 ($n = 10$) long; hooks 3(3') slightly larger, 4–5 (5; $n = 10$) long, base 1 ($n = 10$) long; hooks 4(4') slightly larger, 6 ($n = 10$) long, base 1–2 (1; $n = 10$) long; hooks 5(5') similarly sized, 5–6 (6; $n = 10$) long, base 1 ($n = 10$) long; hooks 6(6') slightly smaller, 4–5 (4; $n = 10$) long, base 1 ($n = 10$) long; hooks 7(7') slightly larger, 5–6 (5; $n = 10$) long, base slightly wider, 2 ($n = 10$) long.

Distinctive basal armature present (Figs. 2C–E, 3C, D); basal hooks uncinete, enlarged, on bothrial surface 4–6 (5 ± 1 ; $n = 4$) long, base 3–4 (4; $n = 4$) long (Figs. 2D, 3C), becoming more falcate on external and internal surfaces (Figs. 2C, 3D), 3–4 (3; $n = 5$) long, base 1 ($n = 5$) long; basal hooks on antibothrial surface uncinete 4 ($n = 2$) long, base 3 ($n = 2$) long (Fig. 2E); hooks prior to basal swelling falcate, 4–5 (4; $n = 6$) long, base 1–2 (2; $n = 6$) long on bothrial surface (Fig. 2D), 5–6 (5; $n = 10$) long, base 1 ($n = 10$) long on antibothrial surface (Fig. 2E); basal swelling present (Figs. 2C, D, 3C–E), with rows of billhooks on antibothrial surface (Fig. 2E), 3–5 (3 ± 1 ; $n = 10$) long, base 1 ($n = 10$) long; billhooks become falcate towards external and internal surfaces (Fig. 2C, E), 5–6 (5; $n = 5$) long, base 1–2 (2; $n = 5$) long; rows of uncinete hooks on bothrial surface (Fig. 2D), of almost similar size, 3–4 (4; $n = 10$) long, base 3–4 (3; $n = 10$) long.

Segments acraspedote; immature segments 15–50 (26 ± 14 ; $n = 8$) long, 95–120 (106 ± 9 ; $n = 8$) wide; terminal mature segments 900–1,595 ($1,306 \pm 256$; $n = 8$) long, 110–140 (124 ± 10 ;

n = 8) wide (Fig. 1E); gravid segment 1.450 (n = 1) long, 280 (n = 1) wide. Genital pore inconspicuous, in posterior third of segment (Fig. 1E); cirrus sac ovoid (Fig. 1E, F), 73–98 (85 ± 8 ; n = 6) long, 53–75 (59 ± 9 ; n = 6) wide; cirrus unarmed; internal seminal vesicle present (Fig. 1F); external seminal vesicle absent; vas deferens obscured by testes. Testes arranged in two columns, exclusively preovarian, in single layer (Fig. 1E), 55–90 (69 ± 12 ; n = 7) in number, 48–82 (61 ± 12 ; n = 7) preporal, 7–10 (8 ± 1 ; n = 7) postporal, 50–55 (53 ± 2 ; n = 10) long, 33–35 (34 ± 1 ; n = 10) wide. Vagina c.10 (n = 1) in width, runs towards genital atrium in sinuous course, enters genital atrium on posterior aspect; vagina with enlarged vaginal sphincter (Fig. 1F); seminal receptacle present, between anterior part of ovarian lobes. Ovary at posterior margin of segment (Fig. 1E), tetra-lobed; ovarian lobes 163–275 (229 ± 39 ; n = 12) long, 18–33 (26 ± 5 ; n = 12) wide in mature segments, 303–335 (n = 2) long, 23–28 (n = 2) wide in gravid segments. Mehlis' gland between posterior parts of ovarian lobes (Fig. 1E), 43–55 (48 ± 5 ; n = 6) in diameter. Vitelline follicles small, circum-medullary, 13–23 (17 ± 3 ; n = 10) in diameter. Uterus median, tubular, simple, extends to anterior extremity of segment; uterine pore absent.

Remarks

The new species is characterised by a very narrow and slender strobila, an acraspedote scolex with two bothria, the presence of prebulbar organs, elongate, muscular bulbs with gland-cells and a retractor muscle inserting at the base of each bulb. The tentacles exhibit a distinctive basal armature with a basal swelling and the metabasal armature is typical heteroacanthous and homeomorphous. The hook rows consisting of seven hooks start on the antibothrial surface and terminate on the bothrial surface. Hook files 1 and 1' are not separated. This combination of morphological characters clearly allocates this species into the genus *Dollfusiella*. One of the most obvious features of *D. angustiformis* n. sp. is the presence of enlarged microtriches covering the scolex peduncle. Ten other species of *Dollfusiella* possess a 'spiny' scolex lined with enlarged microtriches, namely *D. aculeata*, *D. elongata*, *D. litocephala*, *D. micracantha*, *D. ocallaghani*, *D. owensi*, *D. spinulifera*, *D. schmidtii*, *D. spinifer* and *D. tenuispinis*. However, in most species the distribution of the enlarged microtriches extends to the posterior margin of the pars bulbosa or the beginning of the pars proliferans scolecis. In well-fixed material of *D. angustiformis* n. sp. the microtriches expand from between the bothria to the anterior part or mid-level of the pars bulbosa. A similar distribution has been described only for *D. owensi* (i.e. extension to the posterior third of the pars bulbosa) and *D. schmidtii* [not specified in the description, but microtriches are drawn to the mid-level of the pars bulbosa in figure 22 of Heinz & Dailey (1974)]. *Dollfusiella angustiformis* n. sp. differs from *D. owensi* in the length of the

scolex (1.4 vs 1.0 mm, respectively) and in the very distinctive basal armatures; *D. owensi* exhibits large, 'bill-shaped' hooks with small, sharply rebated tips (Beveridge, 1990), which are absent in *D. angustiformis* n. sp. *Dollfusiella schmidt*i possesses a much larger body compared to *D. angustiformis* n. sp. (up to 9.0 vs 2.8 mm, respectively) with more segments (six to ten segments vs three to five segments, respectively) and much larger and wider bulbs ($700 \times 80 \mu\text{m}$ vs $523 \times 65 \mu\text{m}$, respectively). Moreover, *D. schmidt*i possesses many more principle hooks in the metabasal armature [i.e. more than 12 hooks drawn but not specified in the description; see figures 23, 25 in Heinz & Dailey (1974)].

Specimens of this species were obtained from different localities in West and East Kalimantan (Indonesia) and Sabah (Malaysia) and from several host specimens belonging to four different species of *Himantura* Müller & Henle. We therefore consider this species to be highly host specific, only infecting stingrays of the family Dasyatidae.

***Dollfusiella hemispinosa* n. sp.**

Type-host: *Himantura pastinacoides* (BO-12, BO-61).

Additional hosts: *Himantura uarnacoides* (BO-77); *Himantura uarnak* 3 (*sensu* Naylor et al., 2012) (Myliobatiformes: Dasyatidae) (BO-47).

Type-locality: South China Sea off Sematan, Sarawak, Malaysia.

Additional localities: South China Sea off Mukah, Sarawak, Malaysia; Sulu Sea off Sandakan, Sabah, Malaysia.

Site of infection: Spiral intestine.

Type-material: Holotype in MZUM (No. 2013.19); paratypes in MZUM (Nos. 2013.20–22), SAM (Nos. AHC 35708–12), USNPC (Nos. 106917–19) and LRP (Nos. 8198–8217).

Etymology: The specific name *hemispinosa* relates to the posterior distribution of the enlarged microtriches covering the scolex to the border between pars vaginalis and pars bulbosa.

Description (Figs. 4–6)

[Based on 57 whole-mounts, 5 specimens used for SEM and serial sections.] Cestodes small, anapolytic (Fig. 4E); gravid specimens 2.1–5.3 (3.9 ± 1.2 ; $n = 16$) mm long, with 5–9 (8 ± 1 ; $n = 13$) segments. Scolex acraspedote (Figs. 4A, B, 6A, E), 600–1,000 (848 ± 111 ; $n = 16$) long; surface covered with enlarged microtriches extending from between bothria to anterior portion of pars bulbosa (Fig. 4A, B); maximum width at pars bothrialis, 140–220 (175 ± 26 ; $n = 16$) wide;

pars bothrialis 120–165 (138 ± 14 ; $n = 16$) long. Bothria two in number, elongate (Figs. 4B, 6D, F), 130–160 (152 ± 9 ; $n = 10$) long, 70–90 (80 ± 7 ; $n = 10$) wide, with thick, fleshy margins (Fig. 6F); distal bothrial surface covered with capilliform filitriches; capilliform filitriches enlarged at border to proximal bothrial surface; proximal bothrial surface covered with palmate spinitriches and acicular filitriches (Fig. 6B); bothrial pits absent; pars vaginalis longer than pars bothrialis, 290–650 (517 ± 101 ; $n = 16$) long, covered with palmate spinitriches and acicular filitriches (Fig. 6C). Tentacle sheaths sinuous to almost straight; pars bulbosa 290–360 (332 ± 20 ; $n = 16$) long, 90–130 (104 ± 11 ; $n = 16$) wide; prebulbar organs present; bulbs elongate (Fig. 4A–C), 290–350 (320 ± 16 ; $n = 17$) long, 40–60 (49 ± 6 ; $n = 17$) wide; bulb width : length ratio 1.0 : 5.3–8.6 (6.6 ± 0.9 ; $n = 17$); retractor muscle inserts at base of bulb (Fig. 4C); gland-cells numerous, surrounding retractor muscle to anterior third of bulb (Fig. 4C), reaching into anterior part of pars vaginalis in some specimens; scolex ratio (pars bothrialis : pars vaginalis : pars bulbosa) 1.0 : 2.4–4.8 : 2.0–2.9 ($1.0 : 3.8 \pm 0.8 : 2.4 \pm 0.2$; $n = 16$).

