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FISH PARASITOLOGY - ORIGINAL PAPER

Tentaculariid trypanorhynchs (Platyhelminthes: Cestoda) from *Mobula japanica* (Müller & Henle) from Indonesia, with the description of two new species

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Abstract
This study presents new information on tentaculariid trypanorhynchs from the Indo-Pacific region around Bali, Indonesia. Two new tentaculariid species, *Nybelinia balinensis* n. sp. and *N. mobulicola* n. sp., are described from the stomach of their myliobatid host *Mobula japanica* (Müller & Henle). *Nybelinia balinensis* n. sp. is a large-sized tentaculariid (scolex length, 6766–10,991). It can be distinguished from its congeners by a falcate metabasal armature, a unique basal armature of four rows of triangular shaped hooks, craspedote proglottids, and testes arranged in multiple layers in two separate lateral fields. *N. mobulicola* n. sp. can be characterized by short tentacles of 25 rows of hooks and 60 testes not reaching posterior to the ovary. A combination of a shorter basal armature of uncinate hooks without anterior extension of the base and fewer metabasal uncinate hooks with anterior extension of the base distinguishes it from *N. lingualis* (Cuvier, 1817). It differs from *N. balinensis* n. sp. in the possession of uncinate rather triangular shaped basal hooks. The *Nybelinia* Poche, 1926 fauna of *M. japanica* is highly specific, in line with a unique trypanorhynch fauna earlier described for the devil rays. This reflects their unique position as oceanic plankton feeders within the marine food web.

Keywords Tentaculariidae · *Nybelinia* · *Mobula* · Indonesia · Indian and Pacific Ocean

Introduction

The Trypanorhyncha Diesing, 1863 is a cestode order distributed worldwide, characterized by a scolex bearing two or four bothria and a unique tentacular apparatus consisting of four hooked tentacles, tentacle sheaths, retractor muscles, and bulbs (Campbell and Beveridge 1994; Palm 2004). The tentacular armature is characteristic for the different taxa and has been used as a major important character for taxonomic, systematic, and phylogenetic relationships inside the group. Adult trypanorhynchs mainly occur inside the spiral valve or the stomach of their elasmobranch final hosts (Campbell and Beveridge 1994), while the metacestodes infect a wide range of intermediate hosts (Palm 2004; Palm and Caira 2008).

Members of the batoid elasmobranch family Myliobatidae Bonaparte have been reported as common final hosts of the trypanorhynchs (see Palm 2004). Of the five trypanorhynch superfamilies, especially the Eutetrarhynchoidea Guiart, 1927 and the Tentacularioidea Poche, 1926, both belonging to Trypanobatoida Olson, Caira, Jensen, Overstreet, Palm & Beveridge, 2010, infect the myliobatids. Most common

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genera of the former are *Parachristianella* Dollfus, 1946, *Prochristianella* Dollfus, 1946, *Dollfusiella* Campbell and Beveridge 1994, and *Eutetrarhynchus* Pintner, 1913, and of the latter are *Tentacularia* Bosc, 1797, *Kotorella* Euzet & Radujkovic, 1989, and *Nybelinia* Poche, 1926 (see Palm 2004).

Within the myliobatids, the relatively speciose genus *Mobula* Rafinesque includes pelagic and planktivorous rays with a worldwide distribution. Only few studies have been carried out on its trypanorhynch fauna, describing species with a unique morphology. Besides the common eutetrarhynchid *Parachristianella trygonis* Dollfus, 1946, a variety of unique species, namely *Fellicocestus mobulae* Campbell and Beveridge 2006, *Hemionchos maior* Campbell and Beveridge 2006, *H. mobulae* Campbell and Beveridge 2006, *H. striatus* Campbell and Beveridge 2006, *Mobulocestus mollis* Campbell and Beveridge 2006, *M. nephritidis* Campbell and Beveridge 2006, and *M. lepidoscolex* Campbell and Beveridge 2006, have been described from the urogenital tract and spiral valve (see Campbell and Beveridge 2006, 2007)

The members of the Tentaculariidae Poche, 1926 are commonly found inside the stomach of elasmobranchs. Because of their homeoacanthous tentacular armature, they are able to fasten themselves to the stomach wall, which has been recognized as the most common site of infection (Palm 1995). Examination of a stomach from *Mobula japanica* (Müller & Henle) from Bali revealed two new species of tentaculariids, one of them with a very large scolex size and the second of the "*Nybelinia lingualis* type." Both species are described herein, providing further insight into the species richness and morphological plasticity of the tentaculariid trypanorhynch cestodes from the Indo-Pacific region.

