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NYBELINIA POCHE, 1926 (CESTODA: TRYPANORHYNCHA) FROM THE MOÇAMBIQUE COAST, WITH DESCRIPTION OF *N. BEVERIDGEI* SP. NOV. AND SYSTEMATIC CONSIDERATION OF THE GENUS

H. W. PALM, T. WALTER*, G. SCHWERDTFEGER* and L. W. REIMER†*

A total of 247 specimens from 16 fish and one cephalopod species from the coastal waters of Moçambique was investigated for infestation with trypanorhynch cestodes. Postlarvae of six different *Nybelinia* species could be identified: *N. africana*, *N. anthicosum*, *N. beveridgei* sp. nov., *N. gopalai, N. robusta*, and *N. yamagutii*. All represent new locality records. In all, 27 new host records were established. *N. yamagutii* and *N. africana* were the most abundant parasites, infesting seven and six of the examined fish and cephalopod species respectively. The squid *Todarodes angolensis* and the teleost *Ventrifossa nasuta* had the highest prevalence of infestation (79 and 75 % respectively). Whereas the teleost *Saurida undosquamis* was infested with four different *Nybelinia* species, most hosts harboured a single species only. To date, a total of 47 different *Nybelinia* species are known. Of these, 43 are considered to be adequately described. *N. beveridgei* sp. nov. can be distinguished by its large scolex and its homeoacanthous heteromorphous tentacular armature and its characteristic basal armature. For further taxonomic work and to simplify *Nybelinia* identification, a new subdivision of the species is proposed, based on the following 3 characters: metabasal tentacular armature; tentacles with or without a characteristic basal armature; and size of basal hooks in comparison to metabasal hooks. A cladistic analysis revealed no further insights into the phylogeny of the genus.

Trypanorhynch cestodes are characterized by a tentacular apparatus with four eversible armed tentacles and two or four bothridia. In their life cycles, they use small crustaceans as first intermediate hosts and teleosts or other invertebrates such as cephalopods as second intermediate hosts. The occurrence of these cestodes in the flesh of commercially exploited species may reduce their market value (Mehl 1970, Seyda 1976, Deardorff *et al*. 1984). Although they have been found to infest humans only accidentally and causing no serious danger to human health, their presence in the musculature offends potential consumers (Fripp and Mason 1983, Bates 1990).

Investigations of the trypanorhynch fauna from the Indian Ocean along the South-East African coast are scarce. From the coastal waters off South Africa, Linton (1924) reported six trypanorhynchs, *Floriceps saccatus*, *Grillotia erinaceus*, *Hepatoxylon trichiuri*, *Poecilancistrum caryophyllum*, *Tentacularia coryphaenae*, and *Rhynchobothrium* sp.. Later, Botha (1986) and Payne (1986) reported the species *H. trichiuri*, and Botha (1986) reported *Grillotia heptanchi* and *Tetrarhynchus* sp.. Schramm (1989, 1991) found *Grillotia perelica* and *P. caryophyllum* in different mugilids from Transkei (South Africa). From the coastal area off Moçambique, only two investigations have been published. Reimer (1984) found the trypanorhynchs *Parachristianella* sp. and *Prochristianella* sp. in penaeid shrimps and *Callitetrarhynchus gracilis*, *Christianella* sp., *Dasyrhynchus pillersi, Otobothrium crenacolle*, *Parachristianella* sp. and *Pseudogrillotia* sp. from different benthic fish species. Additionally, that author found 11 of 22 fish species examined infested with *Nybelinia* spp., which he did not further identify. Reimer (1989) reported *Parachristianella* sp. and *Prochristianella* sp. in penaeid shrimps and *Nybelinia* sp. in the squid *Todarodes sagittatus angolensis*.

The classification of trypanorhynch cestodes is still considered to be chaotic and confusing (Palm 1997a). Within the genus *Nybelinia*, Schmidt (1986) listed 39 and Beveridge and Campbell (1996) reported 43 species, indicating that this genus includes more species than any other. Additionally, many species descriptions are inadequate. However, the last revision of the genus *Nybelinia* is that by Dollfus (1942), who later described 16 additional species (Dollfus 1960) and arranged them in five different sections on the basis of the following four characters: different kind of hook on bothridial and antibothridial tentacle surfaces; presence of a characteristic basal armature; width of tentacle; and bulb ratio. Since then, though several new species have been de-

* Marine Pathology Group, Department of Fisheries Biology, Institut für Meereskunde an der Universität Kiel, Düsternbrooker Weg 20, D-24105 Kiel, Germany. E-mail: hpalm@ifm.uni-kiel.de
† Am Bahnhof Minden Stadt 4, D-32423 Minden, Germany

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Table I: Fish and cephalopod species examined

Family/species	number examined	Date	Position	Depth (m)
Ommastrephidae				
Todarodes angolensis	33	06 Nov. 1988	21°26´S, 35°41´E	570
		07 Nov. 1988	22°06´S, 35°45´E	520
		08 Nov. 1988	23°09´S, 35°49´E	325
Rajidae				
Raja leopardus	1	13 Jun. 1980	23°19´S, 35°48´E	310
Bothidae				
Chascanopsetta lugubris	11(7*)	19 Jan. 1982	22°21´S, 35°51´E	630
Chaunacidae				
Chaunax pictus	16	01 Feb. 1982	25°50´S, 34°27´E	420
Congridae				
Bassanago albescens	13(11*)	12 Jun. 1980	22°59´S, 35°41´E	200
Gonorhynchidae				
Gonorhynchus gonorchynchus	13	18 Jan. 1982	22°08´S, 35°52´E	760
Lophiidae				
Lophiodes mutilus	8	04 Aug. 1980	20°07´S, 35°54´E	300
Macrouridae				
Coelorinchus braueri	13(13*)	18 Jan. 1982	22°07´S, 35°54´E	750
		10 Feb. 1982	26°01´S, 34°15´E	610
C. flabellispinus	21(16*)	13 Jan. 1982	22°03´S, 35°47´E	545
Ventrifossa nasuta	4	24 Jan. 1982	23°47´S, 35°53´E	750
Paralepididae				
Lestrolepis intermedia	9	27 Oct. 1988	25°29´S, 35°03´E	425
Arctozenus rissoi	6	14 Jun. 1980	23°43´S, 35°51´E	610
Peristediidae				
Peristedion adeni	11(7*)	11 Jan. 1982	24°52´S, 35°27´E	440
Polymixiidae				
Polymixia nobilis	5(5*)	18 Jan. 1982	22°05´S, 35°45´E	530
Sternoptychidae				
Polyipnus polli	55	13 Jan. 1982	21°44´S, 35°36´E	500
		14 Jan. 1982	21°05´S, 35°45´E	520
		16 Jan. 1982	21°38´S, 35°44´E	650
Synodontidae				
Saurida undosquamis	25(11*)	15 Jan. 1982	21°25´S, 35°38´E	425
		29 Oct. 1988	24°38´S, 35°32´E	420
		30 Oct. 1988	24°15´S, 35°40´E	450
Trichiuridae				
Benthodesmus elongatus	3	22 Jan. 1982	23°05´S, 35°58´E	750