Fully everted tentacle 500–550 (533 ± 15 ; $n = 10$) long; tentacle diameter 15–18 (16 ± 1 ; $n = 14$) at base, 23–28 (24 ± 2 ; $n = 14$) at basal swelling, 15–25 (17 ± 3 ; $n = 14$) in metabasal region, 10–18 (14 ± 2 ; $n = 14$) in distal region.

Metabasal armature heteroacanthous (Figs. 5B, C, 6G, J), homeomorphous; hooks hollow, falcate; hook rows consist of 10 hooks (Fig. 5C); rows start on antibothrial surface of tentacle (Figs. 5B, 6G), terminate on bothrial surface (Fig. 5C); hook files 1 and 1' not or only slightly separated (Fig. 5B); hooks 1(1') 3 ($n = 10$) long, base 1 ($n = 10$) long; hooks 2(2') 2–3 (3; $n = 10$) long, base 1 ($n = 10$) long; hooks 3(3') slightly larger, 3–4 (3; $n = 10$) long, base 1 ($n = 10$) long; hooks 4(4') slightly larger, 4–5 (5; $n = 10$) long, base 1–2 (1; $n = 10$) long; hooks 5(5') slightly larger, 5–6 (5; $n = 10$) long, base 1 ($n = 10$) long; hooks 6(6') slightly smaller, 4–5 (4 ± 1 ; $n = 10$) long, base 1 ($n = 10$) long; hooks 7(7') slightly smaller, 3–4 (4; $n = 10$) long, base 1 ($n = 10$) long; hooks 8(8') 3–4 (4; $n = 10$) long, base 1 ($n = 10$) long; hooks 9(9') 3–4 (4; $n = 10$) long, base 1 ($n = 10$) long; hooks 10(10') 3–4 (4; $n = 10$) long, base 1 ($n = 10$).

Characteristic basal armature present (Figs. 5A, D, E, 6H, I); first rows of basal hooks enlarged, uncinata (Figs. 5A, D, E, 6H, I), 5–7 (6 ± 1 ; $n = 10$) long, base 4–5 (4; $n = 10$) long; next rows of hooks prior to basal swelling falcate on antibothrial, external and internal surfaces (Figs. 5A, D, 6I), 6–8 (7; $n = 10$) long, base 1–2 (1; $n = 10$) long, falcate to uncinata on bothrial surface (Figs. 5D, 6H), 4–5 (4; $n = 10$) long, base 2–3 (3; $n = 10$) long; basal swelling present, with c.4–5 rows of hooks; characteristic billhooks on antibothrial surface (Fig. 5A, E), 3–4 (4; $n = 10$) long, base 1 ($n = 10$) long; hooks on internal and external surfaces falcate (Figs. 5A, 6I), 4 ($n = 10$) long, base 1 ($n = 10$) long; hooks on bothrial surface uncinata (Figs. 5D, 6H), 3–4 (4; $n = 10$) long, base 3 ($n = 10$) long; hooks anterior to basal swelling small, uncinata, 2–3 (2; $n = 10$).

long, base 2 ($n = 10$) long on bothrial surface (Figs. 5D, 6H), 1–2 ($n = 10$) long, base 1 ($n = 10$) on antibothrial surface (Fig. 6H); transition to metabasal armature occurs at about hook row 7 anterior to basal swelling.

Segments acraspedote; immature segments wider than long, 10–25 (16 ± 6 ; $n = 8$) long, 70–105 (81 ± 11 ; $n = 8$) wide; late mature segments elongate, 420–980 (613 ± 166 ; $n = 8$) long, 85–150 (113 ± 26 ; $n = 8$) wide (Fig. 4D). Genital pores alternate irregularly, in posterior half of segment (Fig. 4D); pore inconspicuous; cirrus sac ovoid (Fig. 4D, F), thick-walled, 43–70 (56 ± 10 ; $n = 6$) long, 65–98 (80 ± 12 ; $n = 6$) wide; cirrus unarmed; internal seminal vesicle present (Fig. 4D, E), inconspicuous; external seminal vesicle absent; vas deferens not observed; testes arranged in two columns (Fig. 4D), exclusively preovarian, in single layer, 29–35 (31 ± 2 ; $n = 17$) in number, 25–30 (27 ± 2 ; $n = 17$) preporal, 4–6 (5 ± 1 ; $n = 17$) postporal, 45–65 (54 ± 5 ; $n = 15$) long, 28–45 (34 ± 5 ; $n = 15$) wide. Vagina runs towards genital atrium in sinuous course, enters genital atrium from posterior aspect, with enlarged vaginal sphincter (Fig. 4D, F); vaginal sphincter 30–55 (39 ± 9 ; $n = 7$) in diameter (Fig. 4F); seminal receptacle present, small, between anterior part of ovarian lobes. Ovary at posterior extremity of segment, bi-lobed in dorso-ventral view (Fig. 4D); ovarian lobes elongate, 93–193 (124 ± 29 ; $n = 16$) long, 23–40 (28 ± 5 ; $n = 16$) wide; Mehlis' gland between posterior part of ovarian lobes (Fig. 4D), 33–40 (36 ± 4 ; $n = 3$) in diameter. Vitelline follicles small, circum-medullary, 8–14 (10 ± 2 ; $n = 15$) in diameter. Uterus median, tubular, simple, extends to anterior extremity of segment (Fig. 4D); uterine pore absent.

Gravid segments 705–1,570 ($1,034 \pm 323$; $n = 9$) long, 185–340 (241 ± 63 ; $n = 9$) wide; uterus extends to anteriormost extremity, saccate; cirrus sac ovoid, 58–83 (69 ± 8 ; $n = 8$) long, 85–128 (102 ± 14 ; $n = 8$) wide; ovarian lobes 113–195 (163 ± 31 ; $n = 14$) long, 25–83 (41 ± 17 ; $n = 14$) wide.

Remarks

The most obvious and characteristic feature of *D. hemispinosa* n. sp. is the posterior distribution of enlarged, palmate microtriches covering the scolex peduncle to the beginning of the pars bulbosa. This not only differentiates the new species from all other congeners, but furthermore highlights the importance of the posterior microthrix distribution as a specific character within *Dollfusiella*. When compared with other representatives of the genus bearing enlarged microtriches, additional features become apparent, which make *D. hemispinosa* n. sp. unique within the group. The lengths of the scolex and muscular bulbs are smaller than those of most congeners, with the exception of *D. spinulifera*, in which both measurements are even smaller. *Dollfusiella hemispinosa* n. sp. also possesses fewer testes than *D. spinulifera* (i.e. 29–35 vs

34–60, respectively). However, the testes number of *D. hemispinosa* n. sp. matches *D. micracantha* (i.e. 35 testes), which is one of the most poorly known species within the genus. The latter species, however, lacks enlarged hooks at the base of the tentacular armature, which are present in *D. hemispinosa* n. sp., and possesses a smaller scolex (i.e. 1.3–1.9 vs 2.1–5.3 mm, respectively) but larger bulbs (i.e. 400–530 vs 290–350 μ m, respectively).

Dollfusiella hemispinosa n. sp. was found in the spiral valves of three different species of stingrays (Dasyatidae) collected from three different localities in the Malaysian part of Borneo. Given the high number of different species of elasmobranchs observed, the presence of these worms in a single host genus (i.e. *Himantura*) shows a high degree of host specificity.

***Dollfusiella spinosa* n. sp.**

Type-host: *Pastinachus solocirostris* Last, Manjaji & Yearsley (Myliobatiformes: Dasyatidae) (BO-256, BO-165, BO-267, BO-464).

Additional hosts: *Taeniura lymma* 1 (*sensu* Naylor et al., 2012) (Myliobatiformes: Dasyatidae) (BO-131); *Neotrygon kuhlii* 2 (*sensu* Naylor et al., 2012) (Myliobatiformes: Dasyatidae) (BO-409); *Glaucostegus* cf. *typus* (*sensu* Naylor et al., 2012) (Rajiformes: Rhinobatidae) (BO-120).

Type-locality: South China Sea off Mukah, Sarawak, Malaysia.

Additional localities: South China Sea off Sematan, Sarawak, Malaysia; Celebes Sea off Pulau Mabul, Sabah, Malaysia; Kinabatangan River (mouth) near Celebes Sea, Sabah, Malaysia; Sulu Sea off Kampung Tetabuan, Sabah, Malaysia.

Site of infection: Spiral intestine.

Type-material: Holotype in MZUM (No. 2013.23); paratypes in MZUM (Nos. 2013.24–25), SAM (Nos. AHC 35713–19), USNPC (Nos. 106920–23) and LRP (Nos. 8218–25, 8248–71).

Etymology: The specific name *spinosa* relates to the enlarged microtriches covering the scolex posteriorly almost to the pars proliferans scolecis.