Materials and methods

An adult *Mobula japanica* was found at the Kedonganan fish market during the 1st Educational Workshop on Marine Fish Parasites in Indonesia, 21 July to 2 August 2013, and dissected on site. The stomach was transported on ice to the laboratory of the Faculty of Veterinary Science, Udayana University, Denpasar, Bali, and directly opened, and the stomach wall was freed from the stomach contents in a tray. The trypanorhynchs attached to the stomach wall were collected, cleaned in saline solution and fixed, and stored in 70% ethanol following the procedure described in Palm (2004).

Unmounted specimens were stained directly in acetic carmine, dehydrated in an ethanol series, cleared with a graded series of eugenol, and mounted onto slides in Canada balsam. Drawings were made by using an Olympus BX53 with a camera lucida.

For measurement of taxonomically important characters, an ocular micrometer attached to a BH-2 microscope was used. All measurements are reported in micrometers and presented as the range followed by the mean, the standard deviation, the number of the measured worms (*N*), and the total number of measurements for each character (*n*) in parentheses.

The classification follows Palm (2004). Host identity follows Froese and Pauly (2019). The type specimens are deposited in the National Biodiversity Collection, Museum Zoologicum Bogoriense (MZB), Cibinong, Bogor, Java, Indonesia, and the Museum für Naturkunde Berlin (ZMB), Germany.

Results

Two new tentaculariid species, *Nybelinia balinensis* n. sp. and *N. mobulicola* n. sp., are recorded from *Mobula japanica*. Detailed information on the new species with comments on their morphology, taxonomy, and distribution is given below.

Order Trypanorhyncha Diesing, 1863
Suborder Trypanobatoida Olson, Caira, Jensen, Overstreet, Palm & Beveridge, 2010
Superfamily Tentacularioidea Poche, 1926
Family Tentaculariidae Poche, 1926
Genus *Nybelinia* Poche, 1926

***Nybelinia balinensis* n. sp.**

Type host: *Mobula japanica* (Müller & Henle)

Type locality: Kedonganan fish market, Bali, Indonesia.

Site in host: Stomach.

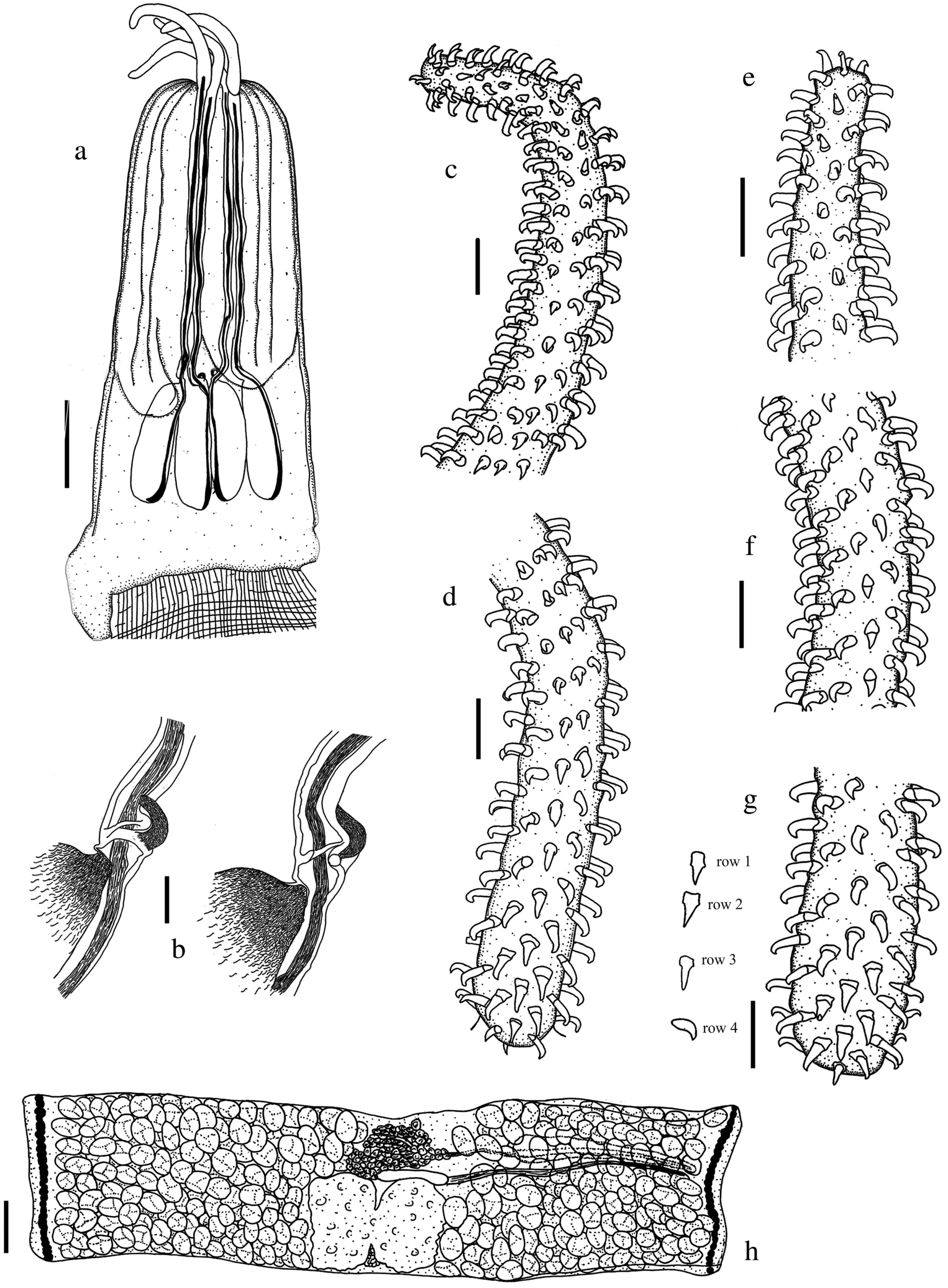
Type material: Holotype (MZB Ca. 207; 1 slide); 3 paratypes (permanent mounts, MZB Ca. 208, ZMB E.7442 and E.7443).