* In Reimer (1984)

scribed, the usefulness of these characters to subdivide different species within the genus *Nybelinia* has not been examined.

The aim of this communication is to present further data on the occurrence of *Nybelinia* species from the south-east African coast off Moçambique. Additionally, most of the *Nybelinia* specimens found by Reimer (1984, 1989) were identified. The present study provides further information on the species composition of a typical subtropical locality in comparison to other recent investigations in the tropical Atlantic Ocean (Palm *et al*. 1994, Palm 1997b). Furthermore, the descriptions of all *Nybelinia* species were examined to establish the usefulness of separating different species into sections, as proposed by Dollfus (1960), and a cladistic analysis of the genus was carried out to provide insights into the phylogeny of the genus.

MATERIAL AND METHODS

Between 1980 and 1988, the viscera of a total of 214 fish belonging to 16 species and 13 families were examined for trypanorhynch cestodes (Table I). Stomach, stomach wall, body cavity, peritoneum and musculature were examined. Additionally, all internal organs and the mantle cavities of 33 specimens of an ommastrephid squid were examined. All were caught

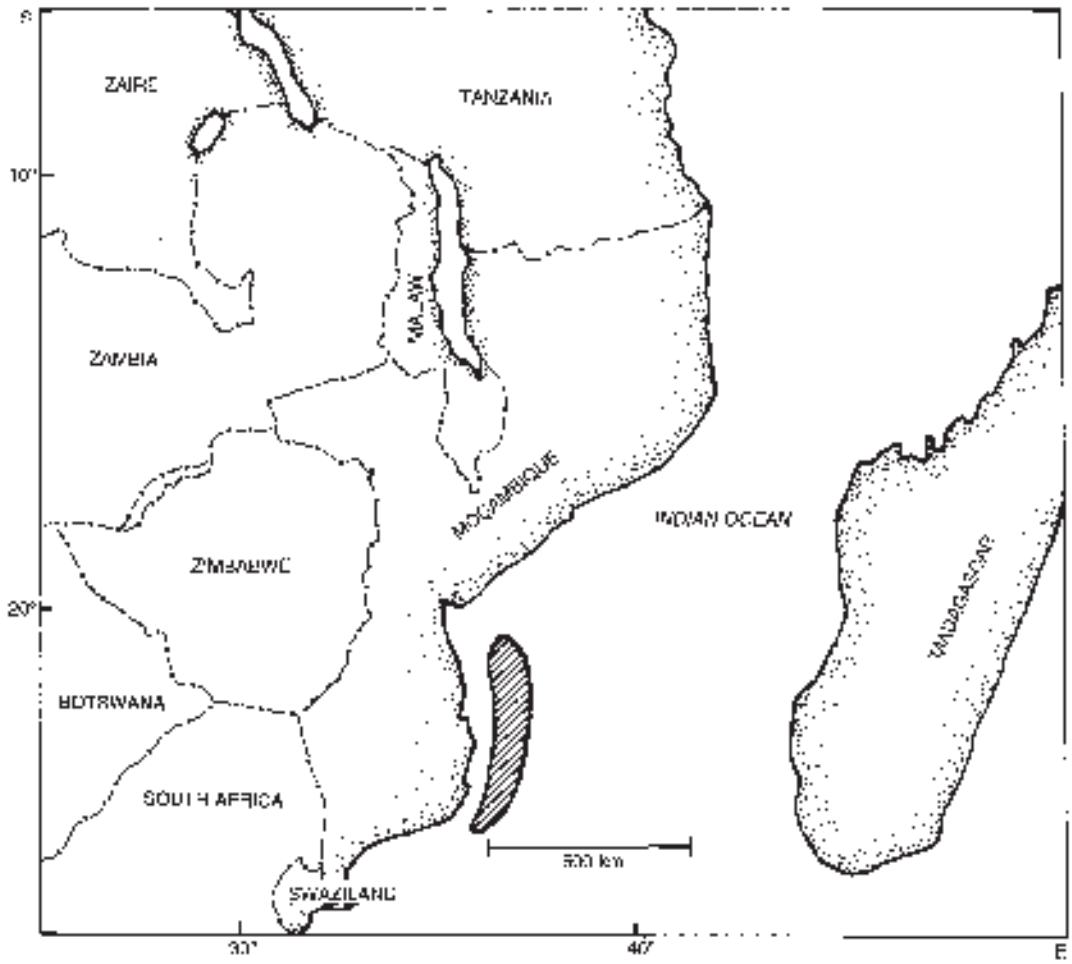

Fig. 1: Map showing area of investigation

on the fisheries research vessel *Ernst Haeckel* as bycatch of shrimp hauls between 34°15′ and 35°58′ E and 20°07′ and 26°01′S (Fig. 1).

All specimens sampled were examined fresh. In the laboratory, they were measured, filleted and the internal organs were removed. The viscera were searched with the aid of a stereoscopic dissecting microscope with 6–10× magnification. Postlarvae were fixed in Demke's fluid and after fixation, they were stained with Carmine and mounted in Canada balsam. The measurements and drawings were made under a Leitz Wetzlar Orthoplan microscope. Additionally, a single *Nybelinia* specimen from *Coelorinchus fasciatus* from the coastal waters of Namibia (21°43′S, 13°04′E) collected by A. A. Kovaljova, ATLANTNIRO Kaliningrad, Russia, on 04.10.1976 was examined for comparison.

