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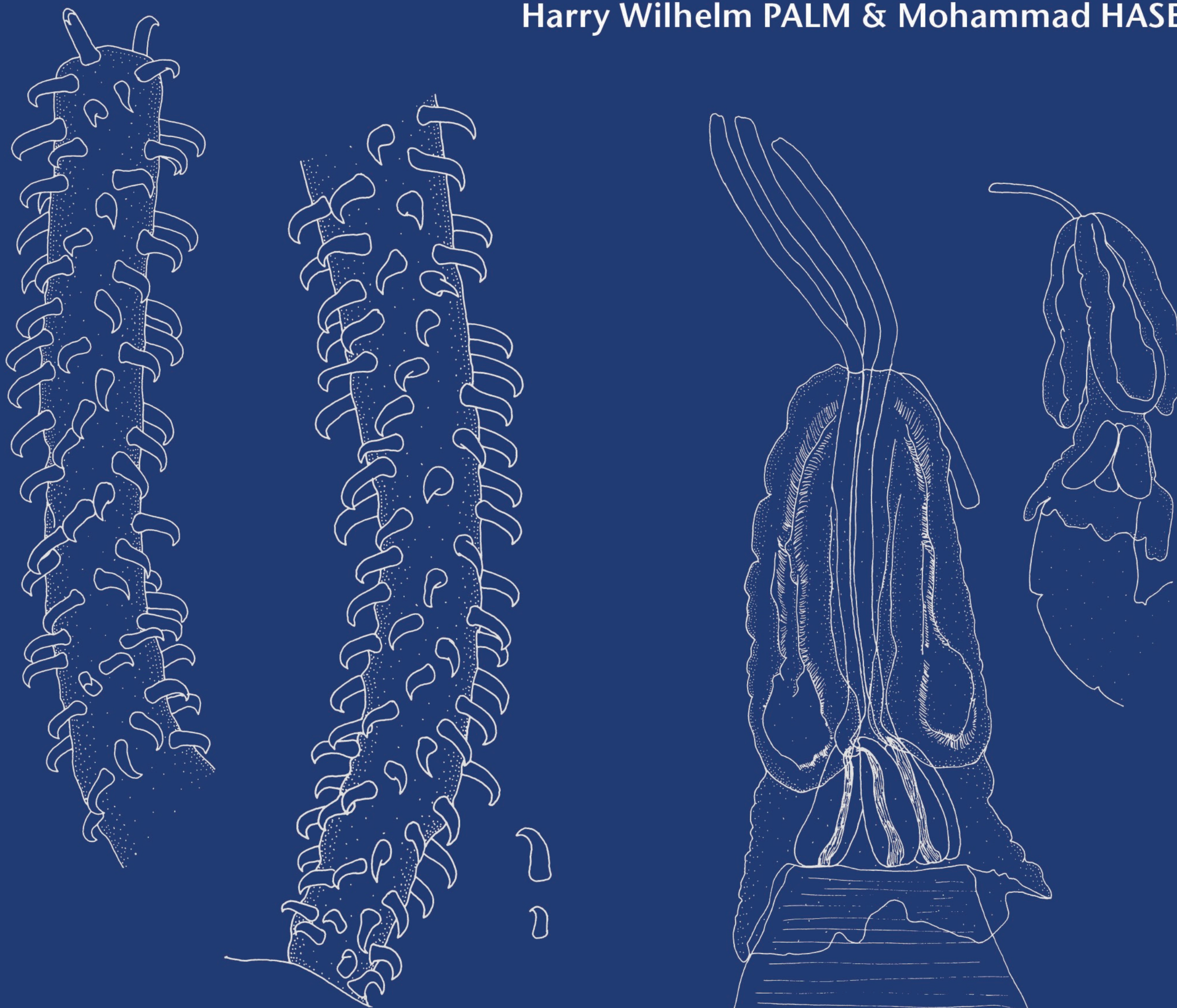

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Couverture / *Cover* :
Homeokotorella anterioporus n. gen., n. sp. ex *Taeniura lymma* 1: scolex; metabasal armature, bothrial surface; and basal towards metabasal armature, bothrial surface.

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Tentaculariids (Cestoda, Trypanorhyncha) of elasmobranchs from Malaysian Borneo

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ABSTRACT
The waters off Borneo, the third-largest island in the world located at the geographic centre of Maritime Southeast Asia, harbour a high diversity of marine cestodes. We examined the tentaculariid species collection of the large-scale sampling endeavours in Malaysian Borneo between 2002 and 2008. Our study resulted in reporting the tentaculariid fauna of the region with greater detail, describing two new species, and erecting a new genus, *Nybelinia pseudafricana* n. sp. and *Homeokotorella anterioporus* n. gen., n. sp. A comparison of *N. sphyrnae* Yamaguti, 1952 from Malaysian Borneo, Australia, New Caledonia, and Japan revealed the synonymy of *N. jayapaulazariahi* Reimer, 1980 with *N. sphyrnae*. Remarks are provided for *N. sphyrnae*, *N. aequidentata* (Shipley & Hornell, 1906) Dollfus, 1930, *Heteronybelinia estigmena* (Dollfus, 1960) Palm, 1999, *Tentacularia coryphaenae* Bosc, 1802, *Kotorella pronosoma* (Stossich, 1900) Euzet & Radujkovic, 1989, and *Kotorelliella* (abbr. *Ko.*) *jonesi* Palm & Beveridge, 2002 and new host records are established for *N. aequidentata* and *Ko. jonesi*. *Nybelinia aequidentata* is reported for the first time from this region. Since most of the trypanorhynch species, including the tentaculariids, reported so far off Borneo are the same as those recorded off Indonesia, it seems that the trypanorhynch fauna of Borneo resembles the one from the Indonesian waters including to date 21 species (36%) of a total of 58 known tentaculariid species and 86 species (26%) of a total of 335 valid trypanorhynch species. These results allow us to better understand the species diversity of the tentaculariid trypanorhynchs off Malaysian Borneo.

KEY WORDS
Southeast Asia, Borneo, Tentaculariidae, elasmobranchs, new synonymy, new species, new genus.

RÉSUMÉ

Tentaculariidés (Cestoda, Trypanorhyncha) des élasmobranches du Bornéo malaisien.

Les eaux au large de Bornéo, la troisième plus grande île du monde située au centre géographique de l'Asie du Sud-Est maritime, abritent une grande diversité de cestodes marins. Nous avons examiné les espèces de tentaculariidés collectées dans le cadre des campagnes d'échantillonnage à grande échelle menées dans la partie malaisienne de Bornéo, entre 2002 et 2008. Notre étude a permis une évaluation plus détaillée de la faune de tentacularidés de la région, avec la description de deux nouvelles espèces et la création d'un nouveau genre, *Nybelinia pseudafricana* n. sp. et *Homeokotorella anterioporus* n. gen., n. sp. Une comparaison de *N. sphyrnae* Yamaguti, 1952 de la partie malaisienne de Bornéo, d'Australie, de Nouvelle-Calédonie et du Japon a révélé la synonymie de *N. jayapaulazariahi* Reimer, 1980 avec *N. sphyrnae*. Des remarques sont fournies pour *N. sphyrnae*, *N. aequidentata* (Shipley & Hornell, 1906) Dollfus, 1930, *Heteronybelinia estigmena* (Dollfus, 1960) Palm, 1999, *Tentacularia coryphaenae* Bosc, 1802, *Kotorella pronosoma* (Stossich, 1900) Euzet & Radujkovic, 1989, et *Kotorelliella* (abbr. Ko.) *jonesi* Palm & Beveridge, 2002 ; de nouveaux signalements d'hôtes sont établis pour *N. aequidentata* et *Ko. jonesi*. *Nybelinia aequidentata* est signalé pour la première fois dans cette région. Comme la plupart des espèces de trypanorhynques, y compris les tentaculariidés, signalées jusqu'à présent au large de Bornéo sont les mêmes que celles signalées au large de l'Indonésie, il semble que la faune de trypanorhynques de Bornéo ressemble à celle des eaux indonésiennes, comprenant à ce jour 21 espèces (36 %) d'un total de 58 espèces de tentaculariidés connues et 86 espèces (26 %) d'un total de 335 espèces de trypanorhynques valides. Ces résultats nous permettent de mieux comprendre la diversité des espèces de trypanorhynques tentaculariidés au large de la partie malaisienne de Bornéo.

MOTS CLÉS
Asie du Sud-Est,
Bornéo,
Tentaculariidae,
élasmobranches,
synonymie nouvelle,
espèces nouvelles,
genre nouveau.

INTRODUCTION

Borneo, the largest island in Asia, is politically divided among Malaysia and Brunei in the North and Indonesia in the South. It borders the Coral Triangle along the western side, a region that contains about ¾ of the world's coral species, and has been recognised as a global centre of marine biodiversity (Allen 2007). Schaeffner & Beveridge (2012a, b, c, 2013a) studied a range of different trypanorhynch taxa from Borneo and identified 50 trypanorhynch species collected from 163 infected host specimens belonging to 17 species of sharks and 26 species of rays (Schaeffner & Beveridge 2014).

Palm (2004) studied the trypanorhynch cestode fauna from the southern Java coast, mainly from teleost hosts. He reported 54 different species from Indonesian waters, among which the abundant ones were the tentaculariids *Tentacularia coryphaenae* Bosc, 1802, *Heteronybelinia estigmena* (Dollfus, 1960) Palm, 1999, *Kotorella pronosoma* (Stossich, 1900) Euzet & Radujkovic, 1989, and a highly abundant species the author identified as *Nybelinia africana* Dollfus, 1960. Schaeffner & Beveridge (2014) reported the following tentaculariid species from Borneo: *H.* cf. *australis* Palm & Beveridge, 2002, *H. estigmena*, *K. pronosoma*, *Kotorelliella jonesi* Palm & Beveridge, 2002, *N. africana sensu* Palm (2004), *N.* cf. *goreensis* Dollfus, 1960, *N.* cf. *mehlhorni* Palm & Beveridge, 2002, *N. sphyrnae* Yamaguti, 1952, and *T. coryphaenae*. Other highly abundant species from the southern Java coast such as *Mixonybelinia lepturi* Palm, 2004 have not been detected by Schaeffner & Beveridge (2014).

In the present study, we erect a new genus to accommodate a species new to science and also revisit *Nybelinia africana* from Indonesian waters as earlier described by Palm (2004), describing it as a new species from Malaysian Borneo and Indonesian waters. A comparison of the specimens of *N. sphyrnae* from Malaysian Borneo, Australia, New Caledonia, and Japan revealed the synonymy of *N. jayapaulazariahi* Reimer, 1980 with *N. sphyrnae*, extending its range of distribution to southern Africa. Additional information and the updated host range from Malaysian Borneo is provided for *N. aequidentata* (Shipley & Hornell, 1906) Dollfus, 1930, *H. estigmena*, *T. coryphaenae*, *K. pronosoma*, and *Ko. jonesi,* based on the new host identifications in the Global Cestode Database by Caira *et al.* (2023). The importance of the Coral Triangle for the distribution patterns of the tentaculariids and the trypanorhynch species diversity is discussed.