Etymology: The specific name refers to Bali Island, Indonesia, where the host was collected.

Description (Fig. 1)

[Based on whole mounts of 4 mature and 1 immature specimens.] Worms large, 15–55 mm (29 ± 18, N = 4) long, with 104 (*N* = 1) proglottids; scolex, craspedote, 6766–10,991 (8890 ± 1920, *N* = 5) long. Scolex width 1963–2336 (2172 ± 156, *N* = 5, *n* = 5) at level of pars bothrialis, 2056–2561 (2284 ± 222, *N* = 5, *n* = 5) at level of pars vaginalis, 2000–2523 (2277 ± 204, *N* = 5, *n* = 5) at level of pars bulbosa.

Fig. 1 *Nybelinia balinensis* n. sp. Scolex (**a**). Anterior part of bulbs with the entrance into the tentacle sheath with muscular ring (**b**). Apical armature (**c**). Basal towards metabasal armature (**d**). Falcate hooks on the apical (**e**) and metabasal (**f**) armature. Details of the basal armature with hook shapes from rows 1–4 (**g**). Mature proglottid (**h**). Scale bars: **a**, 1000 μm; **b**–**g** 100 μm; **h**, 200 μm. In **a**, the four retractor muscles are shown in black color very marginal along the bulbs and attached to the most posterior part of the bulbs. In **h**, the uterus is seen above the vagina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row 4
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Bothria 4 in number, elongate, without thickened rims. Pars bothrialis 3271–3944 (3768 ± 281, *N* = 5) long, slightly overlaps pars bulbosa; pars vaginalis shorter than pars bothrialis, 2841–3738 (3484 ± 394, *N* = 5) long; tentacle sheaths straight (Fig. 1a), 79–104 (91 ± 7, *N* = 5, *n* = 5) in diameter; muscular ring around the basal part of the tentacle sheath present. Pars bulbosa 1402–1589 (1480 ± 74, *N* = 5) long; prebulbar organs and gland cells inside bulbs absent; bulbs 1346–1458 (1400 ± 31, *N* = 5, *n* = 20) long, 336–430 (378 ± 31, *N* = 5, *n* = 20) wide, bulb width to length ratio 1.0:3.3–4.2 (3.7 ± 0.3, *N* = 5, *n* = 20); retractor muscles originate at posterior extremity of bulbs (Fig. 1a); pars post-bulbosa present, 318–748 (493 ± 170, *N* = 5) long. Velum long, overlaps anterior immature proglottids, 561–2991 (1832 ± 1029, *N* = 5) long. Scolex ratio (pars bulbosa to pars bothrialis to pars vaginalis) 1.0:2.2–2.8:1.9–2.7 (1.0:2.5:2.4; *N* = 5).