Description (Figs. 7–9)

[Based on 59 whole-mounts, 5 specimens used for SEM and serial sections.] Mature cestodes small, 2.2–3.4 (2.8 ± 0.5 ; $n = 10$) mm long (Figs. 7E, 9A), with 5–7 (5 ± 1 ; $n = 7$) segments; single gravid specimen 5.6 ($n = 1$) mm long, with 7 ($n = 1$) segments. Scolex acraspedote, very slender, 930–1,190 ($1,030 \pm 72$; $n = 10$) long (Figs. 7A, B, 9A); surface covered with enlarged microtriches extending from between bothria almost to pars proliferans scolecis (Figs. 7A, B,

9E); maximum width at pars bothriialis, 130–205 (151 ± 24 ; $n = 10$) wide; pars bothriialis 130–180 (157 ± 16 ; $n = 10$) long. Bothria two in number, oval (Figs. 7B, 9E), 150–165 (158 ± 7 ; $n = 6$) long, 100–130 (119 ± 12 ; $n = 6$) wide, with thick margins, V-shaped-ridge within bothrium visible in SEM specimens only (Fig. 9E); distal bothrial surface covered with capilliform filitriches (Fig. 9B); proximal bothrial surface covered with palmate spinitriches and acicular filitriches (Fig. 9C); bothrial pits absent; pars vaginalis longer than pars bothriialis, 510–740 (595 ± 65 ; $n = 10$) long, covered with palmate spinitriches and acicular filitriches (Fig. 9D, E). Tentacle sheaths sinuous to irregularly coiled; pars bulbosa 390–470 (438 ± 23 ; $n = 10$) long, 125–155 (138 ± 9 ; $n = 10$) wide; prebulbar organs present; bulbs elongate (Fig. 7A–C), 370–450 (419 ± 20 ; $n = 15$) long, 50–75 (61 ± 8 ; $n = 15$) wide, reach to pars proliferans scolecis in some specimens (Fig. 7B); bulb width : length ratio 1.0 : 5.7–8.4 (7.0 ± 0.7 ; $n = 15$); retractor muscle inserts at base of bulb (Fig. 7C); gland-cells present, mostly in posterior half of bulb (Fig. 7C), reach to anterior third of bulb or even to pars vaginalis in some specimens; scolex ratio (pars bothriialis : pars vaginalis : pars bulbosa) 1.0 : 3.0–4.4 : 2.3–3.3 ($1.0 : 3.8 \pm 0.5 : 2.8 \pm 0.3$; $n = 10$).

Fully everted tentacle 510–530 (520 ± 10 ; $n = 3$) long; tentacle diameter 10–15 (13 ± 1 ; $n = 10$) at base, 16–18 (17 ± 1 ; $n = 10$) at basal swelling, 13–15 (13 ± 1 ; $n = 10$) in metabasal region, 10–13 (11 ± 1 ; $n = 10$) in distal region.

Metabasal armature heteroacanthous (Figs. 8D–F, 9H), homeomorphous; hooks hollow, falcate (Fig. 8D–F); hook rows consist of 8 hooks (Fig. 8E); rows start on antibothrial surface of tentacle (Fig. 8F), terminate on bothrial surface (Fig. 8E); hooks 1 and 1' only slightly spaced (Fig. 8F); hooks 1(1') 2–3 (3; $n = 10$) long, base 1 ($n = 10$) long; hooks 2(2') 2–3 (3; $n = 10$) long, base 1 ($n = 10$) long; hooks 3(3') 3 ($n = 10$) long, base 1 ($n = 10$) long; hooks 4(4') 3 ($n = 10$) long, base 1 ($n = 10$) long; hooks 5(5') larger, 4–6 (5 ± 1 ; $n = 10$) long, base 1 ($n = 10$) long; hooks 6(6') 4–5 (5; $n = 10$) long, base 1–2 (1; $n = 10$) long; hooks 7(7') 5–6 (5; $n = 10$) long, base 1–2 (1; $n = 10$) long; hooks 8(8') 5 ($n = 10$) long, base 1 ($n = 10$) long.

Characteristic basal armature present (Figs. 8A–C, 9F, G, I); first 3–4 rows of basal hooks uncinata, slightly enlarged (Figs. 8A–C, 9F, G, H), 3–4 (4; $n = 10$) long, base 2–3 (3; $n = 10$) long; hooks prior to basal swelling falcate on antibothrial surface (Figs. 8B, 9G), 4–6 (5 ± 1 ; $n = 10$) long, base 1 ($n = 10$) long; hooks prior to basal swelling uncinata on bothrial surface (Figs. 8A, 9F, I), 3–4 (3; $n = 5$) long, base 2–3 (2; $n = 5$) long; hooks prior to basal swelling falcate on internal and external surfaces (Fig. 8C), enlarged, 2–3 (3; $n = 6$) long, base 1 ($n = 6$) long; basal swelling present (Figs. 8A–C, 9F, G, I), with about 5–6 rows of hooks; hooks on antibothrial surface billhook-shaped (Figs. 8B, 9 G), minute, 1–2 (1; $n = 10$) long, base 1 ($n = 10$) long, form cluster anterior to enlarged, falcate hooks; basal swelling with billhooks on

bothrial surface (Figs. 8A, 9F, I), 1–2 (2; n = 10) long, base 1 (n = 10) long, slightly increasing in size towards mid-line; internal and external surfaces with falcate hooks on basal swelling (Figs. 8C, 9I), 2 (n = 10) long, base 1 (n = 10) long; transition to metabasal armature occurs at about hook row 5 anterior to basal swelling.

Segments acraspedote; immature segments wider than long, 10–20 (16 ± 3 ; n = 10) long, 90–125 (105 ± 9 ; n = 10) wide; mature segments elongate, 770–1,760 ($1,188 \pm 301$; n = 10) long, 160–275 (189 ± 37 ; n = 10) wide (Fig. 7D). Genital pores alternate irregularly, in posterior half of segment (Fig. 7D); pore inconspicuous; cirrus sac ovoid (Fig. 7D, F), thick-walled, 55–108 (83 ± 15 ; n = 8) long, 108–150 (126 ± 15 ; n = 8) wide; cirrus unarmed; internal seminal vesicle present (Fig. 7D, F), inconspicuous; external seminal vesicle absent; vas deferens obscured by testes; testes arranged in two columns (Fig. 7D), exclusively preovarian, in single layer, 42–48 (45 ± 2 ; n = 8) in number, 30–36 (33 ± 2 ; n = 8) preporal, 11–13 (12 ± 1 ; n = 8) postporal, 68–88 (75 ± 7 ; n = 10) long, 43–48 (44 ± 2 ; n = 10) wide. Vagina runs towards genital atrium in sinuous course, enters genital atrium on posterior aspect, $c.8$ (n = 2) in width, with large vaginal sphincter (Fig. 7D, F); seminal receptacle present, between anterior part of ovarian lobes. Ovary at posterior extremity of segment (Fig. 7D), bi-lobed in dorso-ventral view; ovarian lobes elongate, 173–263 (225 ± 39 ; n = 10) long, 43–63 (51 ± 6 ; n = 10) wide; Mehlis' gland between ovarian lobes (Fig. 7D), 58–85 (73 ± 8 ; n = 8) in diameter. Vitelline follicles small, circum-medullary, 20–30 (27 ± 3 ; n = 10) in diameter. Uterus median, tubular, simple, extends to anterior extremity of segment (Fig. 7D); uterine pore absent.

Gravid segments 3,150 (n = 1) long, 113 (n = 1) wide; uterus extends to anteriormost extremity; cirrus sac ovoid, 68 (n = 2) long, 113 (n = 2) wide; ovarian lobes 160 (n = 2) long, 40 (n = 2) wide; Mehlis' gland $c.73$ (n = 1) in diameter.

Remarks

The present specimens are allocated to the genus *Dollfusiella*, because they exhibit the typical characteristics of the genus, such as the slender, acraspedote scolex with two, oval bothria lacking bothrial pits, the presence of prebulbar organs and elongate bulbs with gland-cells. The metabasal tentacular armature is heteroacanthous, homeomorphous, with hook rows commencing from the antibothrial to the bothrial surface. Hook files 1 and 1' are slightly separated, although this feature is not as prominent as in species of the closely related genus *Prochristianella*. Furthermore, the specimens of the new species lack the gradation in hook sizes in the metabasal tentacular armature, first increasing and then decreasing in size, which is typical for most species of *Prochristianella*. The microscopically visible microtriches on the scolex

peduncle of *D. spinosa* n. sp. reach posteriorly to the border of the pars bulbosa and pars proliferans scolecis. This posterior distribution of enlarged microtriches was also described for *D. aculeata*, *D. elongata*, *D. micracantha*, *D. litocephala*, *D. ocallaghani*, *D. spinulifera*, *D. spinifer* and *D. tenuispinis*. However, *D. spinosa* n. sp. differs from *D. litocephala*, *D. elongata*, *D. ocallaghani* and *D. spinifer* in having a much smaller scolex and bulbs, whereas these structures are much larger than those in *D. spinulifera*. Lengths of the bulbs also differentiate the new species from *D. tenuispinis* and *D. aculeata*, which have larger bulbs. Specimens of *D. spinosa* n. sp. possess 42 to 48 testes, which is fewer than the testes number of *D. aculeata* (47–63), *D. elongata* (139–215), *D. spinifer* (73–85) and *D. tenuispinis* (c.61), but greater than in *D. micracantha* (c.35). *Dollfusiella spinosa* n. sp. furthermore differs from *D. aculeata*, *D. ocallaghani* and *D. spinifer* in having slightly separated hook files 1 and 1' and from *D. elongata*, *D. micracantha* and *D. ocallaghani* in the possession of enlarged basal hooks. *Dollfusiella spinulifera* and *D. spinifer* exhibit a gradation of metabasal hooks first increasing and subsequently decreasing in size along each principle row, a feature absent in *D. spinosa* n. sp. These differences from congeners as well as the possession of a unique oncotaxy with a characteristic basal armature make *D. spinosa* n. sp. a species new to science.

This species was obtained from several specimens of *Pastinachus solocirostris*, which might indicate a close relationship between the new species and this particular host. However, *D. spinosa* n. sp. was also found in single specimens of two additional dasyatid and one rhinobatid species, reflecting a much wider host spectrum.

***Dollfusiella imparispinis* n. sp.**

Type-host: *Chiloscyllium punctatum* Müller & Henle (Orectolobiformes: Hemiscylliidae) (BO-282).

Type-locality: South China Sea off Mukah, Sarawak, Malaysia.

Site of infection: Spiral intestine.

Type-material: Holotype in MZUM (No. 2013.26); paratypes in MZUM (Nos. 2013.27–28), SAM (Nos. AHC 35720–24), USNPC (No. 106924) and LRP (Nos. 8226–8236).