MATERIAL AND METHODS

Schaeffner & Beveridge (2014) presented the most comprehensive list of trypanorhynch cestodes from different locations around Borneo based on large-scale sampling efforts of elasmobranchs funded by the National Science Foundation and carried out by Janine Caira and Kirsten Jensen between 2002 and 2008 (Caira & Jensen 2017). The taxonomic work was presented in a series of publications (Schaeffner *et al.* 2011; Schaeffner & Beveridge 2012a, b, c, 2013a, 2014; Schaeffner 2014). The revised host identifications (host collection code as BO and collection number, see Naylor *et al.* 2012) and the parasite combinations are accessible from the Global Cestode Database (http://tapewormdb.uconn.edu). The tentaculariid material from Malaysian Borneo prepared by Professor Ian Beveridge was examined, of which some specimens had never been studied. Given the numerous changes in the generic nomenclature of rays in recent years, Last *et al.* (2016a) was also followed, herein.

The elasmobranch hosts were collected off Malaysian Borneo with the help of local fishermen or obtained from fish markets. The stomach and spiral intestine were opened with a

Table 1. — Measurements of *Nybelinia sphyrnae* Yamaguti, 1952 and *N. jayapaulazariahi* Reimer, 1980 in micrometers (µm). Abbreviations: **m**, measured from the types and see Material and methods; **Y**, Yamaguti (1952). Note: since the Japanese type specimens of *N. sphyrnae* are larger and longer than the Bornean specimens, the proglottids with the same size were compared between Bornean vouchers and Japanese type specimens. Regarding the southern Australian specimens of *N. sphyrnae*, immature proglottids could only be observed.

	***Nybelinia sphyrnae* Yamaguti, 1952**				***Nybelinia jayapaulazariahi* Reimer, 1980**		
Characters	**Malaysian Borneo**	**New Caledonia**	**South Australia**	**Japan**	**India (Reimer 1980)**	**India (Palm 1999)**	**Australia (Palm & Beveridge 2002)**
TL (mm)	73.6 (71.0-76.1)	–	–	100 or more Y	–	–	–
SL	686 (500-1019)	974 (884-1025)	888 (762-1013)	800-1000 Y	890	530	1060
PBoL	384 (299-483)	530 (512-555)	634 (537-732)	450-600 Y	–	298	470
PVaL	312 (189-475)	499 (476-518)	436 (354-518)	499 (438-563) m	–	285	450
PBuL	344 (220-525)	399 (360-445)	320 (287-354)	325 Y	–	165	365
BuL	347 (202-535)	388 (332-447)	346 (272-405)	325 Y	228-254	150-165	320-325
BuW	96 (75-121)	78 (69-91)	111 (106-118)	90-150 Y	76-86	54	85-135
BuW : BuL	3.6 (2.2-5.0)	5.0 (4.4-6.2)	3.1 (2.4-3.7)	2.2-3.6 Y	2.9-3.0	2.9	2.4-3.8
VeL	42 (37-49)	63 (51-75)	98 (79-110)	75-130 Y	55	96	–
TeL	700 (603-855)	–	702 (502-840)	350-400 Y	275-289	–	–
TeWBa	35 (32-39)	37 (30-42)	35 (33-36)	34 Y	–	16-18.5	32.5-35
TeWMb	31 (27-36)	36 (30-39)	33 (30-36)	34 Y	–	16-18.5	32.5-35
NHR	30 (28-34)	–	32 (31-34)	32	–	–	–
NHBa	6	6	6	6	–	6	6
NHMb	6	6	6	6 m	–	6	6
BaHL	12 (9-15)	12 (9-14)	11 (9-12)	15 (14-16) m	–	6-7	11-14
BaHB	11 (9-15)	12 (9-15)	11 (8-14)	13 (12-14) m	–	6-7	9-11
MbHL	17 (16-19)	16 (15-20)	17 (12-21)	21 Y	11	10-11	15-16
MbHB	13 (10-15)	13 (11-15)	18 (15-21)	12-15 Y	–	6-7	11-14
PrL	296 (274-317)	–	–	244 m	–	–	–
PrW	753 (744-762)	–	–	793 m	–	–	–
TesL	57 (54-60)	–	–	60 m	–	–	–
TesW	44 (36-51)	–	–	47 (42-51) m	–	–	–
CsL	230 (226-232)	–	–	257 m	–	–	–
CsW	60	–	–	51 m	–	–	–
OvL	135 (120-150)	–	–	105 m	–	–	–
OvW	226 (195-258)	–	–	187 m	–	–	–
ViFoL	33 (28-42)	–	–	34 (30-40) m	–	–	–
ViFoW	25 (19-30)	–	–	27 (18-33) m	–	–	–

longitudinal incision through all the chambers. A subsample of cestodes was immediately fixed in 4% formalin solution buffered in seawater (for morphological study) or 95% ethanol (for DNA analyses). The spiral intestines with worms inside were fixed in 10% seawater-buffered formalin (see Schaeffner & Beveridge 2014). Worms and spiral intestines remained in the formalin solution for up to four weeks and were then transferred into 70% ethanol for long-term storage. Methods for the preparation of the cestodes have been described by e.g. Beveridge (2008), Schaeffner & Beveridge (2012a, b, c, 2013a, b, c) and Schaeffner *et al.* (2011).

The mounted material was analysed and tentatively pre-identified (see Schaeffner & Beveridge 2014). Comparison with voucher material from earlier Indonesian materials (see Palm 2004) in the senior author's collection revealed the presence of two new species (see also Palm *et al.* 2020). *Nybelinia pseudafricana* n. sp. had been earlier identified as *Nybelinia africana* along the southern Indonesian coasts of Java and Bali, and is a common trypanorhynch in *Alopias superciliosus* Lowe as final hosts and many pelagic teleosts as second intermediate or paratenic hosts (Palm 2004). In collecting *N. pseudafricana* n. sp., one specimen of *Trichiurus lepturus* L. was also bought by the first author from the fish market of Pelabuhan Ratu, Indonesia in 2003. The plerocercoids were isolated from the stomach wall, fixed in 10% seawater-buffered formalin, stored in 70% ethanol, stained in acetic carmine, dehydrated in an ethanol series, cleared in methyl salicylate, and mounted on slides in Canada balsam. One plerocercoid of *N. pseudafricana* n. sp., collected earlier by Jakob & Palm (2006) from commercially important fish species from Pelabuhan Ratu, South Java coast, and belonging to a series of voucher slides mainly consisting of *M. lepturi* and *N. pseudafricana* n. sp., was prepared for scanning electron microscopy (SEM) to illustrate details of the armature and surface ultrastructure, as follows: the specimen was transferred to acetone and dehydrated in a graded acetone series, then critical point dried and mounted with a double-sided adhesive carbon tape onto SEM stubs. The stubs were coated with gold-palladium in an argon atmosphere and examined under a LEO 1430 VP SEM at 10-15 kV.

Measurements are in micrometres and are presented as the range followed by the mean, the number of the measured worms (N) and the total number of measurements for each character (n) in parentheses.

Chervy (2009) was followed for the terminology of microtriches.

Type material was deposited in the Lawrence Penner Collection, Storrs, Connecticut, United States (LRP), the Berlin Natural History Museum, Germany (ZMB) (Museum für Naturkunde, catalogue Entozoa, collection Vermes), and the Muséum national d'Histoire naturelle in Paris, France (MNHN). The holotype and a paratype of *N. sphyrnae* from *Sphyrna zygaena* (Linnaeus,

1758) off Nagasaki, Japan, in the collection of Meguro Parasitological Museum, Tokyo, Japan (SY 7201) and some vouchers from Australia (South Australian Museum, AHC 24958), New Caledonia (ZMB E. 7729-32), and Malaysian Borneo (LRP 4367-4371, 11005, 11006; ZMB E. 7726) were also compared.

Abbreviations

Metrical features used in the Table 1

BaHB	basal hook base;
BaHL	basal hook length;
BuL	bulb length;
BuW	bulb width;
BuW: BuL	bulb width: length ratio;
CsL	cirrus sac length;
CsW	cirrus sac width;
MbHB	metabasal hook base;
MbHL	metabasal hook length;
NHBa	number of hooks per half spiral row in basal region;
NHMb	number of hooks per half spiral row in metabasal region;
NHR	number of hook rows along tentacle;
OvL	ovary length;
OvW	ovary width;
PBoL	pars bothrialis length;
PBuL	pars bulbosa length;
PrL	proglottid length;
PrW	proglottid width;
PVaL	pars vaginalis length;
SL	scolex length;
TeL	tentacle length;
TesL	length of testes;
TesW	width of testes;
TeWBa	tentacle width at basal region;
TeWMb	tentacle width at metabasal region;
TL	total length;
VeL	velum length;
ViFoL	vitelline follicle length;
ViFoW	vitelline follicle width.

Institutions

LRP	Lawrence Penner Collection, Storrs, Connecticut;
MNHN	Muséum national d'histoire Naturelle, Paris;
SAM	South Australian Museum, Adélaïde;
SY	Meguro Parasitological Museum, Tokyo;
ZMB	Museum für Naturkunde, catalogue Entozoa, collection Vermes, Berlin.

RESULTS

Order TRYPANORHYNCHA Diesing, 1863
Suborder TRYPANOBATOIDA Olson, Caira, Jensen, Overstreet, Palm & Beveridge, 2010
Superfamily Tentacularioidea Poche, 1926
Family Tentaculariidae Poche, 1926

Genus *Homeokotorella* n. gen.

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Type species. — *Homeokotorella anterioporus* n. gen., n. sp.

Etymology. — The generic name refers to the homeomorphous hooks of the tentacular armature of the type species.

Diagnosis. — Scolex elongated, craspedote. Four elongated bothria, without thickened rims, lateral and posterior bothrial margins not fused with peduncle. Bothrial pits absent; hamulate spinitriches along bothrial margins present. Pars bothrialis overlapping pars bulbosa, pars vaginalis shorter than pars bothrialis. Pars bulbosa with short bulbs. Retractor muscles originating at base of bulbs; prebulbar organs and gland-cells inside bulbs absent. Tentacle sheaths straight. Four elongated, slender tentacles, without basal swelling. Basal and metabasal tentacular armature homeoacanthous, homeomorphous; hooks solid. Characteristic basal armature absent, first rows of basal armature increasing in size. Strobila acraspedote, proglottids wider than long, euapolytic; cirrus unarmed, coiled; cirrus sac lateral and elongate, runs along anterior end of proglottid; genital atrium submarginal, located at anterior end of proglottid; seminal vesicles absent; testes numerous, distributed around central ovary, not reaching anterior to cirrus sac, in single layer; ovary positioned centrally; vitelline follicles circumcortical. Parasitic in dasyatid batoids.

Remarks

Within the Tentaculariidae, unlike in *Tentacularia* Bosc, 1797 with the bothria entirely fused with the scolex peduncle and *Nybelinia* Poche, 1926, *Heteronybelinia* Palm, 1999, *Mixonybelinia* Palm, 1999 and *Reimeriella* Palm, Morales-Ávila, Galván-Magaña & Haseli, 2020 with a robust, muscular scolex and triangular bothria with fused margins, the new genus possesses elongate bothria with free lateral and posterior margins. *Homeokotorella* n. gen. therefore closely resembles the two monotypic genera *Kotorella* Euzet & Radujkovic, 1989 and *Kotorelliella* Palm & Beveridge, 2002 since the members of these three genera possess an elongate scolex, four bothria each with free lateral and posterior margins, a short pars bulbosa, and a homeoacanthous metabasal armature. Nonetheless, the homeomorphous, rather than heteromorphous hooks of the metabasal and basal tentacular armature easily distinguish it from *Kotorella* and *Kotorelliella*. The erection of this genus is consistent with the taxonomy within Tentaculariidae, where each genus possesses its own armature pattern.