Tentacles 1669–2195 (1844 ± 225, *N* = 4, *n* = 5) long; basal swelling absent (Fig. 1d, g); tentacle width 122–165 (145 ± 13, *N* = 5, *n* = 10) at level of the basal region, 85–152 (110 ± 21, *N* = 5, *n* = 9) at level of the metabasal region, and 37–61 (49 ± 17, *N* = 2, *n* = 2) at level of the distal region of tentacle. Hooks solid, tentacles with 33–37 (35 ± 2, *N* = 3, *n* = 3) rows of hooks. Basal armature homeoacanthous, homeomorphous with 4 rows of triangular hooks. Hooks of row 1 smallest, 33–60 (47 ± 12, *N* = 3, *n* = 5) long, base 12–21 (16 ± 3, *N* = 4, *n* = 6) long; hooks of second row 42–60 (50 ± 7, *N* = 4, *n* = 8) long, base 18–27 (24 ± 4, *N* = 4, *n* = 8) long; hooks of third row 48–54 (51 ± 2, *N* = 4, *n* = 8) long, base 15–27 (24 ± 4, *N* = 4, *n* = 7) long; hooks of fourth row 45–60 (55 ± 6, *N* = 4, *n* = 8) long, base 24–27 (25 ± 2, *N* = 4, *n* = 6) long. Metabasal armature homeoacanthous, homeomorphous with falcate hooks, 39–51 (46 ± 4, *N* = 5, *n* = 24) long, base 15–21 (18 ± 2, *N* = 5, *n* = 26) long. Distal region of tentacle with smaller falcate hooks, 27–36 (32 ± 3, *N* = 3, *n* = 8) long, base 6–18 (12 ± 4, *N* = 3, *n* = 8) long. Number of hooks per half spiral row in basal, metabasal, and distal regions of tentacle 5–6 (*N* = 5, *n* = 5), 6–7 (*N* = 5, *n* = 7), and 6 (*N* = 3, *n* = 3) respectively.

Proglottids very slightly craspedote (Fig. 1h), apolytic; immature proglottids 25 (*N* = 1) in number, wider than long. Mature proglottids 24–47 (33 ± 11, *N* = 4) in number, wider than long, terminal proglottid triangular. Mature proglottids 262–1533 (537 ± 336, *N* = 4, *n* = 21) long, with maximum width 1682–3832 (2945 ± 701, *N* = 4, *n* = 14); gravid proglottids observed, 55 in number (*N* = 1), 598–748 (680 ± 60, *N* = 1, *n* = 5) long, with maximum width 4206–4878 (4612 ± 291, *N* = 1, *n* = 4). Genital pore ventro-submarginal (Fig. 1h); cirrus sac elongate and slender, unipartite (Fig. 1h), 610–1220 (805 ± 223, *N* = 4, *n* = 13) long, 30–104 (58 ± 19, *N* = 4, *n* = 13) wide; cirrus straight, uncoiled; seminal vesicles absent; vas deferens not thick, coiled anterior to ovary, 18–43 (30 ± 9, *N* = 2, *n* = 6) in diameter (Fig. 1h); testes in 2 lateral fields, oval, in multiple layers, not observed posterior to ovary (Fig. 1h), 73–110 (96 ± 15, *N* = 4, *n* = 9) long, 61–110 (89 ± 17, *N* = 4, *n* = 9) wide, 292 (*N* = 1, *n* = 1) in number. Uterus thin-walled, anterior to ovary (Fig. 1h); uterine pore not seen; vagina parallel to cirrus sac, uniform in width (Fig. 1h), enters genital atrium at posterior level of cirrus sac (Fig. 1h); seminal receptacle not seen. Ovary posteromedial, with 2 lobes in dorso-ventral view (Fig. 1h), 183–439 (286 ± 74, *N* = 4, *n* = 17) long by 335–854 (558 ± 143, *N* = 4, *n* = 21) wide; Mehlis' gland posterior to ovarian isthmus (Fig. 1h); vitelline follicles circumcortical, 49–104 (70 ± 19, *N* = 3, *n* = 10) long by 30–73 (54 ± 13, *N* = 3, *n* = 10) wide, not interrupted at level of genital atrium (Fig. 1h).

Remarks

Nybelinia balinensis n. sp. from the spinetail devil ray belongs to a group of very large-sized species of *Nybelinia* regularly found in the Indian and especially the Pacific Ocean. However, the new species is easily distinguished from other species with a large scolex, i.e., *N. aequidentata* (Shipley & Hornell, 1906) Dollfus, 1930 and *N. kamegaii* Palm and Bray 2014 from dasyatid stingrays, *N. pintneri* Yamaguti, 1934 from the blue shark *Prionace glauca* (L.), and *N. surmenicola* Okada in Dollfus, 1929 from the salmon shark *Lamna ditropis* Hubbs & Follett, as well as from all other congeners by the presence of a characteristic basal armature with triangular shaped hooks. In comparison with *N. mobulicola* n. sp., in this paper described from *Mobula japanica*, the metabasal armature is falcate and not uncinate.