Etymology: The specific name *imparispinis* relates to the differences in size and shape of the tentacular hooks on the basal swelling.

Description (Figs. 10–12)

[Based on 33 whole-mounts, 4 specimens used for SEM and serial sections.] Cestodes anapolytic (Fig. 10C); gravid specimens 4.3–12.6 (8.6 ± 0.9 ; $n = 13$) mm long (Fig. 10C), with 9–11 (10 ± 1 ; $n = 13$) segments. Scolex acraspedote, slender (Figs. 10A, B, 12A, D), 730–1,040 (894 ± 101 ; $n = 13$) long; surface covered with very enlarged microtriches extending from between bothria to level of pars proliferans scolecis (Figs. 10A, B, 12 A, C, D); maximum width at pars bothrialis, 145–185 (161 ± 14 ; $n = 17$) wide; pars bothrialis 110–200 (144 ± 30 ; $n = 13$) long. Bothria two in number, oval (Figs. 10B, 12B, C), 110–140 (124 ± 10 ; $n = 9$) long, 100–130 (113 ± 10 ; $n = 9$) wide, with thick, free margins (Figs. 10A, 12A, D); distal bothrial surface covered with capilliform filitriches (Fig. 12E); proximal bothrial surface covered with palmate spinitriches and acicular filitriches (Fig. 12F); bothrial pits absent; pars vaginalis longer than pars bothrialis, 460–775 (619 ± 93 ; $n = 13$) long, covered with palmate spinitriches and acicular filitriches (Fig. 12C, G). Tentacle sheaths sinuous to irregularly coiled; pars bulbosa 240–300 (274 ± 19 ; $n = 13$) long, 110–155 (126 ± 14 ; $n = 13$) wide; prebulbar organs present; bulbs relatively small (Fig. 10A, B, E), 230–285 (264 ± 15 ; $n = 22$) long, 40–65 (52 ± 7 ; $n = 22$) wide; bulb width : length ratio 1.0 : 4.0–6.0 (5.1 ± 0.5 ; $n = 22$); retractor muscle inserts at base of bulb (Fig. 10E); gland-cells present, surrounding retractor muscle to mid-bulbar region (Fig. 10E), only very few, tiny gland-cells further anterior; scolex ratio (pars bothrialis : pars vaginalis : pars bulbosa) 1.0 : 2.8–6.2 : 1.3–2.7 ($1.0 : 4.5 \pm 1.0 : 2.0 \pm 0.5$; $n = 13$).

Fully everted tentacle $c.390$ ($n = 1$) long; tentacle diameter 13–15 (15 ± 1 ; $n = 14$) at base, 10–15 (13 ± 2 ; $n = 14$) in metabasal region, 10–13 (12 ± 1 ; $n = 14$) in distal region.

Metabasal armature heteroacanthous (Figs. 11D–F, 12K–N), heteromorphous; hooks hollow; hook rows consist of 12 hooks in posterior metabasal region, decreasing to 11 and 10 hooks per principle row further anteriorly (Fig. 11F); rows start on antiothrial surface of tentacle (Figs. 11E, 12K, M), terminate on bothrial surface (Figs. 11E, 12L); hooks 1 and 1' not separated (Figs. 11E, 12K, M); hooks 1(1') uncinat, with elongate base, 4–5 (5; $n = 10$) long, base 3–4 (3; $n = 10$) long; hooks 2(2') uncinat, 4–5 (4; $n = 10$) long, base 3–4 (4; $n = 10$) long; hooks 3(3') uncinat, erect, 3–4 (3; $n = 10$) long, base narrower, 2–3 (2; $n = 10$) long; hooks 4(4') larger, falcate, with recurved tip (Figs. 11D, 12N), 3–4 (4; $n = 10$) long, base narrower, 1 ($n = 10$) long; hooks 5(5') larger, falcate, with recurved tip, 5 ($n = 5$) long, base 2 ($n = 5$) long; hooks 6(6')–9(9') or 11(11') falcate, smaller, decreasing in size along principle row (Fig. 11F); hooks 6(6') 5 ($n = 5$) long, base 2 ($n = 5$) long; hooks 7(7') 4–5 (5; $n = 10$) long, base 1–2 (1; $n = 10$) long; hooks 8(8') 4–5 (4; $n = 10$) long, base 1–2 (1; $n = 10$) long; hooks 9(9')–11(11') 3–4 (4 ± 1 ; $n = 10$) long, base 1 ($n = 10$) long; hooks 12(12') uncinat, 3 ($n = 10$) long, base 2 ($n = 10$) long.

Characteristic basal armature present (Figs. 11A–C, 12H–J); basal swelling present (Figs. 11A–C, 12H, I), weakly developed; first 2–3 rows of basal hooks uncinat (Figs. 11A–C, 12H, I), enlarged, 4–6 (4 ± 1 ; $n = 10$) long, base 3–4 (4; $n = 10$) long; hooks on external and internal surfaces falcate (Figs. 11C, 12J), 3–5 (4 ± 1 ; $n = 10$) long, base 2 ($n = 10$) long; hooks on bothrial surface in rows 3–8 falcate (Figs. 11B, 12H, I), 3–5 (4 ± 1 ; $n = 10$) long, base 1–2 (1; $n = 10$) long, in rows 9–16 uncinat, increasing in size towards largest hooks in mid-line of bothrial surface (Fig. 11B), 3–4 (3; $n = 10$) long, base 3–4 (3; $n = 10$) long; area with relatively few hooks on antibothrial surface (Fig. 11A), anterior to enlarged basal hooks; hooks small, uncinat to falcate, 1–2 (2; $n = 4$) long, base 1 ($n = 4$) long; next 5 rows of hooks on antibothrial surface erect, spiniform, enlarged, bases reduced (Fig. 11A), 4 ($n = 10$) long, base c.1 ($n = 10$) long; next 5 rows of hooks on antibothrial surface smaller, falcate to spiniform (Figs. 11B, 12H, I), 1–2 (2; $n = 10$) long, base 1 ($n = 10$) long, become more falcate, with recurved tips along each row (Fig. 11A), 2–3 (2; $n = 10$) long, base 1 ($n = 10$) long; hooks on antibothrial surface become falcate anteriorly (Fig. 11A), 3–4 (3; $n = 10$) long, base 1 ($n = 10$) long; transition to metabasal armature at about hook row 25.

Segments acraspedote; immature segments wider than long, 10–25 (16 ± 5 ; $n = 13$) long, 80–130 (102 ± 17 ; $n = 13$) wide; mature segments elongate (Fig. 10D), 510–1,460 (846 ± 271 ; $n = 13$) long, 130–525 (210 ± 100 ; $n = 13$) wide. Genital pores alternate irregularly, in posterior half of segment (Fig. 10D); pore inconspicuous; cirrus sac ovoid (Fig. 10D), thick-walled, 50–98 (76 ± 15 ; $n = 7$) long, 85–110 (100 ± 10 ; $n = 7$) wide; cirrus unarmed; internal and external vesicles absent (Fig. 10D); vas deferens not observed; testes arranged in two columns (Fig. 10D), exclusively preovarian, in single layer, 35–48 (41 ± 4 ; $n = 14$) in number, 30–38 (34 ± 2 ; $n = 14$) preporal, 4–11 (7 ± 2 ; $n = 14$) postporal, 53–63 (58 ± 3 ; $n = 10$) long, 33–43 (38 ± 3 ; $n = 10$) wide. Vagina not observed; seminal receptacle not observed. Ovary at posterior extremity of segment (Fig. 10D), bi-lobed in dorso-ventral view; ovarian lobes almost oval, compact (Fig. 10D), 55–110 (77 ± 19 ; $n = 16$) long, 23–43 (31 ± 6 ; $n = 16$) wide; Mehlis' gland between posterior part of ovarian lobes, 50–70 (62 ± 8 ; $n = 5$) in diameter. Vitelline follicles small, circum-medullary, 20–28 (23 ± 3 ; $n = 10$) in diameter. Uterus median, tubular, simple, extends to anterior extremity of segment (Fig. 10D); uterine pore absent.

Gravid segments 1,720–3,770 ($2,695 \pm 658$; $n = 13$) long, 380–605 (478 ± 76 ; $n = 13$) wide; uterus occupies almost entire medulla (Fig. 10C); cirrus sac ovoid, 80–128 (103 ± 16 ; $n = 7$) long, 115–160 (133 ± 18 ; $n = 7$) wide; ovarian lobes 83–138 (104 ± 20 ; $n = 8$) long, 48–68 (57 ± 7 ; $n = 8$) wide; Mehlis' gland large, 88–120 (100 ± 12 ; $n = 11$) in diameter; vitelline follicle 25–35 (29 ± 4 ; $n = 10$) in diameter; eggs 28–31 (30 ± 1 ; $n = 15$) long, 18–21 (20 ± 1 ; $n = 15$) wide.