Homeokotorella anterioporus n. sp.
(Fig. 1A-F)

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Type material. — **Holotype**. **Malaysia** • 1 specimen; Malaysian Borneo, Sabah, off Semporna (fish market); 04°28'44.09"N, 118°37'00.57"E; from stomach of *Taeniura lymma* 1 (*sensu* Naylor *et al.* 2012) (Myliobatiformes, Dasyatidae) (BO-86); LRP 10983.
Paratypes. **Malaysia** • 1 specimen; same data as for holotype; LRP 4379 • 6 specimens in 5 slides; Malaysian Borneo, Sabah, off Pulau Mabul; 04°14'44.02"N, 118°37'53.32"E; same host as for holotype; LRP 4380, 10984; ZMB E.7744-46.

Etymology. — The specific name refers to the anterior position of the cirrus sac in this species.

Description

[Based on whole mounts of 4 specimens.]

Worms 7800-7875 (7837, N = 2) long, with 37-40 (N = 2) proglottids; scolex slender, craspedote (Fig. 1A, B), 724-781 (739, N = 4) long. Scolex width 290-419 (340, N = 4) at level of pars bothrialis, 282-378 (320, N = 4) at level of pars vagi-

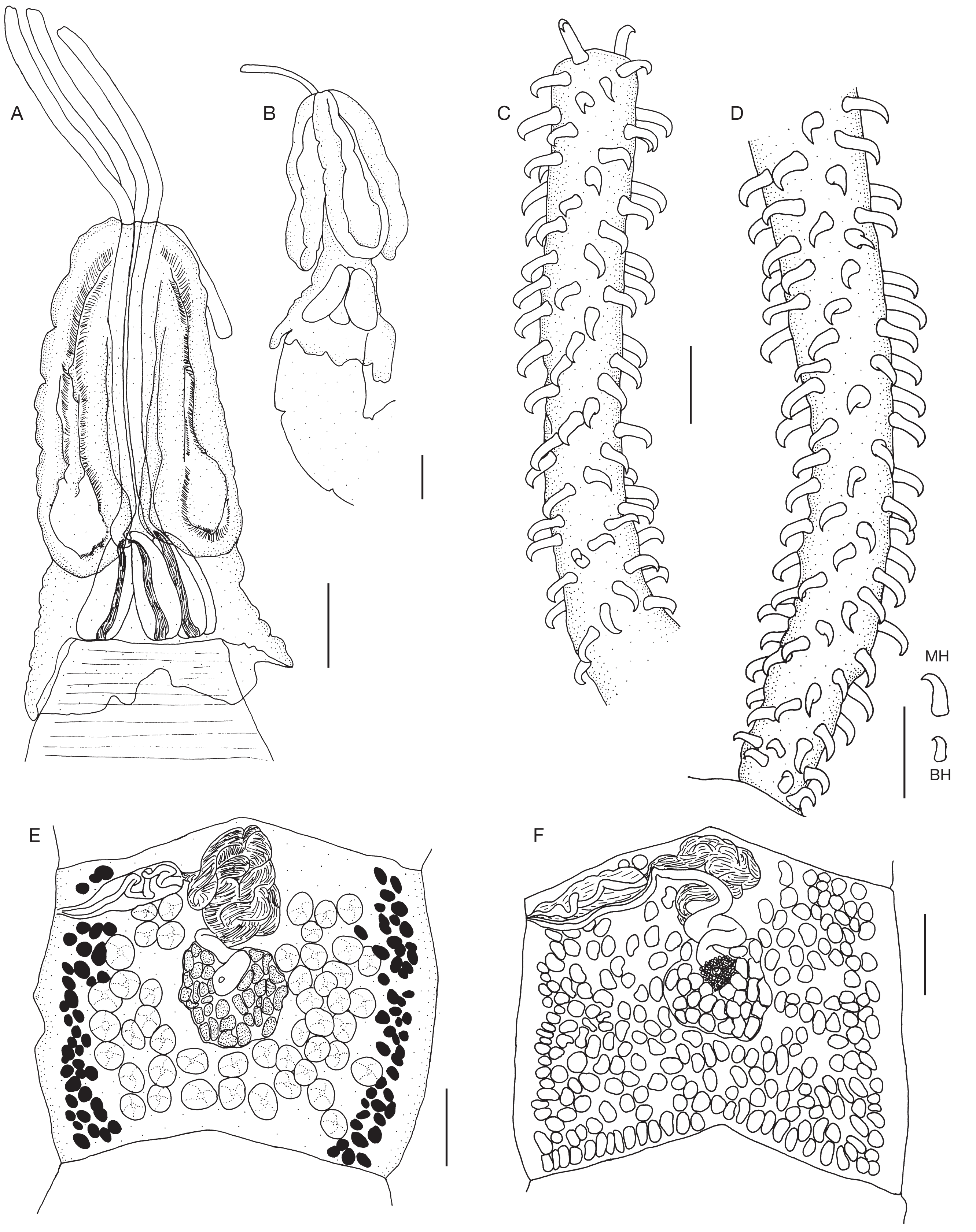

Fig. 1. — *Homeokotorella anterioporus* n. gen., n. sp. ex *Taeniura lymma* 1: **A**, **B**, scolex; **C**, metabasal armature, bothrial surface; **D**, basal towards metabasal armature, bothrial surface (**BH** and **MH** indicate basal and metabasal hooks, respectively); **E**, **F**, mature proglottid, in **F**, **open circles** are vitelline follicles. Scale bars: A, B, E, F, 125 µm; C, D, 20 µm.

nalis, 314-338 (324, N = 4) at level of pars bulbosa. Bothria 4 in number, elongate, with free lateral and posterior margins (Fig. 1B). Hamulate spinitriches present along bothrial borders. Pars bothrialis 451-523 (497, N = 4) long, slightly overlapping pars bulbosa; pars vaginalis shorter than pars bothrialis, 402-499 (441, N = 4) long; tentacle sheaths straight, 20-30 (26, N = 2, n = 4) in diameter; muscular ring around basal part of tentacle sheath present. Pars bulbosa 160-192 (179, N = 4) long; prebulbar organs and gland cells inside bulbs absent; bulbs 152-188 (172, N = 3, n = 11) long, 64-80 (72, N = 3, n = 11) wide, bulb width : length ratio 1.0 : 2.1-2.7 (2.4, N = 3, n = 11); retractor muscles originate at posterior extremity of bulbs; pars post-bulbosa absent. Velum long, 104-160 (130, N = 4). Scolex ratio (pars bulbosa : pars bothrialis : pars vaginalis) 1.0 : 2.4-3.3 : 2.1-2.8 (1.0 : 2.8 : 2.5, N = 4).

Tentacles elongate and slender, 480-500 (490, N = 1, n = 2) long; basal swelling absent; tentacle width 20 (N = 2, n = 2) at level of basal region, 24 (N = 2, n = 2) at level of metabasal region, and 20 (N = 1, n = 1) at level of distal region of tentacle. Hooks solid, tentacles with 27-31 (29, N = 1, n = 2) rows of hooks. Tentacular armature homeoacanthous, homeomorphous (Fig. 1C, D). First four to five rows of basal hooks increasing in size (Fig. 1D), hooks falcate, 4.5-10 (7.0, N = 3, n = 3) long, base 3-4 (4, N = 2, n = 3) long, a single slender uncinate hook with anterior extension of base seen. Metabasal armature with falcate hooks (Fig. 1C), 12-14 (13, N = 3, n = 7) long, base 4-5 (5, N = 2, n = 3) long; distal region of tentacle with falcate hooks, 12 (N = 1, n = 5) long, base 4-5 (5, N = 1, n = 5) long. Number of hooks per half spiral row in basal and metabasal region of tentacle 5-6 (N = 1, n = 2), 6 (N = 1, n = 1) respectively.

Proglottids acraspedote (Fig. 1E, F), euapolytic; immature and mature proglottids wider than long. Mature proglottids 1-5 (3, N = 2) in number, 375-445 (410, N = 2, n = 6) long, with maximum width of 525-650 (572, N = 2, n = 6); gravid proglottids not observed. Genital pore submarginal in mature proglottids, close to anterior end of proglottids. Cirrus sac elongate, running along anterior end of each proglottid, 44-52 (47, N = 1, n = 4) long, 160-192 (179, N = 1, n = 4) wide; cirrus sac length : width ratio 1.0 : 3.5-4.4 (3.8, N = 1, n = 4). Cirrus unarmed, coiled. Seminal vesicles absent. Vas deferens tightly coiled, running anterior medially and posteriorly towards ovarian isthmus. Vagina runs sinuously from ovary towards cirrus sac, then turning laterally along cirrus sac, opening to genital atrium posterior to cirrus sac (Fig. 1F). Testes round to oval, in a single layer, not reaching anterior to cirrus sac, 40-52 (44, N = 2, n = 6) long in diameter, 48 (n = 1) in number (Fig. 1E). Ovary bilobed, located in centre of proglottid, ovarian lobes 160-200 (178, N = 1, n = 4) long, 72-92 (83, N = 1, n = 4) wide. Mehlis' gland posterior to ovarian isthmus, 40-52 (46, N = 1, n = 2) in diameter. Vitelline follicles circumcortical (Fig. 1F), round to oval shaped, 20-40 (30, N = 1, n = 5) in diameter.

Remarks

The specimens from the host described as *Taeniura lymma* 1 are very similar to one another and show only little variability in scolex size, hook sizes and proglottid features. The closely related species *K. pronosoma* and *Ko. jonesi* differ from *H. anterioporus* n. gen., n. sp. in their scolex proportions and bulb ratios (see Palm & Beveridge 2002; Palm 2004) . The tentacular armature of these two species, *K. pronosoma* and *Ko. jonesi*, is homeoacanthous, heteromorphous in the metabasal and/or basal armature. While *K. pronosoma* always shows stout, tightly packed hooks with typical, broad diamond-shaped bases on the bothrial tentacle surface, *Ko. jonesi* has uncinate hooks with an anterior extension of the base on the bothrial and slender spiniform hooks on the antibothrial surface. *Homeokotorella anterioporus* n. gen., n. sp. displays slender falcate hooks without an anterior extension of the base, which are of similar shape on all tentacle surfaces.

Genus *Nybelinia* Poche, 1926

Nybelinia pseudafricana n. sp.
(Figs 2A-D; 3A-G)

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Nybelinia africana Dollfus, 1960: 798 (in part see Palm 2004), **n. syn.**

Type material. — **Holotype**. **Malaysia** • 1 specimen; from stomach of *Lamiopsis tephrodes* (Fowler) (Carcharhiniformes, Carcharhinidae) (BO-74); Malaysian Borneo, Sarawak, off Mukah, 02°53'52.16"N, 112°05'44.12"E; LRP 11007.
Paratypes. Malaysia • 4 specimens; same data as for holotype; LRP 11008, ZMB E.7719-21. **Indonesia** • 2 specimens (plerocercoids); from stomach wall of *Trichiurus lepturus* (Scombriformes, Trichiuridae); South Java, off Pelabuhan Ratu; 06°59'13.9"S, 106°32'37.4"E; MNHN-HEL1926, 1927.