For identification of the species and for systematic consideration, 47 original descriptions of *Nybelinia* species as well as descriptions by Dollfus (1942), Pintner (1927, 1930), and Sáo Clemente and Gomes (1992) were used. With the exception of original descriptions by Cuvier (1817, *N. lingualis*), Linton (1889, *N. bisulcata*), MacCallum (1917, *N. narinari*) and species cited in the present study, further original citations were given by Beveridge and Campbell

Table II: Infestation of *Nybelinia* spp. in fish from coastal waters off Moçambique

Host species	Infestation with *Nybelinia* spp.		
	Site	Level (%)	Species identified
Todarodes angolensis	Mantle, organs, in the stomach wall	78.8	*N. africana, N. anthicosum, N. yamagutii*
Raja leopardus	Stomach	100	*N. robusta*
Chascanopsetta lugubris	Stomach	45 (43*)	*Nybelinia beveridgei* sp. nov.
Chaunax pictus	Stomach wall	32.3	*N. yamagutii*
Bassanago albescens	Peritoneum	23	*N. robusta*
Gonorhynchus gonorhynchus	Body cavity, peritoneum	15.4 (18*)	*N. anthicosum*
Lophiodes mutilus	Stomach wall	37.5	*Nybelinia beveridgei* sp. nov.
Coelorhichus braueri	Body cavity, peritoneum	30.8 (30.8*)	*Nybelinia beveridgei* sp. nov.
C. flabellispinus	Stomach wall		*N. gopalai, N. yamagutii*
	Body cavity, peritoneum	28.6 (37.5*)	*N. gopalai*
Ventrifossa nasuta	Body cavity, peritoneum	75	*N. gopalai*
Lestrolepis intermedia	Stomach	22.2	*N. africana*
Arctozenus rissoi	Stomach wall	16.7	*N. africana*
Peristedion adeni	–	45 (43*)	*N. robusta*
Polymixia nobilis	Stomach wall, peritoneum	60 (60*)	*N. africana, N. yamagutii, N. robusta*
Polyipnus polli	Body cavity, peritoneum	3.6	*N. africana, N. yamagutii*
	Stomach wall		*N. yamagutii*
Saurida undosquamis	Body cavity	45 (27*)	*N. robusta*
	Stomach		*N. anthicosum, N. gopalai, N. robusta*
	Musculature		*N. anthicosum, N. yamagutii*
Benthodesmus elongatus	Stomach wall, peritoneum	33.3	*N. africana, N. yamagutii*

* In Reimer (1984)

(1996). In the taxonomic section of this communication, the following abbreviations are used for the different body parts of the postlarvae: scolex length (*SL*), scolex width at level of pars bothridialis (*SW*), pars bothridialis (*pbo*), pars vaginalis (*pv*), pars bulbosa (*pb*), appendix (*app*), velum (*vel*), bulb ratio (*BR*), ratio of *pbo*:*pv*:*pb* (*SP*), and tentacle width (*TW*). All measurements are given in µm unless otherwise indicated. The range is given in parenthesis. The classification follows that of Palm (1995, 1997a). The orientation of the tentacle surfaces follows that of Campbell and Beveridge (1994).

A cladistic analysis (heuristic search) using PAUP (Phylogenetic Analysis Using Parsimony) 3.1.1 was carried out to provide insights into the phylogeny of the genus. In all 12 characters were used: scolex length >3 000 (0), or ≤3 000 (1); ratio of *pbo* to *pb* >2 (0), or ≤2 (1); pars postbulbosa present (0), or absent (1); bulbs long (length to width ratio ≥4:1) (0), or bulbs short (length to width ratio <4:1) (1); tentacle width >50 (0), or ≤50 (1); basal swelling on tentacle present (0), or absent (1); metabasal armature homeomorphous (0), or heteromorphous (1); metabasal armature, slender hooks with a small basal plate absent (0), or present (1); characteristic basal armature present (0), or absent (1); size of basal hooks smaller (0), equal (1), or larger (2) than metabasal hooks; basal hooks, swollen at middle and strongly recurved at tip, absent (0), or present (1); muscular ring around the basal tentacle sheaths present (0), or absent (1). The tentaculariid *Tentacularia coryphaenae* was chosen as the outgroup. Strobilar characters could not be used, because most species within the genus are described only from postlarvae.

RESULTS

Six different species of the genus *Nybelinia* were found in the fish and cephalopod species investigated (Table II). All parasite species represent novel locality records and 27 represent new host records. In one fish species, *Saurida undosquamis*, four different *Nybelinia* species were present (Table II). *N. yamagutii* and *N. africana* were the most abundant parasites, infesting seven and six different host species respectively. The highest prevalences of infestation (79 and 75%, without considering *N. robusta* in one single ray) were found in the squid *Todarodes angolensis* and the teleost *Ventrifossa nasuta*. The majority of the *Nybelinia* postlarvae were isolated from the stomach, stomach wall and body cavity. The morphological measurements used for species identification, as well as comments on their distribution pattern, are given below.