Remarks

This species possesses an acraspedote scolex, two, oval bothria, prebulbar organs, but lacks bothrial pits. The retractor muscles originate at the base of the bulbs and the tentacular armature is typical heteroacanthous. Hook files 1 and 1' abut and the principle rows of the metabasal armature start on the antibothrial surface and terminate on the bothrial surface, without principle hooks increasing and then decreasing in size. The basal armature is characteristic, with different shapes and sizes of hooks at the base and the weakly developed basal swelling. Following the generic description by Beveridge et al. (2004) this species can be allocated to the genus *Dollfusiella*. The most characteristic features of *D. imparispinis* n. sp. are the reduction in hook numbers, from 12 to 10 hooks per principle row of the metabasal armature along the tentacle anteriorly and the unique, uncinat terminal hooks of each principle row [i.e. either 12(12'), 11(11') or 10(10'), depending on the position on the tentacle]. Another characteristic for this species is the size of the muscular bulbs, which are small compared to the size of the scolex. Among the species of *Dollfusiella* bearing enlarged microtriches on the scolex peduncle, *D. imparispinis* n. sp. is closest to *D. aculeata*, *D. elongata*, *D. micracantha*, *D. litocephala*, *D. ocallaghani*, *D. spinosa*, *D. spinulifera*, *D. spinifer* and *D. tenuispinis*, due to the posterior extension of the microthrix cover to the end of the pars bulbosa and the beginning of the pars proliferans scolecis. It differs from *D. aculeata*, *D. micracantha*, *D. ocallaghani* and *D. spinulifera* in a larger body size, with more segments than in *D. spinosa*, *D. aculeata*, *D. elongata*, *D. ocallaghani* and *D. spinulifera*. However, *D. imparispinis* is much smaller than *D. litocephala* (i.e. 8.3 vs up to 33 mm, respectively), possesses fewer segments (i.e. 9–11 vs 17–50, respectively), a much smaller scolex (i.e. 0.7–1.0 vs 4.4–6.2 mm, respectively) and much smaller bulbs (i.e. 230–285 vs 2,400–3,400 μm , respectively). The scolex of the new species is also smaller than that described for *D. aculeata*, *D. elongata*, *D. ocallaghani*, *D. spinifer* and *D. tenuispinis*, whereas the bulbs are smaller than those of *D. spinosa*, *D. aculeata*, *D. elongata*, *D. micracantha*, *D. ocallaghani*, *D. spinifer* and *D. tenuispinis*. The bulb lengths resemble those of *D. spinulifera*, however, *D. imparispinis* n. sp. possesses a larger scolex (i.e. 0.9 mm vs 0.6 mm, respectively). Specimens in the present study exhibit testes which are smaller but also wider than those of *D. spinosa* (i.e. 58×38 vs 75×27 μm , respectively), whereas the number of testes is fewer than in *D. aculeata*, *D. elongata*, *D. spinifer* and *D. tenuispinis*. The number of principle hooks in the metabasal armature of *D. imparispinis* n. sp. decreases from 12 to 10 hooks per principle row along the length of the tentacle, which represents more hooks per principle row than in *D. spinosa*, *D. aculeata*, *D. elongata*, *D. micracantha*, *D. ocallaghani*, *D. spinulifera*, *D.*

spinifer and *D. tenuispinis*. Moreover, the basal hooks are enlarged in the new species, whereas they are not enlarged in *D. elongata*, *D. micracantha* and *D. ocallaghani*.

Specimens of *D. imparispinis* n. sp. were collected in Malaysian Borneo from the spiral intestine of a single individual of the brownbanded bambooshark, *Chiloscyllium punctatum* (Hemiscylliidae). Although only a single specimen of bambooshark was infected with a relatively high burden of worms, we assume *D. imparispinis* n. sp. to be a relatively uncommon but highly host specific parasite of hemiscylliids.

***Dollfusiella parva* n. sp.**

Type-host: *Himantura gerrardi* (Gray) (Myliobatiformes: Dasyatidae) (BO-23).

Additional hosts: *Himantura pastinacoides* (BO-98); *Himantura walga* (Müller & Henle) (Myliobatiformes: Dasyatidae) (BO-238); *Himantura* cf. *gerrardi* 2 (*sensu* Naylor et al., 2012) (Myliobatiformes: Dasyatidae) (BO-138, BO-158).

Type-locality: South China Sea off Sematan, Sarawak, Malaysia.

Additional localities: South China Sea off Mukah, Sarawak, Malaysia; Sulu Sea off Kampung Tetabuan, Sabah, Malaysia; Celebes Sea off Pulau Mabul, Sabah, Malaysia.

Site of infection: Spiral intestine.

Type-material: Holotype in MZUM (No. 2013.29); paratypes in MZUM (Nos. 2013.30–31), SAM (Nos. AHC 35725–29), USNPC (Nos. 106925–26) and LRP (Nos. 8237–8241).

Etymology: The specific name *parva* relates to the small size of these cestodes.

Description (Figs. 13–14)

[Based on 15 whole-mounts, 5 specimens used for SEM and serial sections.] Cestodes apolytic; mature specimens 1.2–1.9 (1.5 ± 0.2 ; $n = 9$) mm long (Figs. 13B, G, 14A), with 2–4 (3 ± 1 ; $n = 9$) segments. Scolex acraspedote, 620–900 (763 ± 100 ; $n = 9$) long (Figs. 13A, B, 14A); surface covered with enlarged microtriches extending from between bothria to posterior level of pars bulbosa (Figs. 13A, B, 14A); enlarged microtriches readily lost in some specimens; maximum width at level of pars bothriialis, 160–240 (211 ± 25 ; $n = 10$) wide; pars bothriialis 120–180 (149 ± 25 ; $n = 9$) long. Bothria two in number, oval (Figs. 13B, 14E, F), 190–200 ($n = 2$) long, 120–140 ($n = 2$) wide, with thick, fleshy margins (Figs. 13A, 14E, F), V-shaped ridge present within bothrium; distal bothrial surface covered with capilliform filitriches; capilliform filitriches enlarged at border to proximal bothrial surface (Fig. 14H); proximal bothrial surface covered

with palmate spinitriches and acicular filitriches (Fig. 14B); bothrial pits absent; pars vaginalis longer than pars bothrialis, 270–440 (348 ± 75 ; $n = 9$) long, covered with palmate spinitriches and acicular filitriches (Fig. 14C). Tentacle sheaths sinuous; pars bulbosa 340–440 (411 ± 31 ; $n = 9$), 115–160 (136 ± 16 ; $n = 10$) wide; prebulbar organs present, prominent; bulbs elongate (Fig. 13A, B, D), thick-walled, 380–430 (411 ± 17 ; $n = 16$) long, 40–60 (52 ± 6 ; $n = 16$) wide, reach to pars proliferans scolecis in some specimens; bulb width : length ratio 1.0 : 6.7–10.5 (8.1 ± 1.0 ; $n = 16$); retractor muscle originates at base of bulb (Fig. 13D); gland-cells present, surround retractor muscle to between anterior third and anteriormost part of bulb (Fig. 13D); scolex ratio (pars bothrialis : pars vaginalis : pars bulbosa) 1.0 : 1.8–3.6 : 2.4–3.6 ($1.0 : 2.4 \pm 0.5 : 2.8 \pm 0.5$; $n = 9$).

Fully everted tentacle 445–760 (562 ± 121 ; $n = 6$) long; tentacle diameter 15–19 (17 ± 1 ; $n = 11$) at basal swelling, 13–18 (16 ± 1 ; $n = 15$) in metabasal region, 10–15 (14 ± 2 ; $n = 13$) in distal region.

Metabasalar armature heteroacanthous (Figs. 13F, 14G, J), heteromorphous; hooks hollow; hook rows consist of between 12 and 15 hooks (Figs. 13F, 14G, J); rows start on antibothrial surface of tentacle, terminate on bothrial surface (Fig. 14J); hooks 1 and 1' not separated; hooks 1(1') uncinata (Fig. 13F), 2–3 (3; $n = 8$) long, base 2–3 (2; $n = 8$) long; hooks 2(2')–10(10') falcate (Figs. 13F, 14G, J), 2–3 (3; $n = 20$) long, base c. 1 ($n = 20$) long, some hooks with slightly recurved tips (Fig. 14G, J).

Characteristic basal armature present (Figs. 13E, 14I); basal swelling present (Figs. 13E, 14I); first 2–3 rows of hooks uncinata (Figs. 13E, 14I), c. 2 ($n = 5$) long, base 1–2 (2; $n = 5$) long; next 2–3 rows with spiniform hooks, with reduced bases, c. 2–4 (3; $n = 10$) long (Figs. 13E, 14I); basal swelling with c. 7 rows of hooks; hooks on external and internal surfaces falcate (Figs. 13E, 14I), 1–2 (2; $n = 10$) long, base 1 ($n = 10$) long, increasing slightly in size, become more uncinata towards bothrial surface (Figs. 13E, 14I), 2–3 (2; $n = 10$) long, base 1–2 (2; $n = 10$) long; hooks on antibothrial surface elongate, spiniform, erect (Fig. 13E), with reduced bases, 4 ($n = 5$) long; hooks anterior to basal swelling falcate (Figs. 13E, 14I), with slightly broadened base, 2–3 (3; $n = 10$) long, base 1 ($n = 10$) long; transition to metabasalar armature at about hook row 15.

Segments acraspedote; immature segments 20–50 (35 ± 12 ; $n = 7$) long, 70–90 (79 ± 9 ; $n = 7$) wide; terminal mature segments 480–780 (623 ± 114 ; $n = 8$) long, 80–145 (114 ± 20 ; $n = 8$) wide (Fig. 13B, C). Genital pore in posterior half of segment (Fig. 13C), inconspicuous; cirrus sac ovoid (Fig. 13C), 58–75 (67 ± 8 ; $n = 5$) long, 75–98 (84 ± 9 ; $n = 5$) wide; cirrus unarmed; internal and external seminal vesicles absent; vas deferens obscured by testes; testes arranged in two columns, exclusively preovarian (Fig. 13C), in single layer, 21–37 (31 ± 6 ; $n = 7$) in number,

17–29 (25 ± 5 ; $n = 7$) preporal, 4–8 (7 ± 2 ; $n = 7$) postporal, 50–60 (53 ± 3 ; $n = 11$) long, 30–48 (37 ± 7 ; $n = 11$) wide. Vagina enters genital atrium on posterior aspect (Fig. 13C), with large vaginal sphincter (Fig. 13C); seminal receptacle small, $c.25$ ($n = 1$) in diameter, between anterior part of ovarian lobes. Ovary at posterior margin of segment (Fig. 13C), tetra-lobed; ovarian lobes elongate (Fig. 13C), 128–188 (162 ± 23 ; $n = 10$) long, 20–28 (23 ± 2 ; $n = 10$) wide; Mehlis' gland between posterior parts of ovarian lobes (Fig. 13C), 30–38 (33 ± 4 ; $n = 3$) in diameter. Vitelline follicles small, circumcortical, 10–18 (13 ± 2 ; $n = 13$) in diameter. Uterus median, tubular, simple, extends to anterior extremity of segment; uterine pore absent.