Based on the falcate hooks in the metabasal armature, *N. balinensis* n. sp. has similarities with smaller sized *Nybelinia* species, e.g., *N. africana* Dollfus, 1960 mainly from carcharhinids, *N. bilobata* Palm 2004, *N. goreensis* Dollfus, 1960 and *N. syngenes* (Pintner, 1928) Dollfus, 1930 from *Sphyrna lewini* (Griffith & Smith), *N. mehlhorni* Palm & Beveridge, 2002 from *Hemigaleus microstoma* Bleeker, and larval *N. bengalensis* Reimer, 1980 and *N. victoriae* Palm & Beveridge, 2002. The combination of the hook size (L = 39–51), slightly craspedote proglottids, as well as testes arranged in multiple layers and in two separate lateral fields distinguishes the new species from its congeners. All other species have differently shaped metabasal hooks or lack a characteristic basal armature (see Palm 2004).

Nybelinia mobulicola n. sp.

Type host: *Mobula japanica* (Müller & Henle)
Type locality: off Bali, Indonesia.
Site in host: Stomach.
Type material: Holotype (ZMB E.7441).
Etymology: The specific name refers to *Mobula japanica*, the host in which this new species was found.

Description (Fig. 2)

[Based on whole mount of 1 mature specimen.] Worm 36 mm (*N* = 1) long, with 106 (*N* = 1) proglottids; scolex craspedote, 1701 (*N* = 1) long. Scolex width 747–1065 (907 ± 225, *N* = 1, *n* = 2) at level of pars bothrialis, 610–885 (783 ± 150, *N* = 1, n = 3) at level of pars vaginalis, 994 (*N* = 1, *n* = 1) at level of pars bulbosa. Bothria 4 in number, without