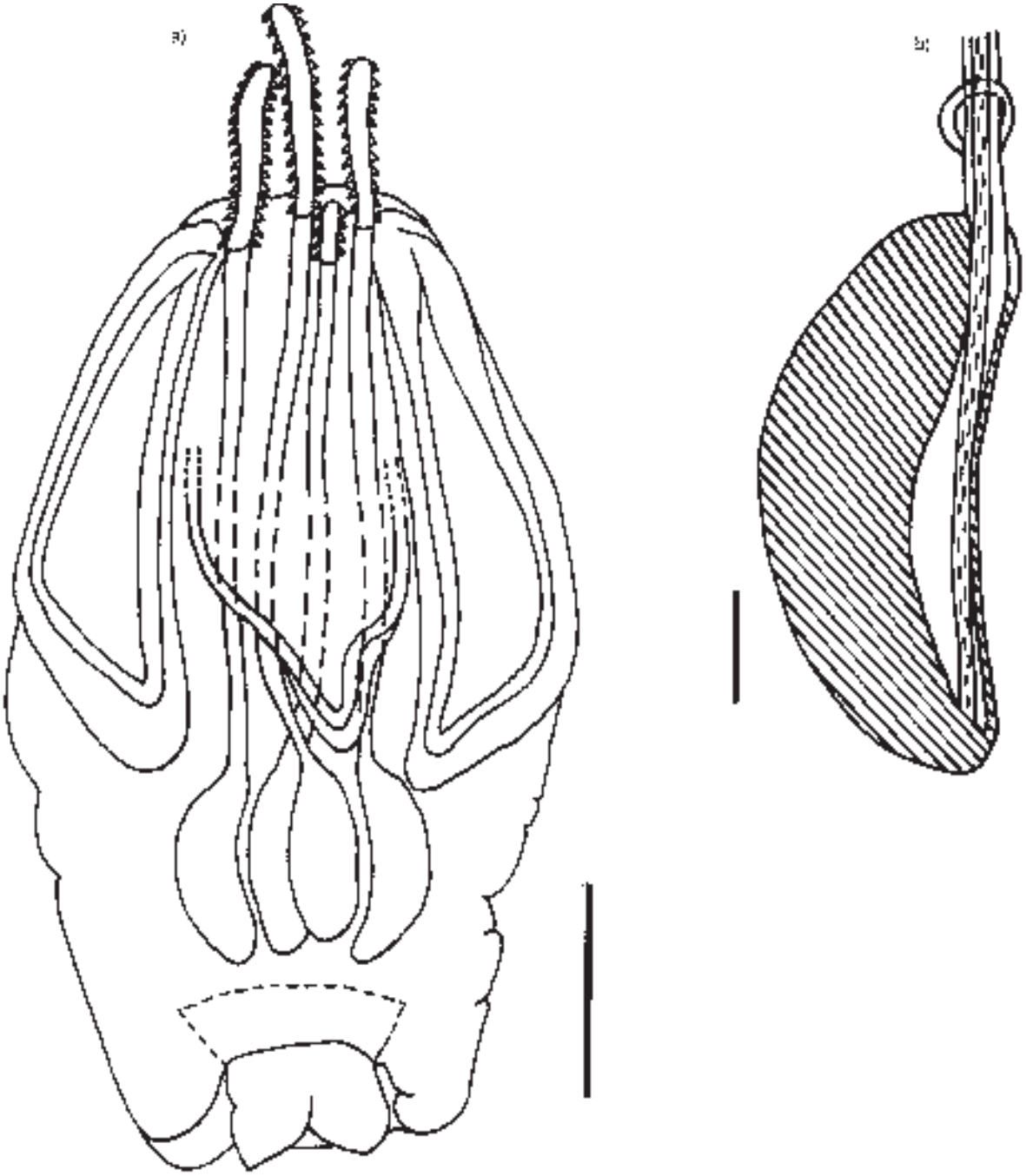

Fig. 2: *Nybelinia beveridgei* sp. nov. – (a) scolex, (b) bulb with retractor muscle and muscular ring around the basal part of the tentacle sheath. Scale bar: (a) = 1 mm, (b) = 200 µm

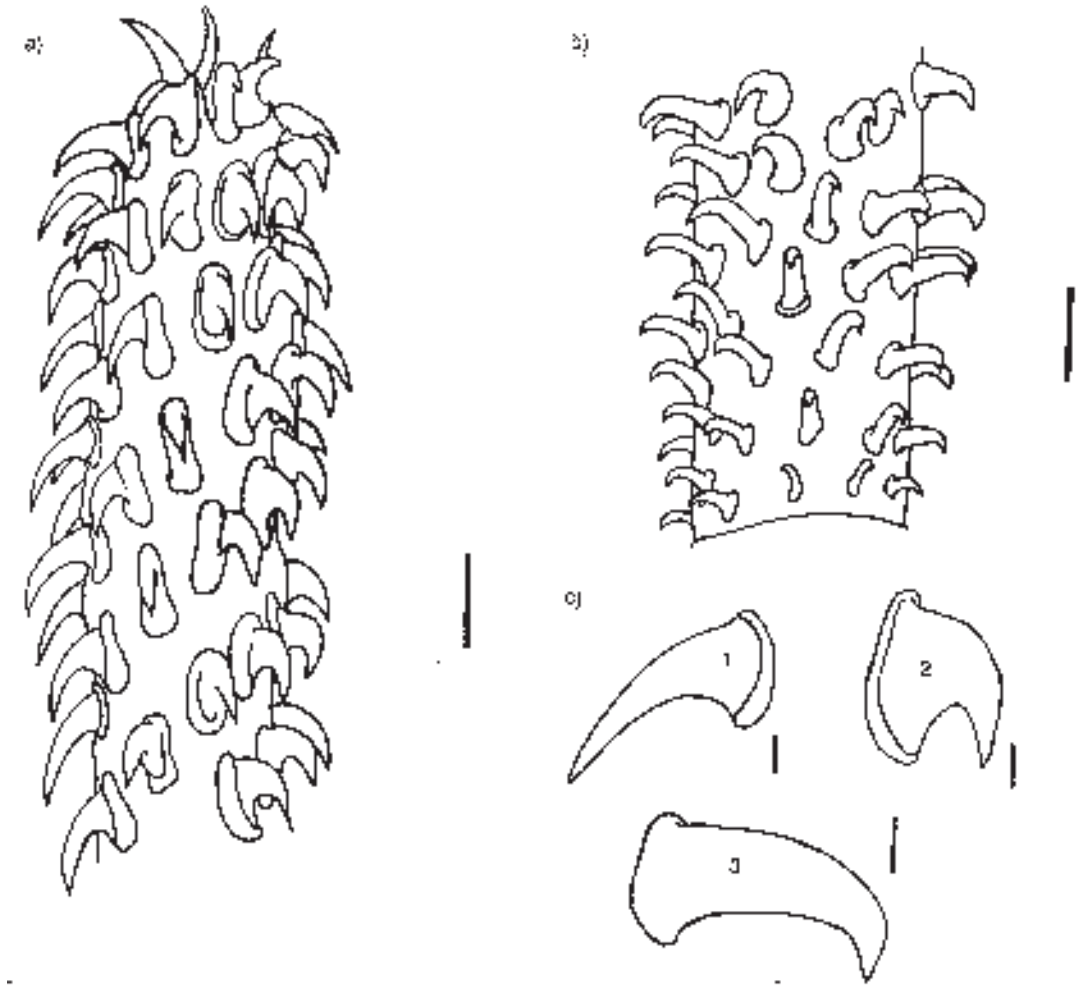

Fig. 3: *Nybelinia beveridgei* sp. nov. (a) tentacle metabasal (Rows 15-21), external surface, antibothridial on right-hand and bothridial on left-hand side, (b) tentacle basal (Rows 1–7), external surface, antibothridial on right hand and bothridial on left hand side, (c) profile of metabasal hook, bothridial (1), antibothridial (2), profile of basal hook (3). Scale bar: (a, b) = 50 µm, (c) = 10 µm