Remarks

This species belongs to the genus *Dollfusiella*, because of its general body morphology. The armature is typical heteroacanthous, with relatively small, hollow hooks in a dense arrangement. The basal armature exhibits slightly enlarged, uncinata hooks directly at the base of each tentacle and a basal swelling with characteristic files of hooks. The metabasal armature consists of uncinata hooks 1 and 1', which are not separated, whereas the remaining hooks of the principle row are falcate. Due to the small size of the tentacular hooks (i.e. less than $4\mu\text{m}$ in length) the metabasal armature appears homeomorphous at first, and depending on the orientation of the tentacle, hooks 1 and 1' are easily overlooked. This species possesses a scolex covered with enlarged microtriches, reaching posteriorly to the level of the pars proliferans scolecis. Although many species of *Dollfusiella* share the same distribution of microscopically visible microtriches, specimens of the present study can be easily differentiated by the small body size (i.e. only 1.5 mm), the short strobila of only two to four segments and relatively few testes (i.e. between 21 and 37). This species also exhibits a smaller scolex and smaller bulbs than most species, such as *D. aculeata*, *D. elongata*, *D. litocephala*, *D. ocallaghani*, *D. spinifer* and *D. tenuispinis*. It can furthermore be differentiated from congeners by the uncinata hooks 1 and 1' and the number of principle hooks in the metabasal armature, which exceeds 12 hooks in present specimens but which is less than 12 in the other species. Given the unique combination of characters of both the body and the oncotaxy, we consider this to represent a species new to science.

Specimens of *D. parva* n. sp. were obtained from four localities in the Malaysian part of Borneo. A total of four different species of stingrays (Dasyatidae), all belonging to the genus *Himantura* were infected. We therefore assume that this parasite is highly host specific, which has also been described for other species of *Dollfusiella*, for example *D. hemispinosa* and *D. angustiformis*.

***Dollfusiella spinulifera* (Beveridge & Jones, 2000) Beveridge, Neifar & Euzet, 2004**

Material examined: Specimens from *Dasyatis* cf. *zugei* (*sensu* Naylor et al., 2012) off Sematan, Sarawak, Malaysia (BO-169); *Himantura lobistoma* Manjaji-Matsumoto & Last off Mukah, Sarawak, Malaysia (BO-247, BO-268); *H. pastinacoides* off Mukah, Sarawak (BO-61), Kampung Tetabuan (BO-247, BO-98, BO-119) and Sandakan (fish market), Sabah (BO-79); *H. uarnacoides* off Sematan (BO-167) and Mukah, Sarawak, Malaysia (BO-258, BO-261); *H. uarnak* (Gmelin) from Pagatan (fish market), South Kalimantan, Indonesia (KA-71); *H. walga* off Santubong (BO-9) and Mukah, Sarawak, Malaysia (BO-66); *Neotrygon kuhlii* 1 (*sensu* Naylor et al., 2012) off Pulau Balambangan, Sabah, Malaysia (BO-321); *Taeniura lymma* 1 (*sensu* Naylor et al., 2012) off Pulau Rabu Rabu, East Kalimantan, Indonesia (KA-420) and Semporna (fish market), Sabah, Malaysia (BO-86).

Site of infection: Spiral intestine.

Remarks

This species was described by Beveridge & Jones (2000) as *Prochristianella spinulifera* Beveridge & Jones, 2000, due to the gradation in hook sizes, first increasing and then decreasing along each principle row in the metabasal armature. However, this species also exhibits hook files 1 and 1' which almost abut and are only slightly separated. Based on these morphological characters, the species represents an intermediate form between the two closely related genera *Prochristianella* Dollfus, 1946 and *Dollfusiella*. Beveridge et al. (2004) described *D. elongata* and redescribed *D. spinifer*; both taxa possessing slightly separated hooks 1 and 1' as well as a slight gradation in hook sizes as it was described for *P. spinulifera* and thus also representing intermediate forms. However, all three species possess general morphological features and oncotaxy patterns similar to species of *Dollfusiella*. For this reason, *P. spinulifera* was transferred to *Dollfusiella*, as *D. spinulifera* (see Beveridge et al., 2004).

The specimens of the present study resemble *D. spinulifera* based on the oncotaxy, both in metabasal and basal armature patterns and the general body morphology. However, the specimens from Borneo possess a smaller number of testes compared to the original description (20–48 testes vs 34–60 testes, respectively). This could be accounted for by intraspecific variability or else it might represent an adaptation to a much wider spectrum of definitive hosts and a different geographical distribution. Other morphological characters, such as the lengths of the scolex and the muscular bulbs, show a much wider range compared to the original

description. The scolex in uncontracted specimens ranged from 460 to 950 μm in length (Fig. 15A), whereas the bulbs ranged from 200 to 500 μm (Fig. 15B). Beveridge & Jones (2000) recorded a scolex length of 490 to 660 μm and individual bulb lengths ranging from 210 to 250 μm . Lengths of the scolex can vary depending on the state of contraction of the pars vaginalis. The length of the muscular bulbs, however, is relatively uniform and such differences have rarely been described in trypanorhynchs. *Pseudogilquinia pillersi* (Southwell, 1929) is one of the very few examples in which the lengths of the scolex and the bulbs varied drastically in specimens from the redescription by Beveridge et al. (2007) and type specimens of the original description (i.e. scolex length: 6.1–12.1 vs 10.1–14.7 mm, respectively; bulb length: 2.0–2.6 vs 3.0–5.5 mm, respectively). Although Beveridge et al. (2007) admitted that the new material might represent a different species of *Pseudogilquinia* Bilqees & Khatoon, 1980, they retained the specimens tentatively in a single species, due to the limited information on variability within the species (Beveridge et al., 2007).

The frequencies of measurements of both scolex lengths and bulb lengths are bimodal. Specimens of *D. spinulifera* could therefore be represented by a group (group 1) with a scolex ranging from 450 to 660 μm in length, and a second group (group 2) with scolex lengths of 660 to 950 μm (Fig. 15A). This particular division can also be identified in the bulb lengths (Fig. 15B) ranging between 200 and 330 μm (corresponding to the original description of *D. spinulifera*) and bulbs with lengths of 330 to 500 μm (Group 2). However, the differences in the metrical data and the separation of the specimens into two groups is not supported by other morphological characters. We consider the oncotaxy as the most important character to differentiate trypanorhynchs at a lower taxonomic level, which is why we retain all specimens as a single, variable species, until further studies can be undertaken to confirm the presence of two groups.

Two definitive hosts previously recorded for this species are *Glaucostegus typus* (Anonymous in Bennett) (Rajiformes: Rhinobatidae) and *Himantura fai* Jordan & Seale (Myliobatiformes: Dasyatidae), collected off Heron Island, Queensland, Australia (Beveridge & Jones, 2000). The present study presents eight additional definitive hosts for *D. spinulifera*. This species was found at nine different localities from Malaysian and Indonesian parts of Borneo that not only represent new geographical records, but also expands our knowledge of the distribution of *D. spinulifera* from tropical Queensland into the Indo-Malayan region. There it might be considered a common parasite of rays, with a much lower host specificity as previously recorded from Australian specimens.

***Dollfusiella michiae* (Southwell, 1929) Beveridge, Neifar & Euzet, 2004**

Material examined: Two specimens from *Glaucostegus thouin* (Anonymous in Lacépède) (Rajiformes: Rhinobatidae) from Pagatan (fish market), South Kalimantan, Indonesia (LRP 8242, 8243; KA-70); 1 specimen from *Himantura lobistoma* off Mukah, Sarawak, Malaysia (LRP 8247; BO-247); 3 specimens from *H. undulata* (Bleeker) (Myliobatiformes: Dasyatidae) from Tawau (fish market), Sabah, Malaysia (LRP 8244–46; BOD-69).

Site of infection: Spiral intestine.

Remarks

Dollfusiella michiae was originally described by Southwell (1929) from the 'Ceylon Pearl Banks' (Sri Lanka), where specimens were obtained from several species of rays. Beveridge (1990) redescribed the species based on Southwell's (1929) material as well as on a single specimen from the Northern Territory, Australia. The latter record greatly expanded the geographical distribution of this parasite in the Indian Ocean. The new records from South Kalimantan (Indonesian Borneo), Sabah and Sarawak (Malaysian Borneo) reported here, further expand the distribution of *D. michiae* in the Indo-Malayan region. The present study also adds three new host records, which doubles the number of definitive hosts for this species.

Key to the species of *Dollfusiella*

For simplicity this key utilises only the most characteristic and easily observable features. Original descriptions and/or re-descriptions should be consulted to confirm individual species identifications.