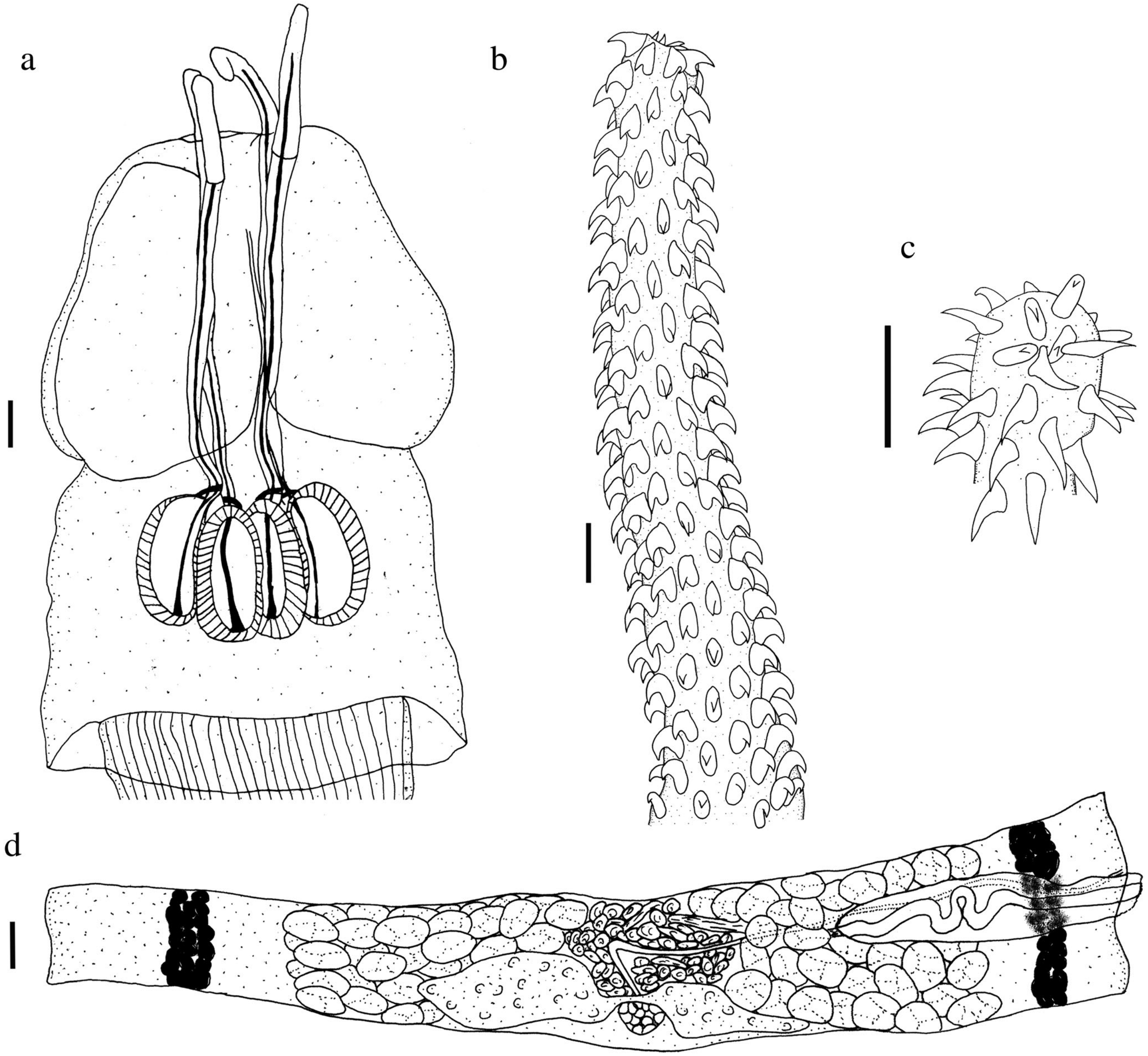

Fig. 2 *Nybelinia mobulicola* n. sp. Scolex (**a**). Basal and metabasal armature (**b**). Distal region of tentacle (**c**). Mature proglottid (**d**). Scale bars: **a**, **d**, 60 μm; **b**, **c**, 30 μm. In **d**, in fact the vagina enters the genital atrium at the anterior level of the cirrus sac. Since the genital atrium could not be seen easily in the mature segment selected for drawing, it seems that it opens outside the genital atrium

thickened rims, 872–887 (880 ± 10, *N* = 1, *n* = 2) long. Pars bothrialis 935 (*N* = 1) long, does not overlap pars bulbosa; pars vaginalis 935 (*N* = 1) long; tentacle sheaths straight (Fig. 2a), 45–58 (52 ± 7, *N* = 1, *n* = 3) in diameter; muscular ring around basal part of tentacle sheath present. Pars bulbosa 423 (*N* = 1) long; prebulbar organs and gland cells within bulbs absent; bulbs oval (Fig. 2a), 372–397 (383 ± 11, *N* = 1, *n* = 4) long, 159–177 (171 ± 8, *N* = 1, *n* = 4) wide, bulb width to length ratio 1.0: 2.2–2.4 (2.2 ± 0.1, *N* = 1, *n* = 4); retractor muscles originate at posterior extremity of bulbs (Fig. 2a); pars post-bulbosa present, 134 (*N* = 1) long. Velum long, overlaps anterior immature proglottids, 305 (*N* = 1, *n* = 1) long. Scolex ratio (pars bulbosa to pars bothrialis to pars vaginalis) 1.0:2.2:2.2 (*N* = 1).

Tentacles 574–604 (589 ± 21, *N* = 1, *n* = 1) long; basal swelling absent (Fig. 2b); tentacle width 67 (*N* = 1) at level of basal region, 46 (*N* = 1) at level of the metabasal region, and 34 (*N* = 1) at level of the distal region. Hooks solid, tentacles with 25–27 (26 ± 1, *N* = 1, *n* = 2) rows of hooks. Basal armature homeoacanthous, homeomorphous with 3 rows of uncinate hooks lacking anterior extension of base (Fig. 2b), 9–18 (15 ± 3, *N* = 1, *n* = 7) long, base 9–18 (14 ± 4, *N* = 1, *n* = 5) long. Metabasal armature homeoacanthous, homeomorphous with uncinate hooks, each with anterior extension of base, 19–

21 (20 ± 1, *N* = 1, *n* = 4) long, base 15–18 (17 ± 1, *N* = 1, *n* = 5) long. Distal region of tentacle with slender uncinate to falciform hooks (Fig. 2c), 16 (*N* = 1, *n* = 4) long, base 9–12 (10 ± 1, *N* = 1, *n* = 4) long. Number of hooks per half spiral row in basal, metabasal, and distal regions of tentacle 4–6 (*N* = 1, *n* = 2), 6 (*N* = 1, *n* = 1), and 5 (*N* = 1, *n* = 1) respectively.