Superfamily Tentacularioidea Poche, 1926
Family Tentaculariidae Poche, 1926
Genus *Nybelinia* Poche, 1926

***Nybelinia africana* Dollfus, 1960**

N. africana was found in five different fish species and for the first time in a cephalopod, *Todarodes angolensis* (Table II). Though the morphometrical measurements of the scolex and tentacles of 23 specimens of six host species were greater than the data given by Dollfus (1960), the bulb ratio as well as scolex proportions were similar. The measurements were as follows: *SL* = 1 343 (1 118–1 568), *SW* = 880 (416–1 344), *pbo* = 891 (715–1 066), *pv* = 657 (416–897), *pb* = 351 (234–468), *app* = 481 (351–611), *vel* = 377 (182–572), *BR* = 2.9:1, *SP* = 2.5:1.9:1, *TW* = 32 – 45. The tentacular armature consisted of short, sharply recurved basal hooks (length = 10–16, base = 7–10) and a homeomorphous metabasal armature with long, slender hooks

(length = 20–32, base = 10–16). *N. africana* has been described from the Mediterranean Sea and from two localities off North-West Africa (Dollfus 1960). The present finding extends the known range of the species to the south-west Indian Ocean.

Nybelinia anthicosum Heinz and Dailey, 1974

Postlarvae of *N. anthicosum* are reported for the first time from two teleost species and the cephalopod *Todarodes angolensis* (Table II). All measurements of the scolex and the metabasal armature of three specimens from three host species lie within the range given for adults by Heinz and Dailey (1974), with the exception of *SW*. The measurements were as follows: *SL* = 1 936 (1 760–2 112), *SW* = 1 120 (864–1 376), *pbo* = 992 (800–1 186), *pv* = 816 (640–992), *pb* = 496 (416–576), *app* = 430 (352–507), *vel* = 387 (325–448), *BR* = 3.4:1, *SP* = 2:1.6:1, *TW* = 48–55. The tentacular armature consisted of homeomorphous hooks, larger in the metabasal region (length = 24–32, base = 13–16) than in the basal region (length = 18, base = 10). The present finding extends the known range of *N. anthicosum* from the Pacific Coast of southern California and northern Mexico (Heinz and Dailey 1974) to the south-west Indian Ocean.

Nybelinia beveridgei sp. nov.

Material described – Holotype and three paratypes from *Chascanopsetta lugubris*, *Coelorinchus braueri* and *Lophiodes mutilus* from coastal waters off Moçambique, and one specimen from *Coelorinchus fasciatus* from the Namibian coast.

Description – with the characters of the genus *Nybelinia*. The scolex is craspedote, massive, with a total length (with velum and without appendix) of 4 640 (4 000–5 280) and width of 2 604 (2 176–3 104) – Fig. 2a. The length of the bothridia is more than half the scolex length. The scolex measurements of the specimens from Moçambique are as follows: *pbo* = 2 912 (2 784–3 040), *pv* = 2 704 (2 368–3 040), *app* = 864 (608–1 120), *vel* = 832 (608–1 120). The bulb ratio is 3.3:1, with a bulb length of 960 (928–992) and width of 288 (256–320). The tentacles are 1 020 long and 81–98 wide, not diminishing in diameter in distal tentacular region. A basal swelling is absent. The tentacle sheaths are 2 730–3 070 long and 95–122 wide. A prebulbular organ is absent, a muscular ring around the basal part of the tentacle sheaths is present (not visible in all specimens) – Fig. 2b. The retractor muscle originates in the basal part of the bulb. *SP* is 3.0:2.8:1. A short pars post-bulbosa 52 (39–65) is present. The measurements of a single specimen of *N. beveridgei* sp. nov. from the coastal waters of Namibia were as follows: *SL* = 5 760, *SW* = 3 040, *pbo* = 3 200, *pv* = 3 520, *pb* = 1 070, *app* = 1 040, *vel* = 975, *BR* = 2.93:1, *SP* = 3.0:3.3:1, *TW* = 117–122.

The massive hooks of the homeoacanthous armature are different in shape and size on bothridial and antibothridial metabasal tentacle surfaces (Fig. 3a). On the antibothridial surface, the tentacular armature consists of strongly recurved and solid hooks with a large base (length = 46–49, base = 39–42, Fig. 3c [2]). On the bothridial surface, the hooks are more slender and slightly curved with a stout base (length = 65–68, base = 33–35, Fig. 3c [1]). A characteristic basal armature consisting of 6 – 7 rows is present (Fig. 3b). The basal hooks are homeomorphous with a stout base, a slender shaft, and strongly recurved at the tip (Fig. 3c [3]). They are smaller than in the metabasal region of the tentacle (length 36 – 39, base 23 – 26), increasing in size towards the metabasal armature. Number of hooks per half row is 6.

TAXONOMIC SUMMARY

Type hosts – *Chascanopsetta lugubris*, *Lophiodes mutilus*, *Coelorinchus braueri*

Site – Stomach, stomach wall, body cavity

Place of collection – 22°21′S, 35°51′E; 20°07′S, 35°54′E; 22°07′S, 35°4′E

Type material – Holotype from the stomach of *Chascanopsetta lugubris* from the coastal waters of Moçambique (19.01.1982, collected by L. W. Reimer, in the British Museum (Natural History), London, number BM (NH) 1997.3.24.1). Three paratypes from the stomach wall, body cavity and peritoneum of *Lophiodes mutilus* and *Coelorinchus braueri* from the coastal waters of Moçambique (04.08.1980 and 18.01.1982, collected by L. W. Reimer, numbers BM (NH) 1997.3.24.2 and 1997.3.24.3–4).