1. Scolex not covered with enlarged, microscopically visible microtriches 2
- Scolex covered with enlarged, microscopically visible microtriches 12
2. Testes in 4 longitudinal columns *D. australis* (Prudhoe, 1969)
- Testes in 2 longitudinal columns 3
3. Pars postbulbosa longer than 20 mm
..... *D. macrotrachela* (Heinz & Dailey, 1974)
- Pars postbulbosa shorter than 200 µm or completely absent 4
4. Bulbs longer than 1,000 µm; strobila with more than 20 segments 5

- Bulbs smaller than 850 μm ; strobila with fewer than 10 segments 7
- 5. Scolex larger than 6 mm; bulbs longer than 3 mm; strobila with more than 50 segments
..... *D. vooremi* (São Clemente & Gomes, 1989)
- Scolex smaller than 5 mm; bulbs smaller than 2.6 mm; strobila with fewer than 35
segments 6
- 6. Metabasal tentacular armature with more than 15 hooks per principle row; strobila with
c.21 segments; bulbs 1,260 to 2,600 μm in length *D. michiae* (Southwell, 1929)
- Metabasal armature with 11 to 12 hooks per row; strobila with 33 to 34 segments; bulbs
1,360 to 1,760 in length μm *D. lineata* (Linton, 1909)
- 7. Scolex larger than 1,500 μm 8
- Scolex smaller than 1,400 μm 9
- 8. Bulbs 700–850 μm in length; metabasal tentacular armature with 9 to 13 hooks per
principle row *D. musteli* (Carvajal, 1974)
- Bulbs 500–700 μm in length; metabasal tentacular armature with 12 hooks per principle
row, decreasing to 9 distally *D. carayoni* (Dollfus, 1942)
- 9. Fewer than 50 testes per segment; external seminal vesicle elongate, 90–180 μm long;
metabasal tentacular armature with c.10 hooks per principle row
..... *D. aetobati* (Beveridge, 1990)
- More than 55 testes per segment; external seminal vesicle smaller than 80 μm or absent;
metabasal tentacular armature with less than 8 hooks per principle row 10
- 10. Metabasal tentacular armature with 5–6 hooks per principle row; enlarged, uncinatate basal
hooks lacking *D. martini* (Beveridge, 1990)
- Metabasal tentacular armature with 7–8 hooks per principle row; enlarged, uncinatate basal
hooks present 11
- 11. Testes more than 100 in number; scolex 1,100–1,400 μm in length
..... *D. geraschmidtii* (Dollfus, 1974)
- Testes fewer than 70 in number; scolex 840–1,270 μm in length
..... *D. bareldsi* (Beveridge, 1990)
- 12. Scolex covered in enlarged microtriches from between bothria to posterior part of pars
bulbosa or anterior pars proliferans scolecis 13
- Enlarged microtriches do not reach to posterior border of pars bulbosa and pars
proliferans scolecis 22
- 13. Scolex more than 4.0 mm long; bulbs longer than 2.2 mm
..... *D. litocephala* (Heinz & Dailey, 1974)
- Scolex less than 2.2 mm long; bulbs smaller than 0.9 mm 14

14. Hook files 1 and 1' with prominent space; gradation in sizes of hooks along principle rows present *D. spinulifera* (Beveridge & Jones, 2000)
- Hook files 1 and 1' abut or only slightly separated; gradation in sizes of hooks along principle rows inconspicuous or absent 15
15. More than 70 testes per segment; testes larger than 130 μm
..... *D. spinifer* (Dollfus, 1969)
- Fewer than 65 testes per segment; testes smaller than 90 μm 16
16. Bulbs small, 230–285 μm *D. imparispinis* n. sp.
- Bulbs longer than 370 μm 17
17. Fewer than 37 testes per segment 18
- More than 42 testes per segment 19
18. Scolex 900–1,140 μm long; bulbs 400–530 μm long; metabasal tentacular armature homeomorphous, with falcate hooks; fewer than 10 hooks per principle row
..... *D. micracantha* (Carvajal, Campbell & Cornford, 1976)
- Scolex 620–900 μm long; bulbs 380–430 μm long; metabasal tentacular armature heteromorphous, with hooks 1(1') uncinat and remaining hooks falcate; more than 12 hooks per principle row *D. parva* n. sp.
19. Basal hooks significantly enlarged *D. tenuispinis* (Linton, 1890)
- Basal hooks not or only slightly enlarged 20
20. Hook files 1 and 1' slightly spaced; internal seminal vesicle present; external seminal vesicle absent; testes 68–88 μm long *D. spinosa* n. sp.
- Hook files 1 and 1' abut; internal seminal vesicle absent; external seminal vesicle present; testes less than 70 μm long 21
21. Basal hooks slightly enlarged; bulbs 420–560 μm long
..... *D. aculeata* Beveridge, Neifar & Euzet, 2004
- Basal hooks not enlarged; bulbs 540–750 μm long
..... *D. ocallaghani* (Beveridge, 1990)
22. Posterior distribution of enlarged microtriches on scolex extends to border of pars vaginalis and pars bulbosa *D. hemispinosa* n. sp.
- Posterior distribution of enlarged microtriches on scolex extends into pars bulbosa 23
23. More than 130 testes per segment; basal hooks not enlarged; hook files 1 and 1' slightly separated *D. elongata* Beveridge, Neifar & Euzet, 2004
- Fewer than 90 testes per segment; basal hooks enlarged; hook files 1 and 1' abut 24

24. Cestodes up to 9.0 mm long; metabasal tentacular armature with more than 10 hooks per principle row *D. schmidt* (Heinz & Dailey, 1974)
- Cestodes less than 3.0 mm long; metabasal tentacular armature with fewer than 8 hooks per principle row 25
25. Scolex smaller than 1,150 μ m; posterior distribution of enlarged microtriches extends to posterior third of pars bulbosa *D. owensi* (Beveridge, 1990)
- Scolex larger than 1,250 μ m; posterior distribution of enlarged microtriches extends from anterior third to mid-level of pars bulbosa *D. angustiformis* n. sp.

Discussion

This study describes five new species of *Dollfusiella* from the Malaysian and the Indonesian parts of Borneo. It also increases the number of valid species of *Dollfusiella* to a total of 26 taxa which is now the most species-rich genus within the Eutetrarhynchidae Guiart, 1927. In addition, new host and locality records are provided for two species, *D. spinulifera* and *D. michiae*, which not only provides new insights into the host ranges and host specificities of these parasites but also expands the distributional patterns from Australia into the Indo-Malayan region. Most species of *Dollfusiella* have a relatively restricted geographical distribution and have been detected in only one geographical area (i.e. 24 species, = 92 %), mostly through opportunistic findings. Apart from the large scale sampling effort in Borneo (by Drs. J. N. Caira, University of Connecticut and K. Jensen, University of Kansas), just two other areas [i.e. Mexico (Baja California) surveyed by Drs. J. N. Caira and K. Jensen and several parts of Australia surveyed by B. Robertson] have been intensively studied for elasmobranch cestodes on a global scale. Therefore it is not surprising that nine species of *Dollfusiella* (i.e. 35%) are recorded from off the Australian continent (i.e. *D. geraschmidt*, *D. bareldsi*, *D. martini*, *D. ocallaghani*, *D. australis*, *D. michiae*, *D. owensi*, *D. aetobati* and *D. spinulifera*), whereas seven species (27%) were found in waters off Borneo (i.e. *D. spinulifera*, *D. michiae*, *D. angustiformis*, *D. hemispinosa*, *D. spinosa*, *D. imparispinis* and *D. parva*). Six species of *Dollfusiella* (23%) have been described from off the North American continent by different authors. Three of these species were found off the east coast (i.e. *D. tenuispinis*, *D. lineata* and *D. micracantha*; see Linton, 1890, 1909 and Carvajal et al., 1976, respectively), whereas the other three taxa have been found off the west coast (i.e. *D. litocephala*, *D. macrotrachela* and *D. micracantha*; see Heinz & Dailey, 1974). Only two representatives of *Dollfusiella* (8%), *D. vooremi* and *D. musteli*, are known from the South American continent [see São Clemente & Gomes (1989) and Carvajal (1974),

respectively]. *Dollfusiella carayoni* has been found in the Atlantic off Arcachon, France (Dollfus, 1942), whereas three other species are recorded from the Mediterranean Sea: *D. spinifer* from off Sète, France (Dollfus, 1969), and *D. elongata* and *D. aculeata* from off northern Africa (Tunisia) (Beveridge et al., 2004). Overall, the Australasian region represents the most species-rich area for species of *Dollfusiella*, with a total of 14 species (54%). *Dollfusiella michiae* and *D. spinulifera* represent the species with the widest geographical distribution reported thus far. The first species has been recorded in Sri Lanka, Borneo and northern Australia, whereas the latter is distributed from the Malaysian part of Borneo to the Great Barrier Reef (Queensland, Australia).

Host specificity varies between species of *Dollfusiella*. Eight species (31%) appear to be highly host specific (i.e. *D. elongata*, *D. aculeata*, *D. geraschmidtii*, *D. vooremi*, *D. angustiformis*, *D. hemispinosa*, *D. imparispinis* and *D. parva*), infecting either a single host species or several species of one host genus. However, almost the same number of species (i.e. 35%) are less host specific (i.e. *D. martini*, *D. ocallaghani*, *D. australis*, *D. michiae*, *D. owensi*, *D. spinosa*, *D. spinulifera*, *D. litocephala* and *D. schmidtii*). These taxa infect a wider spectrum of hosts, ranging from two to ten different species, most frequently incorporating several genera of elasmobranchs. With ten and nine different host species respectively, *D. spinulifera* and *D. martini* represent the two species with the widest spectrum of hosts and therefore the lowest host specificity. For the remaining species (i.e. *D. bareldsi*, *D. spinifer*, *D. aetobati*, *D. carayoni*, *D. tenuispinis*, *D. lineata*, *D. macrotrachela*, *D. micracantha* and *D. musteli*) it is not possible to ascertain the host specificity, because they have only been detected in one or two host species and are accounted for as opportunistic findings.

Recent studies on the molecular phylogeny of trypanorhynchs by Palm et al. (2009) and Olson et al. (2010) have shown that the genus *Dollfusiella* is paraphyletic. However, only relatively few taxa were included in both analyses and the results are not conclusive. Furthermore, the paraphyletic state of *Dollfusiella* is not supported by morphology. More taxa need to be included in additional analyses focussing specifically on the genus, in order to clarify the current morphological division with one group possessing enlarged, microscopically visible microtriches on their scoleces and another group entirely lacking such microtriches.

