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Nybelinia Poche, 1926, *Heteronybelinia* gen. nov. and *Mixonybelinia* gen. nov. (Cestoda, Trypanorhyncha) in the collections of The Natural History Museum, London

HARRY W. PALM

Marine Pathology Group, Department of Fisheries Biology, Institut für Meereskunde an der Universität Kiel, Düsternbrooker Weg 20, D-24105 Kiel, Germany

SYNOPSIS. With a total of 43 adequately described species, the cosmopolitan genus *Nybelinia* is the most species-rich genus within the order Trypanorhyncha. As an initial part of a revision of the genus, the present study was carried out to examine unidentified and identified *Nybelinia* specimens deposited at The Natural History Museum London. A total of 17 different species was found, four new species are described and 2 new genera, *Heteronybelinia* gen. nov. and *Mixonybelinia* gen. nov., are erected: *Nybelinia aequidentata* (Shipley & Hornell, 1906); *N. africana* Dollfus, 1960; *N. jayapaulazariahi* Reimer, 1980; *N. lingualis* (Cuvier, 1817); *N. riseri* Dollfus, 1960; *N. sakanariae* sp. nov.; *N. schmidti* sp. nov.; *N. scoliodoni* (Vijayalakshmi, Vijayalakshmi & Gangadharam, 1996) comb. nov.; *Nybelinia* sp.; *Heteronybelinia elongata* (Shah & Bilqees, 1979) comb. nov.; *H. estigmena* (Dollfus, 1960) comb. nov.; *H. heteromorphi* sp. nov.; *H. minima* sp. nov.; *H. robusta* (Linton, 1890) comb. nov.; *H. yamagutii* (Dollfus, 1960) comb. nov.; *Mixonybelinia beveridgei* (Palm, Walter, Schwerdtfeger & Reimer, 1997) comb. nov. and *M. southwelli* (Palm & Walter, 1999) comb. nov.. *Tentacularia scoliodoni* is transferred to the genus *Nybelinia*. Nine new locality and 15 new host records were established. The adults of *Heteronybelinia estigmena* and *H. yamagutii* are reported for the first time. It is proposed that the morphological variation within the different species is much higher than considered in the recent literature. Many species within the genus have a world-wide distribution pattern and a low host specificity, both in their fish second intermediate/paratenic hosts and in their final hosts.

INTRODUCTION

Trypanorhynchs are cosmopolitan marine cestodes and mature in the stomach or the spiral valve of marine elasmobranchs, while their postlarvae are parasitic in teleosts and invertebrates, with the first intermediate hosts being crustaceans (Palm, 1997a, Sakanari & Moser, 1989). Within the order Trypanorhyncha, the genus *Nybelinia* Poche, 1926 is particularly difficult to study. Palm *et al.* (1997) listed 43 adequately described species while leaving 4 as species of uncertain status. Jones & Beveridge (1998) added a further species, *N. queenslandensis*, and Palm & Walter (1999) described *N. southwelli*, and synonymised *Nybelinia dakari* Dollfus, 1960 and *N. herdmani* (Shipley & Hornell, 1906) with *N. perideraeus* (Shipley & Hornell, 1906) and *Kotorella pronosoma* (Stossich, 1901) respectively. Thus, with a total of 43 adequately described species, the genus *Nybelinia* is the most species-rich genus within the order Trypanorhyncha.

In contrast our knowledge of their biology is poor. The first intermediate hosts are unknown and the occurrence of postlarvae in marine plankton (Dollfus, 1974) is enigmatic. Postlarvae of these robust worms are found in unusual sites such as the human palatine tonsil (Kikuchi *et al.*, 1981) as well as in anadromous *Lampetra japonica,* 1000–3000 km away from the sea in the Amur river (Shulman, 1957). Additionally, members of the genus *Nybelinia* infest the fish flesh (Oshmarin *et al.*, 1961, Palm, 1997b), and parasitic infestation of the musculature of commercially important fish species causes heavy losses to the fish processing industry (Arthur *et al.*, 1982, Deardorff *et al.*, 1984).