Other material – For comparison, the single specimen from *Coelorhinchus fasciatus* from the coastal waters of Namibia, accessioned as BM (NH) 1997.3.24.5.

Etymology – The new species was named after I. Beveridge, University of Melbourne, in honour of his taxonomic work on the order Trypanorhyncha.

REMARKS

Nybelinia beveridgei sp. nov. is characterized by a homeoacanthous armature of heteromorphous metabasal hooks (on opposite tentacle surfaces) and a characteristic basal armature of homeomorphous hooks. Several other members of the genus have a heteromorphous metabasal armature. *N. karachii* Khurshid and Bilqees, 1988 as well as *N. alloiotica*, *N. cadenati*, *N. dakari*, *N. estingmena*, *N. eureia*, *N. punctatissima* and *N. senegalensis*, all described by Dollfus (1960), can be distinguished from *N. beveridgei* sp. nov. by having a much smaller scolex size, a different size and shape of hooks, different *SP* and lack of a characteristic basal armature. Species of *Nybelinia* with heteromorphous hooks together with a characteristic basal armature are *N. herdmani* Shipley and Hornell, 1906, *N. nipponica* Yamaguti, 1952, *N. rougetcampanae* Dollfus, 1960 and *N. yamagutii* Dollfus, 1960. These species differ from *N. beveridgei* sp. nov. in having a basal armature consisting of heteromorphous hooks.

Nybelinia gopalai Chandra and Hanumantha Rao, 1985

N. gopalai was found in four teleosts (Table II). All morphometric measurements of the scolex and tentacle armature of 10 specimens from three host species lie within the range given by Chandra and Hanumantha Rao (1985). The measurements were as follows: *SL* = 1 692 (1 144–2 240), *SW* = 761 (416–1 105), *pbo* = 767 (520–1 014), *pv* = 956 (611–1 300), *pb* = 501 (286–715), *app* = 241 (156–325), *vel* = 104 (65–143), *BR* = 7.1:1, *SP* = 1.5:1.9:1, *TW* = 16–35. The tentacular armature of the metabasal region consisted of homeomorphous, solid, small (length = 8) hooks. The basal hooks, on a basal tentacular swelling, differ from the metabasal hooks; they are larger (length = 16, base = 5–8), somewhat swollen in the middle and strongly recurved at the tip. The first finding of *N. gopalai* was from the Bay of Bengal (Chandra and Hanumantha Rao 1985). The present record extends the known distribution of the species to the south-west Indian Ocean.

Nybelinia robusta (Linton, 1890)

N. robusta was found in a single elasmobranch and four teleosts (Table II). Although the morphometric measurements of the scolex and tentacles of 27 specimens from all five host species were larger than the data of Linton (1890), the bulb ratio and scolex proportions were similar. The measurements were as follows: *SL* = 2 064 (1 600–2 528), *SW* = 944 (416–1 472), *pbo* = 1 092 (832–1 352), *pv* = 982 (767–1 472), *pb* = 511 (384–637), *app* = 841 (273–1 408), *vel* = 162 (117–608), *BR* = 4.4:1, *SP* = 2.1:1.9:1, *TW* = 29 – 33. The tentacular armature consisted of homeomorphous hooks in the metabasal region (length = 16, base = 10–13). A characteristic basal armature with smaller (length = 8, base = 7), more recurved hooks was present. Therefore, with this finding of *N. robusta*, its distribution is extended from the North-West Atlantic (Linton 1890), eastern Atlantic (Dollfus, 1942) and the northern Indian Ocean (Kyan-Myint 1968, cited in Bates 1990) to the south-west Indian Ocean.

Nybelinia yamagutii Dollfus, 1960

N. yamagutii was found in six teleosts and for the first time in the cephalopod *Todarodes angolensis* (Table II). All morphometric measurements of the scolex and the metabasal armature of 20 specimens from seven host species were within the range given by Dollfus (1960), with the exception of some specimens which were smaller or larger than those given by Dollfus (1960). The measurements were as follows: *SL* = 2 544 (1 183–3 904), *SW* = 993 (546–1 440), *pbo* = 1 240 (529–1 888), *pv* = 1 353 (689–2 016), *pb* = 927 (286–1 568), *app* = 341 (169–512), *vel* = 161 (65–256), *BR* = 6.7:1, *SP* = 1.3:1.5:1, *TW* = 42–80. The metabasal hooks of the homeoacanthous armature were heteromorphous. The strongly recurved hooks on the antibothridial surface were larger (maximum: length = 65, base = 21). On the bothridial surface, the claw-like hooks (length = 45, base = 17) were smaller. The hooks on the basal region of the tentacle (length = 26–39, base = 10–13) also appeared different from the hooks of the metabasal region; they were swollen in the middle and had a strongly recurved tip. The present finding extends the known range of *N. yamagutii* from the North American Atlantic coast (Stunkard 1977) and West African (Dollfus 1960) coasts to the south-west Indian Ocean.

Dollfus (1960) described *N. yamagutii* as having differently formed hooks on the internal and external tentacle surfaces. In contrast to this, the specimens in the present study showed different hooks on the antibothridial/bothridial tentacle surfaces.

Cladistic analysis

The heuristic search gave no clear result. As more species were added, the more the species changed

their positions on the resulting tree. Although the 12 listed characters appeared to be useful to separate between different species on a morphological basis, the number of characters is too few to provide a cladistic analysis.