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Captions to figures

Fig. 1 Line drawings of *Dollfusiella angustiformis* n. sp. from *Himantura uarnacoides* (Bleeker) (KA-146) in the Java Sea. A, scolex, lateral view; B, scolex, dorso-ventral view; C, bulb; D, outline of entire cestode; E, mature segment; F, detail of cirrus-sac, composite line drawing from serial sections. *Abbreviations:* c, cirrus, cs, cirrus-sac, isv, internal seminal vesicle, mg, Mehlis' gland, ov, ovary, t, testis, va, vagina, vit, vitelline follicle, vs, vaginal sphincter

Fig. 2 Line drawings of tentacular armature of *Dollfusiella angustiformis* n. sp. from *Himantura uarnacoides* (Bleeker) (KA-146) in the Java Sea. A, metabasal tentacular armature, antibothrial surface; B, metabasal tentacular armature, bothrial surface—note opposing tentacular surface to tentacle illustrated in (A); C, basal tentacular armature, external surface; D, basal tentacular armature, bothrial surface; E, basal tentacular armature, antibothrial surface

Fig. 3 Scanning electron micrographs of *Dollfusiella angustiformis* n. sp. from *Himantura uarnacoides* (Bleeker) (KA-146) in the Java Sea. A, complete specimen, lateral view; B, detailed view of bothrium—note enlarged, capilliform filitriches lining border between distal and proximal bothrial surfaces; C, basal tentacular armature, bothrial surfaces; D, basal tentacular armature, external surface; E, metabasal tentacular armature, bothrial to external surface; F, metabasal tentacular armature, antibothrial surface; G, palmate spinitriches covering proximal bothrial surface; H, enlarged, palmate spinitriches covering scolex peduncle; I, anterior part of scolex, lateral view; J, metabasal tentacular armature, external surface. *Symbols:* *, position on proximal bothrial surface where microthrix micrograph (G) was taken; +, position on pars vaginalis where microthrix micrograph (H) was taken

Fig. 4 Line drawings of *Dollfusiella hemispinosa* n. sp. from *Himantura pastinacoides* (Bleeker) (BO-12) in the South China Sea. A, scolex, lateral view; B, scolex, dorso-ventral view; C, bulb; D, mature segment; E, outline of entire cestode; F, detail of cirrus-sac, composite line drawing from serial sections. *Abbreviations:* c, cirrus, cs, cirrus-sac, isv, internal seminal vesicle, mg, Mehlis' gland, ov, ovary, t, testis, vit, vitelline follicle, vs, vaginal sphincter

Fig. 5 Line drawings of tentacular armature of *Dollfusiella hemispinosa* n. sp. from *Himantura pastinacoides* (Bleeker) (BO-12) in the South China Sea. A, basal tentacular armature, external surface; B, metabasal tentacular armature, antibothrial surface; C, metabasal tentacular armature, bothrial surface—note opposing tentacular surface to tentacle illustrated in (B); D, basal tentacular armature, bothrial surface; E, basal tentacular armature, antibothrial surface

Fig. 6 Scanning electron micrographs of *Dollfusiella hemispinosa* n. sp. from *Himantura pastinacoides* (Bleeker) (BO-12) in the South China Sea. A, scolex, lateral view; B, palmate spinitriches covering proximal bothrial surface; C, enlarged, palmate spinitriches covering scolex peduncle; D, anterior part of scolex, dorso-ventral view; E, scolex, dorso-ventral view; F, anterior part of scolex, lateral view; G, metabasal tentacular armature, antibothrial surface; H, basal tentacular armature, bothrial surface; I, basal tentacular armature, antibothrial surface; J, metabasal tentacular armature, external surface. *Symbols*: *, position on proximal bothrial surface where microthrix micrograph (B) was taken; +, position on pars vaginalis where microthrix micrograph (C) was taken

Fig. 7 Line drawings of *Dollfusiella spinosa* n. sp. from *Pastinachus solocirostris* Last, Manjaji & Yeatsley (BO-267) in the South China Sea. A, scolex, lateral view; B, scolex, dorso-ventral view; C, bulb; D, mature segment; E, outline of complete specimen; F, detail of cirrus-sac, composite line drawing based on serial sections. *Abbreviations*: at, genital atrium, c, cirrus, cs, cirrus-sac, isv, internal seminal vesicle, mg, Mehlis' gland, ov, ovary, t, testis, ut, uterus, vd, vas deferens, vit, vitelline follicle, vs, vaginal sphincter

Fig. 8 Line drawings of the tentacular armature of *Dollfusiella spinosa* n. sp. from *Pastinachus solocirostris* Last, Manjaji & Yeatsley (BO-267) in the South China Sea. A, basal tentacular armature, bothrial surface; B, basal tentacular armature, antibothrial surface—note opposing tentacular surface to tentacle illustrated in (A); C, basal tentacular armature, external surface; D, metabasal tentacular armature, internal surface; E, metabasal tentacular armature, bothrial surface; F, metabasal tentacular armature, antibothrial surface—note opposing tentacular surface to tentacle illustrated in (E)

Fig. 9 Scanning electron micrographs of *Dollfusiella spinosa* n. sp. from *Pastinachus solocirostris* Last, Manjaji & Yeatsley (BO-267) in the South China Sea. A, complete specimen, dorso-ventral view; B, capilliform filitriches covering distal bothrial surface; C, palmate spinitriches covering proximal bothrial surface; D, enlarged, palmate spinitriches covering

scolex peduncle; E, anterior part of scolex, lateral to dorso-ventral view; F, basal tentacular armature, bothrial surface; G, tentacular armature on basal swelling, antibothrial surface; H, metabasal tentacular armature, internal surface; I, basal tentacular armature, bothrial to external surface. *Symbols*: #, position on distal bothrial surface where microthrix micrograph (B) was taken; *, position on proximal bothrial surface where microthrix micrograph (C) was taken; +, position on pars vaginalis where microthrix micrograph (D) was taken

Fig. 10 Line drawings of *Dollfusiella imparispinis* n. sp. from *Chiloscyllium punctatum* Müller & Henle (BO-282) in the South China Sea. A, scolex, lateral view; B, scolex, dorso-ventral view; C, outline of complete specimen; D, mature segment; E, bulb. *Abbreviations*: c, cirrus, cs, cirrus-sac, ov, ovary, t, testis, ut, uterus, vit, vitelline follicle

Fig. 11 Line drawings of the tentacular armature of *Dollfusiella imparispinis* n. sp. from *Chiloscyllium punctatum* Müller & Henle (BO-282) in the South China Sea. A, basal tentacular armature, antibothrial surface; B, basal tentacular armature, bothrial surface—note opposing tentacular surface to tentacle illustrated in (A); C, basal tentacular armature, external surface; D, metabasal tentacular armature, internal surface; E, metabasal tentacular armature, antibothrial surface; F, metabasal tentacular armature, bothrial surface

Fig. 12 Scanning electron micrographs of *Dollfusiella imparispinis* n. sp. from *Chiloscyllium punctatum* Müller & Henle (BO-282) in the South China Sea. A, scolex, lateral to dorso-ventral view; B, anterior part of scolex, lateral view; C, anterior part of scolex, dorso-ventral view; D, scolex, lateral view; E, capilliform filitriches covering distal bothrial surface; F, palmate spinitriches covering proximal bothrial surface; G, enlarged, palmate spinitriches covering scolex peduncle; H, basal tentacular armature, internal to bothrial surface; I, basal tentacular armature, external to bothrial surface; J, tentacular armature on basal swelling, internal surface; K, apical tentacular armature, antibothrial surface; L, metabasal tentacular armature, bothrial surface; M, detailed view of bothrial surface—note hooks 1 and 1' abut; N metabasal tentacular armature, internal surface. *Symbols*: #, position on distal bothrial surface where microthrix micrograph (E) was taken; *, position on proximal bothrial surface where microthrix micrograph (F) was taken; +, position on pars vaginalis where microthrix micrograph (G) was taken

Fig. 13 Line drawings of *Dollfusiella parva* n. sp. from *Himantura gerrardi* (Gray) (BO-23) in the South China Sea (A, D–G) and from *Himantura* cf. *gerrardi* 2 (BO-138) in the Celebes Sea (B, C). A, complete specimen (immature), lateral view; B, complete specimen, dorso-ventral

view; C, mature segment; D, bulb; E, basal tentacular armature, external surface; F, metabasal tentacular armature, external surface; G, outline of complete specimen. *Abbreviations*: at, genital atrium, c, cirrus, cs, cirrus-sac, mg, Mehlis' gland, ov, ovary, t, testis, vit, vitelline follicle, vs, vaginal sphincter

Fig. 14 Scanning electron micrographs of *Dollfusiella parva* n. sp. from *Himantura* cf. *gerrardi* 2 (BO-138) in the Celebes Sea. A, complete specimen, lateral view; B, palmate spinitriches covering proximal bothrial surface; C, enlarged, palmate spinitriches covering scolex peduncle; D, metabasal tentacular armature, antibothrial surface; E, anterior part of scolex, dorso-ventral view; F, anterior part of scolex, dorso-ventral to lateral view; G, metabasal tentacular armature, external surface; H, detailed view of posterior bothrial margin—note enlarged, capilliform filitriches lining border between distal and proximal bothrial surfaces; I, basal tentacular armature, bothrial surface; J, metabasal tentacular armature, bothrial surface. *Symbols*: *, position on proximal bothrial surface where microthrix micrograph (B) was taken; +, position on pars vaginalis where microthrix micrograph (C) was taken

Fig. 15 Frequency distributions of scolex length (A) and bulb length (B) for specimens of *Dollfusiella spinulifera* (Beveridge & Jones, 2000) examined in the present study. Interrupted grey line represents a possible division of specimens of *D. spinulifera* into two groups: *D. spinulifera* of original description (left) and group 2 (right) with larger specimens and with larger bulbs

A **B**

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