Voucher Material. — Scolex (plerocercoid) of *N. pseudafricana* n. sp. (voucher specimen) from the stomach wall of *Gempylus serpens* Cuvier, Pelabuhan Ratu, Indonesia (Jakob & Palm 2006), prepared for SEM.

Additional specimens studied. — Several specimens of *N. africana* (ZMB E. 7722-25, 5 slides) from *Mullus surmuletus* Linnaeus off Kalâat el-Andalous, Tunisia.

Etymology. — The specific name is related to the similarity of the new species to *N. africana*.

Description

[Based on whole mounts of 3 specimens; plerocercoid from *Gempylus serpens* observed with SEM.]

Worms 28 875-48 500 (37 283, N = 3) long, with 160-246 (N = 2) proglottids; scolex compact (Figs 2A; 3A), craspedote (Fig. 2A), 555-724 (628, N = 3) long. Scolex width 427-451 (440, N = 3) at level of pars bothrialis, 427-451 (440, N = 3) at level of pars vaginalis, 288-338 (319, N = 3) at level of pars bulbosa. Bothria 4 in number, sessile and elongate. Lineate spinitriches along bothrial borders present. Scolex and bothrial surface covered with capilliform (3-5) and papilliform (1) filitriches. Pars bothrialis 282-386 (346, N = 3) long, overlapping pars bulbosa; pars vaginalis shorter than pars bothrialis, 185-370 (252, N = 3) long; tentacle sheaths straight anteriorly, each with a single coil immediately anterior to bulb, 36-52 (47, N = 3, n = 10) in diameter; muscular ring around basal part of tentacle sheath not seen. Pars bulbosa 217-266 (241,

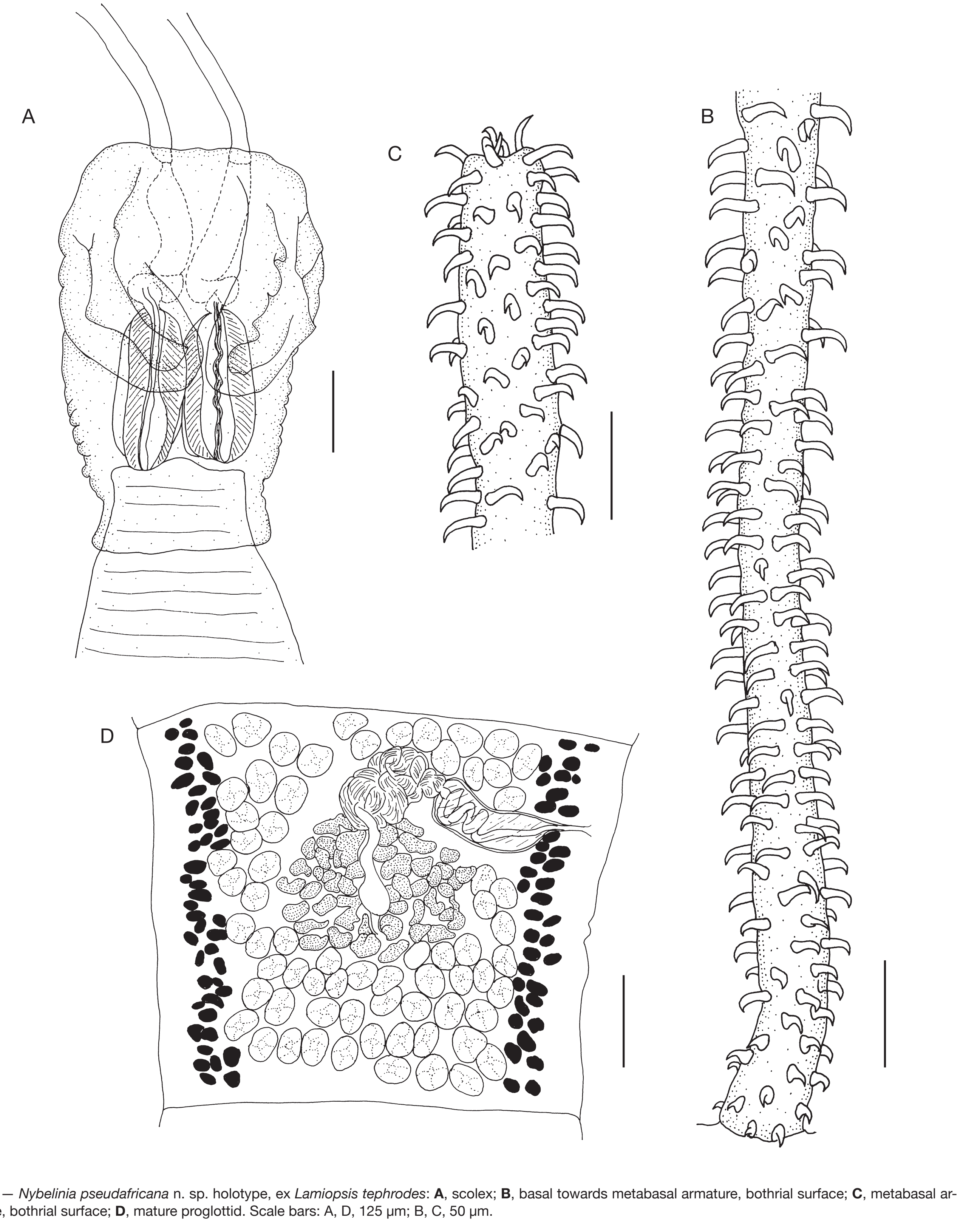

Fig. 2. — *Nybelinia pseudafricana* n. sp. holotype, ex *Lamiopsis tephrodes*: **A**, scolex; **B**, basal towards metabasal armature, bothrial surface; **C**, metabasal armature, bothrial surface; **D**, mature proglottid. Scale bars: A, D, 125 µm; B, C, 50 µm.

N = 3) long; prebulbar organs and gland cells inside bulbs absent; bulbs 240-252 (246, N = 3, n = 6) long, 96-104 (99, N = 3, n = 6) wide, bulb width : length ratio 1.0 : 2.3-2.5 (2.5, N = 3, n = 6); retractor muscles originating at posterior extremity of bulbs; pars post-bulbosa absent. Velum elongate, straight or scalloped, 80-113 (99, N = 3) long. Scolex ratio (pars vaginalis : pars bothrialis : pars bulbosa) 1.0 : 1.0-2.0 : 0.6-1.4 (1.0 : 1.5 : 1.1, N = 3).

Tentacles elongate, 720-1000 (900, N = 1, n = 3) long with *c.* 40 rows of hooks; basal swelling absent; tentacle width 32-36 (N = 1, n = 2) at level of basal region, 40-42 (N = 1, n = 2) at level of metabasal region. Hooks solid. Tentacular armature homeoacanthous, homeomorphous (Fig. 2B, C). Metabasal armature differing distinctly from basal armature. 2-3 rows of basal armature with uncinate hooks with distinct anterior extension of base, 10-12 (11, N = 2, n = 6) long, base 8-10 (9, N = 2, n = 5) long; metabasal hooks larger, slender falcate with small base and regularly curved tip, 20-25 long (22, N = 3, n = 14); base 6-8 (7, N = 3, n = 15) long; apical hooks of not fully everted tentacles 22 (N = 1) long, base 7-8 (7, N = 1, n = 2) long. Number of hooks per half spiral row in basal and metabasal region of tentacle 5-6 (5, N = 2, n = 2) and 6-7 (6, N = 2, n = 3), respectively.

Proglottids acraspedote (Fig. 2D), apolytic; immature and mature proglottids wider than long. Mature proglottids 2-3 (N = 2) in number, 400-1125 (690, N = 2, n = 5) long, 675-2500 (999, N = 2, n = 4) wide. Gravid proglottids 1000-1375 (N = 1, n = 2) long, 2625 wide (N = 1, n = 1). In mature proglottids, genital pore in anterior third of proglottid; genital pores alternate irregularly. Cirrus sac submarginal, elongate, 56-72 (64, N = 1, n = 2) long, 168-220 (194, N = 1, n = 2) wide, not reaching anterior end of proglottid; cirrus sac length : width ratio 1.0 : 2.3-3.9 (3.1, N = 1, n = 2). Cirrus unarmed, coiled. Seminal vesicles absent. Vas deferens tightly coiled, running anteriorly medially and then posteriorly towards ovarian isthmus. Testes oval in shape, around 40 in diameter, arranged in single layer; testes number 70-75 (73, N = 2, n = 2) per proglottid, 9 testes anterior to cirrus sac (n = 1). Ovary bilobed, located in centre of proglottid, 68-189 (106, N = 2, n = 4) long, 140-280 (189, N = 2, n = 4) wide. Vitelline follicles circumcortical, round to oval in shape, 24-44 (33, N = 2, n = 5) long; 12-24 (18, N = 2, n = 5) wide.

Remarks

The specimens presented here as a new species are those identified by Schaeffner & Beveridge (2014) as *N. africana* from *Lamiopsis tephrodes* (BO-74). *Nybelinia pseudafricana* n. sp. most closely resembles *N. africana*. Both species can be characterized by the presence of several rows of uncinate hooks at the base of the tentacular armature and the presence of falcate hooks along the tentacle. Nonetheless, the new species is distinguished from *N. africana* by the length of the metabasal hooks (20-25 vs 12.5-16) and the tentacle length (720-1000 vs 200) (see Palm 2004). In this respect, several Tunisian specimens of *N. africana* isolated from *Mullus surmuletus* caught off Kalâat el-Andalous, were also used for comparison with their characteristics as follows: scolex 632-828 (751, N = 12) long; bulbs 186-270 (213, N = 9, n = 9) long, 72-96 (86, N = 9, n = 9) wide, bulb width : length ratio 1.0: 1.9-3.0 (2.5, N = 9, n = 9); velum 240-345 (277, N = 8 n = 8) long; number of rows of hooks 17-19 (18, N = 5); metabasal hooks 12-17 (15, N = 5, n = 5) long, base 3-6 (5, N = 5, n = 5) long; tentacles 258-321 (294, N = 4, n = 4) long. *Nybelinia pseudafricana* n. sp., considering the Tunisian specimens, is also different from *N. africana* in the number of rows of hooks (40 vs 17-19). It is worth mentioning that this feature was not mentioned in the original description of *N. africana* (see Palm 2004).

Regardless of variation in scolex length as can be seen in species of *Nybelinia* (see Palm 2004), it is of note that the specimens earlier identified as *N. africana* in Indonesia, including the adult specimens isolated from *Alopias superciliosus* Lowe as well as *Carcharhinus* sp. and the plerocercoids isolated from *Alepisaurus ferox* Lowe, *Brama dussumieri* Cuvier, *Conger cinereus* Rüppell, *Coryphaena hippurus* L., *Gempylus serpens* Cuvier, *Thyrsitoides marleyi* Fowler, and *Trichiurus lepturus* (see Palm 2000, 2004; Jakob & Palm 2006), are re-identified as *N. pseudafricana* n. sp., and that this species is very common along the southern Java coast, Indonesia.