DISCUSSION AND SYSTEMATICS

During the present study, six different *Nybelinia* species from the Moçambique coast were found in one cephalopod and 16 fish species investigated. Only *N. gopalai* was found previously in *Saurida undosquamis* (Chandra and Hanumantha Rao 1985), which was found earlier to be infested with *Nybelinia* sp. (Paruchin and Skryabin 1989) at a prevalence of 96%. All other findings represent new host records, because Reimer (1984, 1989) and Paruchin and Skryabin (1989) reported parasites as *Nybelinia* sp., which they did not further identify. Together with the occurrence of *Nybelinia* sp. in *Malacocephalus laevis*, *Merluccius capensis*, *Psenes arafurensis* and *Thyrsitoides marleyi* (Reimer 1984), 21 different hosts from the Moçambique coast are known to harbour these trypanorhynchs, and 15 fish species were not infested.

Most *Nybelinia* specimens were found in the stomach, stomach wall or the body cavity, which appear to be the preferred sites of the postlarvae. This corresponds to the site preferrence of the adults, which often infest the stomach of their elasmobranch final hosts (Bates 1990, Palm 1995). Musculature infestation was detected in only a single case: *Saurida undosquamis* harboured postlarvae of *N. anthicosum*. Together with *N. erythraea* (see Dollfus 1960), *N. surmenicola* (see Arthur *et al*. 1982) and *N. indica* (see Chandra 1986), four *Nybelinia* species are known to infest the musculature. However, as several reports of *Nybelinia* sp. from the musculature have not been identified to species (Bates 1990) and others have been described only as adults, further findings of flesh-infesting *Nybelinia* species can be expected.

All six *Nybelinia* species collected inhabit different localities, and with the exception of *N. gopalai* (restricted to the Indian Ocean) different oceans. For example, *Nybelina yamagutii* has been reported from several regions of the Atlantic (Kinne 1990) and from the Indian Ocean and might be considered cosmopolitan. Similarly, *N. africana*, *N. anthicosum* and *N. robusta* have an interoceanic and perhaps a worldwide distribution. With the transoceanic record of *N. edwinlintoni*, *N. rougetcampanae* and *N. senegalensis* from the south-west American coast (Palm 1997b, Sáo Clemente and Gomes 1992) and *N. alloiotica* from the Gulf of Mexico (Palm 1995), six of the 16 species described by Dollfus (1960) have been found far away from the place of their original description. Additionally, species such as *N. beveridgei* (detected from the Moçambique and Namibian coast in the present study), *N. indica*, *N. perideraeus* and *N. surmenicola* (Dollfus 1942, Palm 1997b) have wide distribution. It appears that the genus comprises many species with a cosmopolitan distribution pattern. This is supported by the fact that adults of *Nybelinia* spp. have been recorded from sharks such as *Carcharhinus* spp., *Isurus oxyrinchus*, *Lamna ditropis*, *Mustelus canis*, *Prionace glauca* and *Sphyrna* spp. (Bates 1990), all of which have a wide zoogeographical distribution (Compagno 1984). Additionally, most teleosts found to be infested during the present study are transoceanic to worldwide in their distribution (*Arctozenus rissoi*, *Benthodesmus elongatus*, *Chascanopsetta lugubris*, *Chaunax pictus*, *Coelorinchus braueri*, *C. fasciatus*, *Gonorhynchus gonorhynchus*, *Lestrolepis intermedia*, *Lophiodes mutilus*, *Polymixia nobilis*, *Saurida undosquamis*; Hureau and Monod 1973, Quéro *et al*. 1990, Smith and Heemstra 1986). Interestingly, this contrasts to other trypanorhynch genera such as *Eutetrarhynchus*, of which many species parasitize locally distributed hosts, for example endemic rays (see Beveridge 1990, Last and Stevens 1994).

The prevalence of infestation found during this study was highly variable, ranging between 28.6 and 75.0% for *N. gopalai* and from 3.6 to 78.8% for *N. africana* and *N. yamagutii*. This is a typical infestation pattern for trypanorhynch cestodes at a single locality. However, the host-specificity of the six *Nybelinia* species was low; all were found in more than a single host species. For example, *N. yamagutii* had a wide host range, infesting six of the 16 fish species as well as the cephalopod *Todarodes angolensis.* The reports of *N. yamagutii* from other squid, such as *Sthenoteuthis pteropus* (Gaevskaya and Nigmatullin 1978), *S. oualaniensis* (Gaevskaya and Shukhgalter 1992), *Todaropsis eblanae*, *Illex coindetii* (Pascual *et al*. 1996) and *I. illecebrosus* (Stunkard 1977) support the suggestion of low host specificity. This finding is in contrast to the results of investigations on nontentaculariid cestodes (Palm 1997b), for which only a few species infested more than a single host at a single locality. It appears that tentaculariid postlarvae have a low host specificity in combination with a wide oceanic distribution. Therefore, besides morphological differences between these tentaculariid cestodes and other trypanorhynchs, such as a lack of a blastocyst (Campbell and Beveridge 1994) and a different

preferred site of infestation (Palm 1995), it is proposed that these worms additionally have evolved a different life cycle strategy. The development of different life cycles within trypanorhynch cestodes has been earlier described by Mattis (1986).

Postlarvae of tentaculariid trypanorhynchs are common parasites of cephalopods (Palm 1997a). Kinne (1990) listed five different *Nybelinia* species from squid, namely *N. africana*, *N. bisulcata*, *N. lingualis*, *N. surmenicola* and *N. yamagutii*, and together with *N. anthiciosum*, six *Nybelinia* species as infesting cephalopods. In the present study, a similar parasite fauna was found in the fish and in *Todarodes angolensis*. Cephalopods can be considered versatile predators that feed on most available food items (Rodhouse and Nigmatullin 1996). Therefore, the similar parasite fauna indicates that the squid served as a paratenic host for *N. africana*, *N. anthicosum* and *N. yamagutii* off the coast of Moçambique.

Beveridge and Campbell (1996) listed about 43 *Nybelinia* species, and in the present study, 47 species descriptions were considered. *N. beveridgei* sp. nov. is described here, Chandra and Hanumantha Rao (1985) described *N. gopalai* and Yang *et al.* (1995) described *N. rhynchobatus*. The descriptions of *N. macrocephala* by Asmi (1983, cited in Bilqees and Khurshid 1987) and *N. trisulcata* in Reimer (1980) were not included, because the description of Asmi was never published and *N. trisulcata*, listed in Reimer (1980) as being described in Subhapradha (1955), refers to *Nybelinia* sp. in Subhapradha (1955, pp. 48–49). It was not described under the name *N. trisulcata* and the morphological characters are similar to those from *N. oodes* Dollfus, 1960.