Proglottids acraspedote (Fig. 2d), apolytic; immature proglottids 36 (*N* = 1) in number, wider than long. Mature proglottids 12 (*N* = 1) in number, wider than long. Mature proglottids 149–187 (164 ± 18, *N* = 1, *n* = 4) long, with maximum width 1308–1458 (1364 ± 81, *N* = 1, *n* = 3); gravid proglottids observed, 58 in number, 224–747 (444 ± 225, *N* = 1, *n* = 4) long, with maximum width 1420–1682 (1528 ± 110, *N* = 1, *n* = 4). Genital pore ventro-submarginal (Fig. 2d); cirrus sac elongate, unipartite (Fig. 2d), 332–453 (404 ± 51, *N* = 1, *n* = 4) long, 75–91 (87 ± 7.5, *N* = 1, *n* = 4) wide; cirrus coiled; seminal vesicles absent; vas deferens not thick, coiled anterior to ovary (Fig. 2d), 18–24 (22 ± 3, *N* = 1, *n* = 5) in diameter; testes in 2 lateral fields, round to oval, 60 (*N* = 1, *n* = 1) in number, in multiple layers, not observed posterior to ovary (Fig. 2d), 75–91 (81 ± 7, *N* = 1, *n* = 4) long, 45–60 (54 ± 7, *N* = 1, *n* = 4) wide. Uterus thin-walled, anterior to ovary; uterine pore not seen; vagina ventral to cirrus sac, relatively uniform in width (Fig. 2d), enters genital atrium at anterior level of cirrus sac (Fig. 2d); seminal receptacle not seen. Ovary posteromedial, with 2 lobes in dorso-ventral view (Fig. 2d), 92–110 (100 ± 9, *N* = 1, *n* = 3) long by 488–518 (498 ± 18, *N* = 1, *n* = 3) wide; Mehlis' gland posterior to ovarian isthmus (Fig. 2d), 57–61 (59 ± 2, *N* = 1, n = 4) long, 52–55 (54 ± 1, *N* = 1, *n* = 4) wide; vitelline follicles circumcortical (Fig. 2d), 51–60 (56 ± 5, *N* = 1, *n* = 3) long by 30–36 (34 ± 3, *N* = 1, *n* = 3) wide, not interrupted at level of genital atrium (Fig. 2d).

Remarks

Nybelinia mobulicola n. sp. from the spinetail devil ray is a smaller sized *Nybelinia* species with a scolex length below 2 mm, resembling *N. lingualis* (Cuvier, 1817) and similar species by the presence of rose thorn–shaped or uncinate hooks along the entire tentacle. Following the description of *N. lingualis* in Palm (2004), the presence of three basal rows of uncinate hooks without extension of the base compared with rose thorn–shaped metabasal hooks with anterior basal extension defines *N. mobulicola* n. sp. as a species with a characteristic basal armature.

Following the key to the genus *Nybelinia* in Palm (2004), the new species is most similar to *N. pintneri*, *N. lingualis*, and *N. riseri* Dollfus, 1960. The basal armature of the similar sized *N. pintneri* has uncinate hooks with an anterior extension of the base and the metabasal armature consists of slender uncinate hooks with a simple oval base. The number of hook rows is 33 vs 25–27 in the new species, the number of testes extending posterior to the ovary is 100–120 vs 60 not extending posterior to the ovary, and *N. pintneri* was found in a blue shark compared with *N. mobulicola* n. sp. from a devil ray.

N. mobulicola n. sp. differs from *N. lingualis* and *N. riseri* by the number of rows of basal uncinate hooks lacking an anterior extension of the base, that is fewer compared with *N. lingualis* and *N. riseri* (3 vs 7–8 and 10 rows, respectively). In addition, the number of hook rows along the tentacle is smaller (25) compared with *N. lingualis* (31–35), and *N. riseri* has been described mainly from rajiform rays. Unlike *N. mobulicola* n. sp. in which the size of the uncinate hooks increases towards the metabasal armature, the size of the uncinate hooks decreases drastically in *N. basimegacantha* Carvajal, Campbell & Cornford, 1976. It can be distinguished from the other species of *Nybelinia* with rose thorn–shaped hooks (e.g., *N. africana*, *N. bilobata*) because these species have either differently shaped hooks in the metabasal or in both the basal and metabasal armature (e.g., *N. aequidentata*, *N. jayapaulazariahi* Reimer, 1980). It also lacks, rather than possesses, the testes posterior to the ovary as seen in *N. manazo* Yamaguti, 1952, *N. queenslandensis* Jones & Beveridge, 1998, and *N. hemipristis* Palm & Beveridge, 2002, and unlike *N. strongyla* Dollfus, 1960 and *N. sphyrnae* Yamaguti, 1952, the new species has acraspedote rather than craspedote proglottids.