Likewise, the specimens reported as *N. africana* off Mozambique by Palm *et al.* (1997) are re-identified as *N. pseudafricana* n. sp. based on the scolex measurements and the length of their metabasal hooks (20-32). Thus, whereas *N. pseudafricana* n. sp. occurs in the Indo-Pacific region, the distribution of *N. africana* still remains mainly around Western Africa and in the Mediterranean Sea.

Examination of the scolex with SEM identified several rows of tiny pores (Fig. 3B, D), each parallel to one hook row, and serially placed along the tentacle. This is a novel feature, which had not earlier been described from trypanorhynchs. However, pores have been earlier reported already from the hooks of *Molicola horridus* (Goodsir, 1841) Dollfus, 1935 and *Gymnorhynchus isuri* Robinson, 1959 (see Knoff *et al.* 2004, 2007).

Nybelinia sphyrnae Yamaguti, 1952

Nybelinia sphyrnae Yamaguti, 1952: 56.

Nybelinia jayapaulazariahi Reimer, 1980: 226, **n. syn.**

Material examined. — **Malaysia** • 5 specimens; from *Sphyrna* cf. *lewini* (Griffith & Smith) (BO-69) (Carcharhiniformes: Sphyrnidae); Malaysian Borneo, off Mukah, Sarawak; 02°53'52.16"N, 112°05'44.12"E; LRP 4367-4371 • 1 specimen; same data; ZMB E. 7726 • 1 specimen; from *Sphyrna lewini* 1 (*sensu* Naylor *et al.* 2012) (BO-60); off Mukah, Sarawak; 02°53'52.16"N, 112°05'44.12"E; LRP 11005.
Japan • holotype and 1 paratype; from *S. zygaena* off Nagasaki; off Nagasaki; SY 7201.
South Australia • 3 specimens; from *S. zygaena* off Goolwa; SAM; AHC 24958.
Malaysia • 1 specimen; from *Urogymnus polylepis* (Bleeker) (BO-108) (Myliobatiformes: Dasyatidae); Malaysian Borneo, off Kampung Abai, Kinabatangan River, Sabah; 05°41'10.81"N, 118°23'08.35"E; LRP 11006.
New Caledonia • 7 plerocercoids; from *Saurida undosquamis* (Richardson) (Aulopiformes: Synodontidae); off New Caledonia; ZMB E. 7729-32.

Remarks

Nybelinia sphyrnae was described by Yamaguti (1952) from *Sphyrna zygaena* off Nagasaki, Japan. Beveridge & Campbell (1996) reported three specimens of this species from *S. zygaena* from Goolwa, South Australia, providing additional drawings

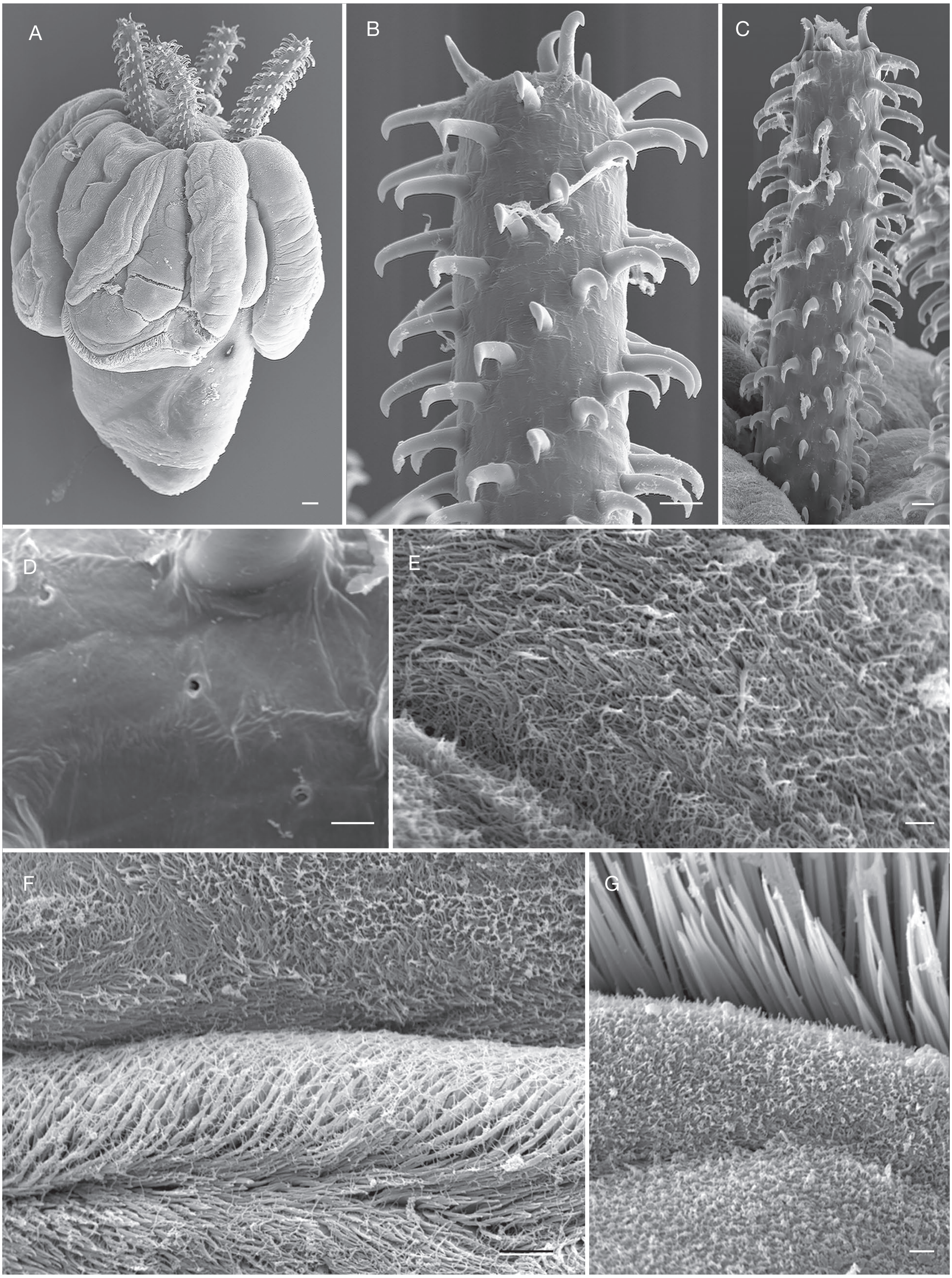

Fig. 3. — Surface ultrastructure of *Nybelinia pseudafricana* n. sp.: **A**, typical muscular scolex with triangular shaped bothria; **B**, metabasal armature; **C**, basal and metabasal armature; **D**, series of pores at the base of tentacular hooks; **E**, capilliform filitriches between the bothria; **F**, lineate spinitriches along bothrial borders with capilliform filitriches on proximal bothrial surface; **G**, lineate spinitriches at bothrial border with papilliform filitriches on distal bothrial surface. Scale bars: A, 30 μm; B, C, 10 μm; D-F, 2 μm; G, 6 μm.

of the scolex and mature proglottid and the first drawing of the tentacle with its hooks. Palm (2004) also reported this species from *S. zygaena* from Goolwa, South Australia, in his parasite-host checklist. Thereafter, Schaeffner & Beveridge (2014), during a large-scale study focusing on the parasite diversity of elasmobranchs from Malaysian and Indonesian Borneo, reported specimens of *N. sphyrnae* from *S. lewini* off Malaysian Borneo, the hosts having been registered in the Global Cestode Database as *Sphyrna lewini* 1 (BO-60) and *S.* cf. *lewini* (BO-69).

In the present study, in addition to examining the specimens of *N. sphyrnae* earlier identified by Schaeffner & Beveridge (2014) from *S. lewini* 1 and *S.* cf. *lewini* (BO-60, 69), we also measured the holotype as well as one paratype from Japan, some specimens from New Caledonia, and those South Australian specimens mentioned in the parasite-host checklist of Palm (2004) to clarify the range of measurements for *N. sphyrnae* (see Table 1). Furthermore, on the basis of recent examinations and the measurements at hand a proposal for a synonymy of the two species *N. sphyrnae* and *N. jayapaulazariahi* is made, both of which have a homeoacanthous, homeomorphous tentacular armature with uncinate hooks, which increase in size towards the metabasal part of the tentacle. In both species, the pars bothrialis is larger than the pars bulbosa and the retractor muscles originate at the base of the bulbs.

In Table 1, the measurements of *N. jayapaulazariahi* from different studies are compared with those of the types and vouchers of *N. sphyrnae* from different localities. The ranges of the taxonomically important characters of *N. jayapaulazariahi* overlap with those of *N. sphyrnae*. Regarding the variation seen for the bulb width to length ratio in the Malaysian Bornean and New Caledonian specimens of *N. sphyrnae* in comparison to other conspecifics, it is worth mentioning that in all the specimens of *N. sphyrnae* the values measured for the pars bulbosa as well as the length of bulbs are uniform, for which such differences have rarely been described in trypanorhynchs (see Schaeffner & Beveridge 2013a), but a variation is seen in the width of the bulbs, which depends on the state of contraction during fixation. This situation can also be considered for the length of the tentacles, however, by re-measuring this character from figure 7 drawn by Reimer (1980), this value is 335 at maximum size and is very close to the lower bound of the range measured (350-400) by Yamaguti (1952). None of the taxonomic works carried out on *N. jayapaulazariahi* mentioned the number of the hook rows along the tentacle. However, about 30 rows can be counted at least from figure 7 of Reimer (1980), which is close to the number of the hook rows counted for the Malaysian Bornean and South Australian specimens of *N. sphyrnae*. Although Yamaguti (1952) described 12 hook rows along the tentacle for the types, from figure 83 drawn by him, at least 24 rows can be counted. By examining the type specimens, we could count 32 rows of hooks. According to these findings we consider *N. jayapaulazariahi*, the descriptions of which were based on the larval forms, a new synonym for *N. sphyrnae*.

Nybelinia aequidentata (Shipley & Hornell, 1906) Dollfus, 1930 (Fig. 4A, B)

Tetrarhynchus equidentatus Shipley & Hornell, 1906: 83.

Nybelinia aequidentata – Dollfus 1930: 210.

Material examined. — **Malaysia** • 5 specimens; from *Rhinoptera jayakari* Boulenger (BO-83) (Myliobatiformes: Rhinopteridae); Malaysian Borneo, off Sabah, Semporna fish market; 04°28’44.09”N, 118°37’00.57”E; LRP 4375-4378, 11002 • 1 specimen; same data; ZMB E. 7713 • 1 specimen; from *Maculabatis pastinacoides* (Bleeker) (BO-76) (Myliobatiformes: Dasyatidae); Malaysian Borneo, off Sabah, Kampung Tetabuan; 06°01’10.32”N, 117°42’14.76”E; ZMB E. 7712.