The first workable classification of species within the genus *Nybelinia* was presented by Dollfus (1960), amending his subdivision of the genus into the two subgenera *Nybelinia* and *Syngenes* (Dollfus 1942). While the characters "different kind of hooks on tentacle surfaces and characteristic basal armature" appear to be useful for species subdivision, the characters "width of tentacle and bulb ratio" are of dubious value. The width of the tentacles can vary in different parts of the tentacles and some species described can be placed in more than one section. *N. gopalai* has a tentacle between 19 µm wide in the basal and 15 µm in the metabasal region of the tentacle, therefore not fitting in any of the ranges proposed by Dollfus (1960). *N. nipponica* has a tentacle width of 30 – 60 µm (Yamaguti 1952), which corresponds to both Sections 1 and 2. Similarly, *N. anguillae*, with a tentacle width of 30-75 µm (Yamaguti 1952), falls between Sections 1 and 2. The bulb ratio (*BR*) can be variable. For example, *N. robusta* was found to have a ratio of 4.4:1 in the present study, in contrast to 3.6:1 reported in the original description (Linton 1890). Similarly, the *BR* of different varieties of *N. africana* range between 2.6:1 and 3.4:1 (Dollfus 1960).

Species such as *N. anantaramanorum* Reimer, 1980 and *N. gopalai* Chandra and Hanumantha Rao, 1985 do not fit into any of the sections suggested by Dollfus (1960). To simplify further taxonomic studies within the genus, a new subdivision of 43 adequate described *Nybelinia* species is proposed on the basis of the following three main characters: (a) metabasal tentacular armature, (b) tentacles with or without a characteristic basal armature, and (c) size of basal hooks in comparison to metabasal hooks.

I Metabasal tentacular armature homeoacanthous homeomorphous (Homeoacanths Type I in Campbell and Beveridge 1994)

A – Without characteristic basal armature
- a – Size of basal hooks smaller than metabasal hooks: *N. aequidentata*, *N. anthicosum*, *N. edwinlintoni*, *N. goreensis*, *N. lingualis*, *N. palliata*, *N. riseri*, *N. sphyrnae*, *N. thyrsites*
- b – Size of basal hooks equal to metabasal hooks: *N. anantaramanorum*, *N. bengalensis*, *N. elongata*, *N. jayapaulazariahi*, *N. oodes*, *N. pintneri*, *N. rhynchobatus*, *N. strongyla*, *N. surmenicola*, *N. syngenes*, *N. tenuis*
- c – Size of basal hooks larger than metabasal hooks: *N. basimegacantha*

B – With characteristic basal armature
- a – Size of basal hooks smaller than or equal to metabasal hooks: *N. africana*, *N. anguillae*, *N. bisulcata*, *N. erythraea*, *N. indica*, *N. manazo*, *N. perideraeus*, *N. robusta*
- b – Size of basal hooks larger than metabasal hooks: *N. gopalai*

II Metabasal tentacular armature homeoacanthous heteromorphous (Homeoacanths Type II in Campbell and Beveridge 1994)

A – Without characteristic basal armature
- a – Size of basal hooks smaller than metabasal hooks: *N. alloiotica*, *N. cadenati*, *N. estingmena*, *N. eureia*, *N. karachii*, *N. punctatissima*, *N. senegalensis*
- b – Size of basal hooks equal to or larger than metabasal hooks: *N. dakari*

B – With characteristic basal armature
a – Size of basal hooks smaller than or equal to metabasal hooks: *N. beveridgei*, *N. herdmani*, *N. nipponica*, *N. rouget-campanae*, *N. yamagutii*

Nybelinia beveridgei sp. nov. is similar to four species in Group IIBa, sharing the homeoacanthous and heteromorphous tentacular armature together with a characteristic basal armature and smaller or equal basal hooks than metabasal hooks. However, *N. beveridgei* clearly differs from the other species in the section by having a homeomorphous basal armature and characteristically shaped tentacular hooks. Not included in this list are the following four species of uncertain status: *N. congri*, because of its poor description (Guiart 1935); *N. infulata,* because of its poor description (Molin 1858) and the synonymy of this species with *N. lingualis* (Dollfus 1942); *N. lamontae*, because of its poor description (Nigrelli 1938) and the similarity of this species to *Tentacularia coryphaenae* Bosc, 1797; and *N. narinari* MacCallum, 1917, owing to the synonymy of this species with *N. robusta* (Dollfus 1930). Following Campbell and Beveridge (1994), the division of the genus into two subgenera *Nybelinia* and *Syngenes* by Dollfus (1942) was not followed as a result of the lack of information on strobila characters of most *Nybelinia* species (see Beveridge and Campbell 1996). Similarly, the subdivision of the genus into the *Nybelinia* Poche, 1926 and *Pleronybelinia,* described by Sezen and Price (1969), was not followed, corresponding to Heinz and Dailey (1974).

The present study has demonstrated that the genus *Nybelinia* consists of several subgroups of species with corresponding morphological characters, which might warrant a separation of the genus into several different subgenera. However, two main reasons can be given against the erection of subgenera with the current stage of knowledge. A revision of the whole genus *Nybelinia* is needed to ensure the validity of many species within the genus. Considering the high variation of scolex morphology within a single trypanorhynch species (Palm *et al*. 1993) and the minor difference between several species (especially see Dollfus 1960), some species might be solely variations of earlier described species. The second reason is the lack of knowledge on strobilar characters and the small number of useful taxonomic characters available using scolex morphology. A total of 12 different characters was used in the attempt to analyse the genus within a cladistic framework. However, the characters appear to be insufficient for analysing the genus, and as more species were added, the tree became more and more unstable.

Within the Trypanorhyncha, the genus *Nybelinia* remains the most difficult genus to study. However, this contrasts with its obviously enormous distribution in the world oceans, together with great abundances in different geographical regions. Further studies on species within the *Nybelinia* are encouraged, which should give further insight into understanding of the development of different types of tentacular armatures within the genus. This can be seen as essential for future classifications within the Tentacullariidae as well as within the whole order.

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