Discussion

With the description of *Nybelinia balinensis* n. sp. and *N. mobulicola* n. sp., 31 species are considered valid in the genus *Nybelinia* (see Palm 2004; Palm and Bray 2014; Beveridge et al. 2017). Together with *Heteronybelinia* Palm, 1999 and *Mixonybelinia* Palm, 1999, this group of tapeworms belongs to one of the most speciose trypanorhynch families. The character combinations, especially the scolex dimensions, tentacle length, and armature patterns shed some light into the zoogeographical distribution, morphological plasticity, and phylogenetic relationships of these cestodes.

Nybelinia balinensis n. sp. belongs to the larger sized *Nybelinia* species that have been recorded from the Indian and the Pacific Oceans. The metabasal armature with its characteristic falcate hooks resembles its large sized congeners *N. aequidentata* and *N. kamegaii* from dasyatid stingrays. The host, *M. japanica*, also has an Indo-Pacific distribution, similar to those of *N. aequidentata*, and such a distribution might be also true for *N. balinensis* n. sp. Its basal armature is unique among *Nybelinia* species and has little resemblance to the cosmopolitan tentaculariid *Tentacularia coryphaenae* Bosc, 1802, with two small extensions flanking the central hook prong (see Palm 2004, page 102, Figure 35 b–d). *N. mobulicola* n. sp., according to its general morphology (e.g., scolex size, short bulbs) as well as its tentacular armature, strongly resembles *N. lingualis*, a species that also infects stingrays (batiforms) as final hosts. However, the tentacles are shorter and the number of hook rows is significantly fewer.

Although with the single specimen we could not genetically characterize the new species, it is likely that both might be also phylogenetically related.

Regardless of some variation seen in the position of the ovary and the cirrus sac as well as the distribution of the testes in *Nybelinia*, the absence of testes posterior to a central ovary and the preequatorial cirrus sac were utilized in the generic diagnosis of the genus (see Palm 2004). However, the position of the ovary can be also posterior, e.g. in *N. balinensis* n. sp., *Nybelinia gopalai* Chandra & Hanumantha Rao, 1985, *N. mobulicola* n. sp., *N. sphyrnae*, and *N. surmenicola*, where testes are absent behind the ovary or only very few testes are present posterior to the lateral parts of the ovary (in *N. gopalai*). Furthermore, except for *N. balinensis* n. sp. which has an equatorially oriented cirrus sac containing a straight cirrus, all other species of *Nybelinia* possess a preequatorial cirrus sac with a coiled cirrus. It is difficult to judge if the generic diagnosis of *Nybelinia* requires amendment to meet all current descriptions or this character helps to classify different *Nybelinia* groups in the future. It is evident that most known characters within the tentaculariids demonstrate distinct morphological variability, and their reliability as generic characters needs to be verified.

The tentaculariids are unique among the Trypanorhyncha as specialized parasites in the stomach of elasmobranchs (Palm 1995). *Nybelinia* so far infects 53 species of 12 batoid and 23 shark genera (Palm 2004; Schaeffner and Beveridge 2014; Haseli et al. 2010; Palm and Bray 2014). Palm and Caira (2008) demonstrated the low host specificity within this genus, especially in the second intermediate host, allowing them to be widely distributed in many teleosts and cephalopods worldwide (Palm 2004). Combined with the unique infection site, these trypanorhynchs were able to switch hosts, from originally batoid hosts into a wide range of different sharks (Palm et al. 2009). Because of the uniqueness of the homeoacanth tentacular armature with both homeomorphous and heteromorphous hooks on the different parts of the tentacles, and the co-occurrence of different species with different armature patterns inside the same final host, it is not clear which factors have led to this high degree of species radiation. Palm et al. (2009) demonstrated that morphology within the tentaculariids can be highly plastic even between phylogenetically closely related species within the same final host (e.g. *Nybelinia* cf. *africana* and *Mixonybelinia lepturi* Palm 2004 in *Alopias superciliosus* Lowe, Alopiidae). Though we could not collect genetic data from the new species, the characteristic ecology of the devil rays and the uniqueness of the already-recorded trypanorhynch fauna from these hosts suggest that this might be also the case in the morphologically highly different *Nybelinia balinensis* n. sp. and *N. mobulicola* n. sp. Consequently, neither the armature pattern nor the final host species so far seem to be reliable in matching the morphological characters with the phylogenetic relationships within this group of interesting trypanorhynchs.

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Conflict of interest The authors declare that they have no conflict of interest.

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