Measurements

Long worms, 7850-11 776 (10 154, N = 4) long. Scolex 2411-3271 (2867, N = 5) long; scolex width 841-1121 (979, N = 4, n = 11) at level of pars bothrialis, 518-1147 (816, N = 5, n = 1) at level of pars vaginalis, 744-1128 (947, N = 5, n = 10) at level of pars bulbosa. Bothria 1287-1415 (1358, N = 3, n = 5) long. Pars bothrialis 1342-1433 (1391, N = 5) long; pars vaginalis 854-1464 (1174, N = 5) long; tentacle sheaths 75-121 (92, N = 5, n = 13) in diameter. Pars bulbosa 884-1013 (947, N = 5) long; bulbs 793-982 (900, N = 5, n = 10) long, 183-232 (202, N = 4, n = 8) wide, bulb width : length ratio 1.0 : 3.7-5.4 (4.5, N = 4, n = 8); pars post-bulbosa present, 42-67 (54, N = 5) long. Velum very lobate in its posterior margin (Fig. 4A), 43-537 (400, N = 5, n = 11) long. Scolex ratio (pars bulbosa : pars bothrialis : pars vaginalis) 1.0 : 1.4-1.6 : 1.0-1.5 (1.0 : 1.5 : 1.2, N = 5).

Tentacles 1726-2025 (1871, N = 3, n = 3) long with 37-43 (39, N = 2, n = 4) rows of hooks; tentacle width 51-97 (76, N = 5, n = 7) at level of basal region and 69-97 (80, N = 5, n = 8) at level of metabasal region. Metabasal armature homeoacanthous, homeomorphous (Fig. 4B); characteristic basal armature absent. Basal hooks 8-21 (15, N = 5, n = 10) long, base 5-12 (9, N = 5, n = 10) long. Metabasal hooks 30-43 (36, N = 5, n = 19) long, base 10-18 (14, N = 5, n = 19) long. Number of hooks per half spiral row in basal and metabasal region of tentacle 7 (N = 3, n = 5).

Anterior-most immature proglottid 12-18 (15, N = 4, n = 4) long, 640-1006 (809, N = 4, n = 4) wide; posterior-most proglottid 165-317 (239, N = 4, n = 4) long, 598-769 (683, N = 4, n = 4) wide.

Remarks

Historically, Shipley & Hornell (1906) described this species as *Tetrarhynchus equidentatus* Shipley & Hornell, 1906 from *Brevitrygon walga* (Müller & Henle) (therein referred as *Himantura walga*) off Sri Lanka. After Pintner (1927) redescribed the type, it was transferred to *Nybelinia* by Dollfus (1930). Wenchuan *et al.* (1995) reported *N. aequidentata* from *Hemitrygon akajei* (Müller & Henle) (therein referred as *Dasyatis akajei*) from the Taiwan Strait (see also Wenchuan 2007). Palm (1999) redescribed a plerocercoid of this species from *Lepturacanthus savala* (Cuvier), off Sagar Island, Bay of

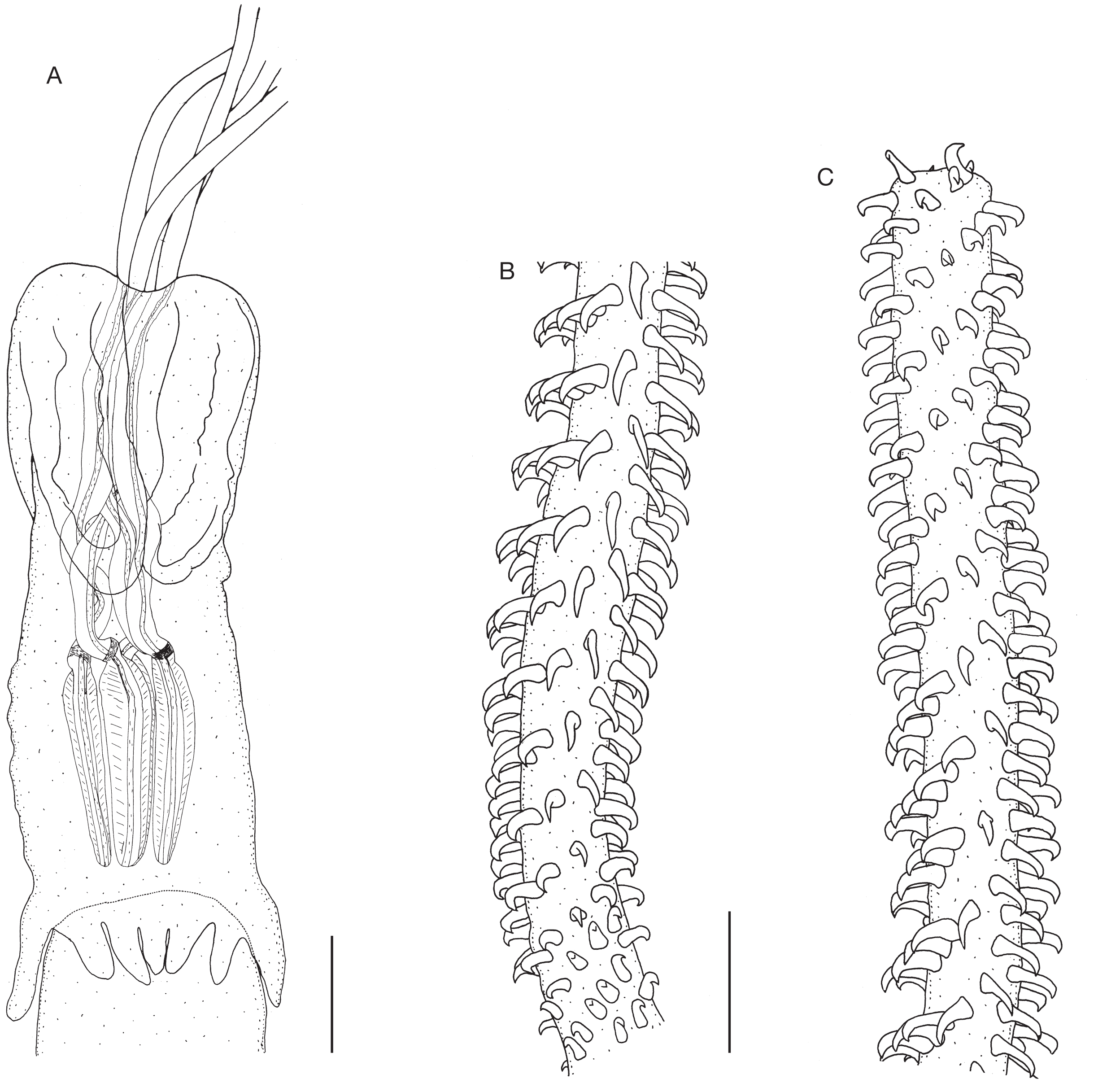

Fig. 4. — *Nybelinia aequidentata*: **A**, scolex with lobate velum; **B**, basal (left illustration) towards metabasal armature of a tentacle cut in two parts, bothrial surface. Scale bars: A, 500 µm; B, 100 µm.

Bengal. Palm & Beveridge (2002) presented measurements of a postlarva as *N. aequidentata* isolated from *Dendrochirus zebra* (Cuvier) off New Caledonia (see also Beveridge *et al.* 2014). Nonetheless, Palm (2004) stated that the specimens identified and described as *N. aequidentata* by Palm & Beveridge (2002) were synonymous with *N. syngenes* (Pintner, 1928) Dollfus, 1930, based on the hook sizes and the length of the bulbs. In the present study, five specimens were collected from *Rhinoptera jayakari* (BO-83) off Malaysian Borneo. *Rhinoptera jayakari* is a new host record for *N. aequidentata* and a new locality record is also established for this parasite off Malaysian Borneo. Although the examined material was strobilate, the internal organs were invisible and we missed the opportunity to describe the proglottid anatomy of this species.

Nybelinia aequidentata most closely resembles *N. syngenes*, both of which are characterized by a large scolex size, the large metabasal falcate hooks decreasing in size towards the apical and basal regions of tentacle, and the overlapping measurements of the scolex. Despite the fact that *N. aequidentata* is distinguished from *N. syngenes* by its acraspedote, rather than craspedote, proglottids, identifying the plerocercoids of these two species is very difficult solely relying on scolex morphology and hook shape. Palm & Bray (2014: 299, plate III) provided a photograph of the scolex of the type of *N. aequidentata*, in which the velum is very lobate in its posterior margin, a character obviously overlooked in earlier treatments of this taxon. The velum in all our specimens off Malaysian Borneo was also very lobate (Fig. 4A). Therefore, the lobate velum and the acraspedote proglottids are the two main characters distinguishing *N. aequidentata* from *N. syngenes*. It is of note that the lobate velum was only described in the adults and that it cannot be clarified so far if it is also characteristic for larvae. Nonetheless, the scolex morphology of trypanorhynchs is usually the same in transition from the larval to the adult stage (see Palm 2004) and hence we herein reidentify the postlarval specimen identified by Palm (1999) as *N. aequidentata*, lacking the lobate velum, with *N. syngenes*.

Given that the type material of *N. syngenes* is not known, there is no information on the number of hook rows along its tentacle and from this point of view, it is currently not possible to distinguish *N. aequidentata* (37-43 hook rows along the tentacle in our specimens from Malaysian Borneo) from *N. syngenes*.

Unidentified material

The following material was examined but was unable to be assigned to a species of *Nybelinia*: 2 specimens (ZMB E. 7714, 7715) from *Chiloscyllium punctatum* Müller & Henle (BO-282) (Orectolobiformes: Hemiscylliidae) off Mukah, Sarawak, Malaysian Borneo (02°53'52.16"N, 112°05'44.12"E); 1 specimen (LRP 11003) from *Carcharhinus sealei* (Pietschmann) (BO-55) (Carcharhiniformes: Carcharhinidae) off Mukah, Sarawak, Malaysian Borneo (02°53'52.16"N, 112°05'44.12"E); 1 specimen (LRP 11004) from *Carcharhinus sorrah* (Müller & Henle) (BO-70) off Mukah, Sarawak, Malaysian Borneo (02°53'52.16"N, 112°05'44.12"E).

Genus *Heteronybelinia* Palm, 1999

Heteronybelinia estigmena (Dollfus, 1960) Palm, 2004

Nybelinia estigmena Dollfus, 1960: 831.

Heteronybelinia estigmena – Palm 2004: 151.

Material examined. — **Malaysia** • 7 specimens; from *Carcharhinus* cf. *leucas* (Müller & Henle) (BO-75, 97, 101) (Carcharhiniformes: Carcharhinidae); Malaysian Borneo, off Sabah, ; 06°01'10.32"N, 117°42'14.76"E; LRP 10976-10982 • 2 specimens; same data; ZMB E. 7717, 7718 • 4 specimens; from *Carcharhinus* cf. *limbatus* (Müller & Henle) (BO-54, 58); Malaysian Borneo, off Mukah, Sarawak; 02°53'52.16"N, 112°05'44.12"E ; LRP 4372-4374, 10975 • 1 specimen; same data; ZMB E. 7716.

Measurements

Long worms, 25 140-40 654 (30 112, N = 5) long with 188-206 (197, N = 2) proglottids. Scolex 787-1324 (1097, N = 5) long; scolex width 305-720 (585, N = 11, n = 11) at level of pars bothrialis, 348-549 (478, N = 11, n = 1) at level of pars vaginalis, 305-518 (423, N = 11, n = 11) at level of pars bulbosa. Bothria 396-567 (469, N = 11, n = 13) long. Pars bothrialis 384-622 (494, N = 11) long; pars vaginalis 342-518 (424, N = 11) long; tentacle sheaths 33-48 (43, N = 11, n = 11) in diameter. Pars bulbosa 348-451 (398, N = 11) long; bulbs 308-417 (350, N = 11, n = 27) long, 85-121 (103, N = 11, n = 27) wide, bulb width : length ratio 1.0 : 2.9-4.3 (3.4, N = 11, n = 27); pars post-bulbosa present, 24-159 (72, N = 11) long. Velum 165-305 (218, N = 11, n = 11) long. Scolex ratio (pars bulbosa : pars bothrialis : pars vaginalis) 1.0 : 0.9-1.5 : 0.8-1.3 (1.0 : 1.2 : 1.1, N = 11).

Tentacles 528-690 (595, N = 11, n = 14) long with 31-36 (33, N = 5, n = 5) rows of hooks; tentacle width 27-39 (33, N = 11, n = 11) at level of basal region and 27-36 (32, N = 11, n = 11) at level of metabasal region. Metabasal armature homeoacanthous, heteromorphous; characteristic basal armature absent. Basal uncinate hooks on bothrial tentacle surface 8-10 (9, N = 5, n = 5) long, base 10-12 (11, N = 5, n = 5) long; basal uncinate hooks on antibothrial tentacle surface 5-6 (6, N = 5, n = 5) long, base 7-8 (7, N = 5, n = 5) long; metabasal uncinate hooks on bothrial tentacle surface 14-15 (15, N = 5, n = 5) long, base 13-14 (14, N = 5, n = 5) long; metabasal uncinate hooks on antibothrial tentacle surface 10-12 (11, N = 5, n = 5) long, base 9-10 (9, N = 5, n = 5) long. Number of hooks per half spiral row in basal and metabasal region of tentacle 5-6 (N = 3, n = 5).

Mature proglottids 66-78 (72, N = 2) in number, 152-518 (387, N = 8, n = 8) long, with maximum width of 281-793 (462, N = 8, n = 8). Cirrus sac 45-66 (52, N = 9, n = 9) long, 172-302 (236, N = 9, n = 9) wide; cirrus sac length : width ratio 1.0 : 3.3-6.0 (4.6, N = 9, n = 9). Testes 21-67 (39, N = 11, n = 14) long, 16-43 (27, N = 11, n = 14) wide; testis number around 80 per proglottids (N = 1), 3-9 (6, N = 10, n = 10) testes anterior to cirrus sac. Ovary 120-135 (127, N = 2, n = 2) long, 52-75 (64, N = 2, n = 2) wide. Vitelline follicles 12-52 (25, N = 11, n = 11) long, 9-18 (13, N = 11, n = 11) wide.

Remarks

Schaeffner & Beveridge (2014) reported *H. estigmena* from *C. limbatus* (BO-54, 58) off Malaysian Borneo. *Heteronybelinia estigmena* is a well described and a cosmopolitan tentaculariid species (see Palm 2004). The scolex measurements of the Malaysian Bornean specimens fall within the range of the measurements given by Palm (1999) and Palm & Beveridge (2002). This case is also seen for the measurements of the strobila.

Genus *Tentacularia* Bosc, 1797

Tentacularia coryphaenae Bosc, 1797

Tentacularia coryphaenae Bosc, 1797: 9.

Material examined. — **Malaysia** • 2 specimens; from *Carcharhinus falciformis* (Müller & Henle, 1839); BO-132, 133; (Carcharhiniformes: Carcharhinidae); Malaysian Borneo, off Sabah; 04°14'44.02"N, 118°37'53.32"E; LRP 11009, 11010.

Remarks

Tentacularia coryphaenae is well described and a cosmopolitan tentaculariid species (see Palm 2004). Schaeffner & Beveridge (2014) reported *T. coryphaenae* from *Carcharhinus falciformis* (BO-133) from Malaysian Borneo. Another shark specimen of *C. falciformis* (BO-132) was also infected with *T. coryphaenae*.

Genus *Kotorella* Euzet & Radujkovic, 1989

Kotorella pronosoma (Stossich, 1900) Euzet & Radujkovic, 1989

Rhynchobothrium pronosomum Stossich, 1900: 100.

Kotorella pronosoma – Euzet & Radujkovic 1989: 421.

Material examined. — **Malaysia** • 4 specimens; *Pastinachus solocirostris* Last, Manjaji & Yearsley (BO-164, 256) (Myliobatiformes: Dasyatidae); Malaysian Borneo, off Mukah; Sarawak; 02°53'52.16"N, 112°05'44.12"E; ZMB E. 7741 • 1 specimen; same data; LRP 10991 • 3 specimens; same data; Sematan, Sarawak; 01°48'15.45"N, 109°46'47.17"E; LRP 10988-10990 • 1 specimen, from *Pateobatis uarnacoides* (Bleeker) (BO-118, 261) (Myliobatiformes: Dasyatidae); Malaysian Borneo, off Sabah; 06°01'10.32"N, 117°42'14.76"E; LRP 10987 • 1 specimen; same data; Mukah, Sarawak; 02°53'52.16"N, 112°05'44.12"E; ZMB E. 7742 • 1 specimen; same data; 10992 1 specimen; from *Maculabatis gerrardi* (Gray) (BO-49) (Myliobatiformes: Dasyatidae); Malaysian Borneo, off Mukah, Sarawak; 02°53'52.16"N, 112°05'44.12"E; LRP 10986 • 2 specimens; from *Himantura tutul* Borsa, Durand, Shen, Alyza, Solihin & Berrebi (BO-47) (Myliobatiformes: Dasyatidae); Malaysian Borneo, off Mukah, Sarawak; 02°53'52.16"N, 112°05'44.12"E; LRP 10985 • 3 specimens; same data; ZMB E. 7743.

Remarks

Kotorella pronosoma is a well described and cosmopolitan tentaculariid species (see Palm 2004). The material examined herein is that identified by Schaeffner & Beveridge (2014). The hosts of *K. pronosoma* presented by Schaeffner & Beveridge (2014) and also registered in the Global Cestode Database were *Himantura tutul* (therein referred as *Himantura uarnak* 3) (BO-47), *Maculabatis gerrardi* (therein referred as *Himantura gerrardi*) (BO-23, 49, 88), *Maculabatis macrura* (Bleeker) (therein referred as *H. gerrardi* 1) (BO-92, 93, 337, 400), *Neotrygon orientalis* Last, White & Serét (therein referred as *Neotrygon kuhlii* (Müller & Henle) (BO-321, 322, 360, 368), *Pastinachus solocirostris* (BO-164, 165, 177, 256, 267, 464), *Pateobatis uarnacoides* (therein referred as *Himantura uarnacoides*) (Bo-8, 77, 78, 91, 96, 117, 118, 149, 167, 258, 261, 489), and *Taeniura lymma* 1 (Bo-81, 84, 86, 87, 122, 125, 131). It is of note that BO-360 and BO-368 were absent in the Global Cestode Database and BO-489 is a code for *Pastinachus solocirostris* and not *Pateobatis uarnacoides*.

Genus *Kotorelliella* Palm & Beveridge, 2002

Kotorelliella jonesi Palm & Beveridge, 2002

Kotorelliella jonesi Palm & Beveridge, 2002: 74.

Material examined. — **Malaysia** • 7 specimens; from *Neotrygon orientalis* Last, White & Serét (BO-366, 368) (Myliobatiformes: Dasyatidae); Malaysian Borneo; LRP 10997-11001 • 1 specimen; same data; ZMB E. 7740 • 3 specimens; from *Neotrygon orientalis* (BO-27); Malaysian Borneo; off Sematan, Sarawak; 01°48'15.45"N, 109°46'47.17"E; LRP 10993-1099 • 1 specimen; same data; ZMB E. 7738 • 1 specimen, LRP 10996 from *Pateobatis* cf. *jenkinsii* (Annandale) (BO-339) (Myliobatiformes: Dasyatidae); Malaysian Borneo, off Sarawak; 02°30'07.34"N, 110°40'16.82"E • 1 specimen; same data; ZMB E. 7739 • 1 specimen, from *Maculabatis macrura* (BO-93, 337) (Myliobatiformes: Dasyatidae); Malaysian Borneo, off Sarawak; 02°30'07.34"N, 110°40'16.82"E • 1 specimen; same data; Sabah, off Kudat; 06°48'60.00"N, 116°53'54.00"E; ZMB E. 7736, 7737.

Measurement

Long worms, 17 625-21 000 (19 312, N =) long with 46-69 (60, N = 3) proglottids. Scolex 1320-1666 (1446, N =) long; scolex width 330-427 (373, N = 3, n = 3) at level of pars bothrialis, 241-330 (274, N = 3, n =) at level of pars vaginalis, 322-402 (330, N = 3, n = 3) at level of pars bulbosa. Pars bothrialis 515-668 (604, N = 3) long; pars vaginalis 724-1046 (869, N = 3) long. Pars bulbosa 266-322 (290, N = 3) long; bulbs 240-304 (265, N = 3, n = 12) long, 84-108 (96, N = 3, n = 12) wide, bulb width : length ratio 1.0 : 2.3-3.6 (2.8, N = 3, n = 12). Velum 250-314 (287, N = 3, n = 3) long. Scolex ratio (pars bulbosa : pars bothrialis : pars vaginalis) 1.0 : 1.8-2.4 : 2.7-3.2 (1.0 : 2.1 : 2.9, N = 3).

Metabasal armature homeoacanthous, heteromorphous. Metabasal armature with uncinate hooks on bothrial surface, 14-16 (15, N = , n = 10) long, base 8-10 (9, N = 2, n = 10) long; antibothrial hooks of metabasal armature falcate, 14-15 (14, N = 2, n = 5) long, base 4-5 (4, N = 1, n = 5) long. Basal hooks heteroacanthous atypical. Bothrial hooks of basal armature 8-10 (9, N = 1, n = 5) long, base 6-8 (7, N = 1, n = 5) long; antibothrial hooks of basal armature 4-8 (6, N = 1, n = 5) long, base 1-2 (1, N = 1, n = 5) long.

Mature proglottids wider than long, 175-275 (224, N = 1, n = 5) long, 650-700 (680, N = 1, n = 5) wide; fully gravid proglottids longer than wide, 750-1150 (920, N = 1, n = 5) long, 400-625 (510, N = 1, n = 5) wide, size increasing towards end of strobila. Testes 52-60 (57, N = 1, n = 10) in diameter, 35-50 (42, N = 1, n = 10) in number. Vitelline follicles 20-24 (22, N = 1, n = 5) in diameter.

Remarks

Palm & Beveridge (2002) erected the monotypic genus *Kotorelliella* to accommodate *Ko. jonesi* by describing a single plerocercoid from *Taeniura lymma* (Forsskål) off Heron Island, Queensland, Australia. Although the specimens of Malaysian Borneo were adult, because of the poor condition of the strobilae, the internal anatomy of the proglottids could not be easily seen and hence there was no opportunity to describe the proglottids.

Schaeffner & Beveridge (2014) reported *Ko. jonesi* from *Pateobatis jenkinsii* (therein referred as *Himantura jenkinsii*) (BO-335) and *Pateobatis* cf. *jenkinsii* (therein referred as *Himantura jenkinsii*) (BO-339) from Malaysian Borneo. The host specimens coded as BO-366 and BO-368 have been identified morphologically as *Neotrygon kuhlii* but not registered in the Global Cestode Database. BO-27 is a code for *Ne. orientalis* in the Global Cestode Database. The only species of *Neotrygon* known from Borneo is *Ne. orientalis*. *Neotrygon kuhlii* is now known only from the region of the Solomon Island (Last *et al.* 2016b). The record cited from Schaeffner & Beveridge (2014) predates the revision of the host species by Last *et al.* (2016b), but all of the records from Borneo are now referable to *Ne. orientalis*, not to *Ne. kuhlii*. Therefore, a new host record, *Ne. orientalis*, is established for *Ko. jonesi*.

Compared to the holotype of *Ko. jonesi*, which is a plerocercoid, the adult specimens of the present study have a smaller scolex size (1320-1666 vs 1910). Other scolex features are also smaller. Such a situation was also reported for other trypanorhynchs, e.g. *Progrillotia dasyatidis* Beveridge, Neifar & Euzet, 2004 (see Beveridge *et al.* 2004; Marques *et al.* 2005). This may relate to the size and the physiological condition of the intermediate host, from which it is transmitted by predation into its definitive hosts.

DISCUSSION

With the description of *Nybelinia pseudafricana* n. sp. and the synonymy of *N. jayapaulazariahi* with *N. sphyrnae*, 31 species are considered valid in the genus *Nybelinia* (see Palm 2004; Palm & Bray 2014; Beveridge *et al.* 2017a; Palm *et al.* 2019; present study). Together with *Heteronybelinia* (15 species), *Mixonybelinia* (6), *Reimeriella* (2) and the monotypic genera, *Tentacularia* (1), *Kotorella* (1), *Kotorelliella* (1), and *Homeokotorella* n. gen. (1), the Tentaculariidae family comprises 58 different species and belongs to the most speciose trypanorhynch families.

The description of the new genus *Homeokotorella* n. gen. brings the number of valid tentaculariid genera with a slender elongate scolex and long bothria with free lateral margins and short bulbs to three. *Homeokotorella* n. gen., *Kotorella*, and *Kotorelliella* can be distinguished by having a homeomorphous basal and metabasal armature (*Homeokotorella* n. gen.), a heteromorphous basal and metabasal armature (*Kotorella*) and a heteromorphous basal and homeomorphous metabasal armature (*Kotorelliella*). This diversity is similar to the tentaculariids with a robust, muscular scolex with more triangular bothridia without free margins. A homeomorphous basal and metabasal armature is characteristic for *Nybelinia*, a heteromorphous basal and metabasal armature for *Heteronybelinia*, a homeomorphous basal and heteromorphous metabasal armature for *Mixonybelinia* and a heteromorphous basal and homeomorphous metabasal armature for the most recently described *Reimeriella* (Palm 2004; Palm *et al.* 2020). It is most likely that species with a homeomorphous basal and heteromorphous metabasal armature also occur in the "*Kotorella*-like" tentaculariids and might be described in future. This illustrates the dependency of the taxonomy within the Tentaculariidae on the characteristic kind of armature and requires a more detailed examination of the diversity of armature patterns known to date.

Beside the recognised four different principal armature patterns, other characteristics such as the number of hooks per half spiral row (see Palm 2004), the length of the tentacles in terms of number of hook rows along the tentacles (e.g. Palm *et al.* 2020) and differences in size and/or shape of the hooks along the basal, metabasal, and apical part of the tentacles are of taxonomic importance. For *Homeokotorella* n. gen. and the species of *Nybelinia* presented here, we used the word 'homeomorphous' in the descriptions of the hooks in the tentacular armature, in spite of the difference in the size of the hooks with the same shape along the tentacle (*Homeokotorella* n. gen.) and the presence of a distinctive basal armature (*N. pseudafricana* n. sp.). In *Homeokotorella anterioporus* n. gen., n. sp., all the tentacular hooks are falcate but first four to five rows of the basal hooks increase in size anteriorly. This issue is also seen in *N. aequidentata*, in which the basal hooks are smaller than the metabasal hooks but all hooks are the same in shape. In *N. pseudafricana* n. sp., the metabasal armature with the slender falcate hooks differs distinctly from the basal armature with the uncinate hooks. To prevent chaos in using the word 'homeomorphous' in taxonomic descriptions, we suggest that within the tentaculariids, the armature patterns must be explained more clearly in order to better describe species diversity and distinguish among the species. Since the shape of hooks is determined by the proportion of blade and base, the armature is heteromorphous where this proportion changes on opposite tentacular surfaces in some hook rows, and it is homeomorphous where the size is similar or changes but the hook proportions remain the same. Since the word 'homeomorphous', used frequently in trypanorhynchs, means conceptually the sameness in shape, and not in size, it must be clarified especially in homeoacanth or heteroacanth typical armature types, when hooks of all rows in the metabasal or basal armature have the same shape and/or the same size along each row of hooks. In many *Nybelinia* species, the metabasal hooks do not change in shape along the tentacle from the metabasal to the distal region, and the basal hooks are smaller but can still be recognised as similar in shape to the other hooks along the tentacle. This is the usual use of the homeoacanthous, homeomorphous armature in the generic diagnosis of the speciose genus *Nybelinia* (see Palm 2004). However, *Nybelinia lingualis* (Cuvier, 1817) Dollfus, 1929, as the type species, has homeoacanthous hooks that are homeomorphous around the tentacle but differ between the basal, metabasal and apical part. Also, in *N. thyrsites* Korotaeva, 1971, *N. balinensis* Palm, Palm & Haseli, 2019, and *N. mobulicola* Palm, Palm & Haseli, 2019, the shape of the hooks in the metabasal armature is different compared to those in the basal and distal tentacle region. Likewise, some *Nybelinia* species have clearly distinct basal hooks (characteristic basal armature), such as *N. basimegacantha* Carvajal, Campbell & Cornford, 1976 with enlarged rosethorn-shaped hooks and *N. anguillicola* Yamaguti, 1952 with rows of small uncinate hooks followed by 2-3 rows of billhooks.

We herewith complete the description of tentaculariids from Malaysian Borneo, a region with a recorded high species diversity of marine organisms. The Coral Triangle is an area of the tropical marine waters with a rich biodiversity (Allen 2007), including elasmobranchs as final hosts for trypanorhynchs, where southern Indonesian waters together with Malaysian Borneo waters are within this recognised zone. Of the 335 valid trypanorhynch species known to date (Haseli & Malekpour Fard 2017; Beveridge *et al.* 2017a; Schaeffner 2018; Beveridge & Schaeffner 2018; Schaeffner & Marques 2018; Shafiei & Haseli 2019; Palm *et al.* 2019, 2020; Beveridge *et al.* 2021; Haseli *et al.* 2021; Oosthuizen *et al.* 2021; Herzog & Jensen 2022; present study), a total of 86 different species (26%) have been recorded until now from Indonesia, and of the 58 tentaculariid species, 21 species (36%) occur in Indonesian waters (Palm 2004; Palm *et al.* 2009, 2019, 2020; Schaeffner *et al.* 2011; Schaeffner & Beveridge 2012a, b, c, 2013a, b, c, 2014; present study). Since most of the trypanorhynch species reported so far off Borneo (see Schaeffner & Beveridge 2014; Palm *et al.* 2020; present study) have also been recorded from Indonesia other than its Bornean part, it seems that the trypanorhynch fauna of Borneo resembles the one from Indonesian waters, since both areas are within the Coral Triangle.

The Coral Triangle lies within a broader ecological zone, the Indo-West Pacific, stretching from the west Pacific to the Persian Gulf, and hence it can have impact on the trypanorhynch fauna of its neighbouring areas. This issue is partly explained by the number of the species in each tentaculariid genus known from the Coral Triangle (CT), the west Pacific outside of the Coral Triangle (wP), and the Indian Ocean outside of the Coral Triangle (I) with its most north-western part, the Persian Gulf (Palm 2004; Wenchuan 2007; Palm *et al.* 2009, 2019, 2020; Justine *et al.* 2010, 2012; Olson *et al.* 2010; Haseli *et al.* 2011; Schaeffner & Beveridge 2014; Beveridge *et al.* 2014, 2017b; Biserova *et al.* 2016; Jun *et al.* 2018; Zhokhov *et al.* 2020; Kleinertz *et al.* 2022). Regarding *Nybelinia*, 20 species occur in the Indo-West Pacific, of which 10 species were reported from the Coral Triangle (3 CT, 3 CT+wP, 4 CT+wP+I, 9 wP, 1 I). Of the five species distributed in the Indian Ocean, four species also occur in the Coral Triangle, one of which was reported from the Persian Gulf. This issue shows the impact of the Coral Triangle on the *Nybelinia* fauna of the Indian Ocean. It seems that this impact is less on the fauna of the west Pacific, since of the 16 species of *Nybelinia* occurring in the west Pacific, only seven species are also known from the Coral Triangle. Regarding *Heteronybelinia*, nine species occur in the Indo-West Pacific, of which seven species are also known from the Coral Triangle (3 CT+wP, 3 CT+I, 1 CT+wP+I, 1 Wp, 1 wP+I). It seems that the fauna of *Heteronybelinia* in the Coral Triangle has a significant impact on the fauna of both the Indian Ocean and the west Pacific, because, of the five species occurring in the Indian Ocean, four species were also reported from the Coral Triangle and of the six species occurring in the west Pacific, four species were also known from the Coral Triangle. Regarding *Mixonybelinia*, the two out of four species distributed in the Indo-west Pacific also occur in the Coral Triangle (1 CT+wP, 1 CT+wP+I, 1 wP, 1wP+I). The occurrence of one species of *Heteronybelinia* as well as *Mixonybelinia* in both the Indian Ocean and the west Pacific and their absence in the Coral Triangle may indicate the lack of enough sampling effort. In contrast to the speciose tentaculariid genera, *Kotorella* and *Tentacularia* are distributed from the west Pacific to the Persian Gulf, *Reimeriella varioacantha* Palm, Morales-Ávila, Galván-Magaña & Haseli, 2020 and *Homeokotorella* n. gen. occur only in the Coral Triangle, and *Kotorella Jonesi* is distributed in the Coral Triangle and the west Pacific. Accordingly, the comprehensive studies on the trypanorhynch fauna of the Persian Gulf and the Gulf of Oman (Haseli *et al.* 2010, 2011; Haseli 2013) also reveal the profound impact of the trypanorhynch fauna of the Coral Triangle on the western Indian Ocean, especially in the Persian Gulf with a low diversity of tentaculariids. This demonstrates the importance of Indonesian waters including the Coral Triangle for the generally high trypanorhynch species diversity observed and its global distribution. Therefore, in general, it seems that the tentaculariid fauna of the Coral Triangle has more impact on the fauna of the Indian Ocean than on that of the west Pacific.

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