One of the biggest problems for taxonomic work within the genus *Nybelinia*, apart from incomplete original descriptions, remains the lack of information on material deposited in museum collections. The genus has not been revised since 1942, and due to the morphological similarity of several species, many *Nybelinia* specimens found have not been identified to species level, and consequently have been deposited as *Nybelinia* sp. Additionally, several species descriptions are based on single specimens.

The present study was carried out to examine unidentified species of *Nybelinia* deposited at The Natural History Museum, London. Measurements and drawings of most specimens are given as verification of the identifications made. Beside the establishment of new host and locality records, species identifications provide further insight into the zoogeographical distribution. The comparison of the scolex measurements with those from original descriptions allows comments to be made on the level of intraspecific morphological variation of some *Nybelinia* species, data which are necessary for further taxonomic studies within the genus. The description of adult specimens allows comparative investigations on strobilar morphology within the genus.

MATERIAL AND METHODS

Standard measurements and drawings of the scoleces of *Nybelinia* specimens deposited in the Parasitic Worms Division, The Natural History Museum, London (BMNH), were made using a Leitz Wetzlar Dialux 20 microscope with an ocular micrometer. Special attention was given to unidentified specimens deposited simply as *Nybelinia* sp., while other deposited and identified material was also exam-

ined. As additional material, slides from the Natural History Museum, Vienna (NHMV No. 2111) and from the U.S. National Parasite Collection, Beltsville (USNPC No. 7727 (M130–6)) were borrowed. Similarly, deposited *Nybelinia* species were studied in the Muséum National d´Histoire Naturelle, Paris (MNHN Paris), for comparison.

The following measurements were made: Scolex length (SL), scolex width at level of pars bothridialis (SW), pars bothridialis (pbo), pars vaginalis (pv), pars bulbosa (pb), pars postbulbosa (ppb), velum (vel), appendix (app), bulb length (BL), bulb width (BW), bulb ratio (BR), proportions of pbo/pv/pb (SP), tentacle width (TW), and tentacle sheath width (TSW). If possible, the tentacle length was estimated. Additionally, the tentacular armature was described as follows: armature homeomorphous or heteromorphous, hooks per half spiral row (hsr), total hook length (L) and the total length of the base of the hooks (B). The abbreviation nm (not measured) indicates that no measurement was taken.

All measurements are given in micrometers unless otherwise indicated. Specimens belonging to the same species from different hosts or localities were measured in the same order as the specimens are listed under Material examined. If more than two measurements were taken, the mean is given with the range in parentheses, unless otherwise indicated. Illustrations are provided if useful for future identification of the species; otherwise the reader is referred to illustrations of other authors. The classification follows that of Palm (1995, 1997a) and the orientation of the tentacular surfaces follows that of Campbell & Beveridge (1994).

RESULTS

A total of 17 species was identified, and 4 new species are described. Nine new locality and 15 new host records were established. The information on the single specimens measured with comments on their taxonomy and distribution are given below.

Superfamily **TENTACULARIOIDEA** Poche, 1926
Family **TENTACULARIIDAE** Poche, 1926
Genus ***NYBELINIA*** Poche, 1926

1. *Nybelinia aequidentata* (Shipley & Hornell, 1906) (Figs 1–2)

MATERIAL EXAMINED. BMNH 1992.7.1.193–196, A. Roy *leg.*, 1 postlarva from *Lepturacanthus savala*, Sugar Island, Bay of Bengal.

DESCRIPTION. The type material of *N. aequidentata*, which is deposited at the Natural History Museum, Vienna, was re-described by Pintner (1927). The scolex and tentacular armature of the present specimen is given in Figs 1–2. Measurements: SL=3400; SW=1700; pbo=1510; pv=1890; pb=813; ppb=57; vel=530; app=585; BL=780 (756–813); BW=237 (227–265); BR=3.3:1; SP=1.9:2.3:1. TW metabasal=54–58, TW apical=46–51. A basal tentacular swelling is absent. The tentacle sheaths are straight; TSW=33–38. Prebulbar organs are absent, muscular rings around the basal part of the tentacle sheaths are present. The retractor muscles originate in the basal part of the bulbs.

The armature is homeoacanthous, homeomorphous, and a characteristic basal armature is absent. The massive hooks of the metabasal armature are similar in shape (Fig. 2), diminishing in size from the 6th row towards the basal part of the tentacle. The size of the hooks also diminish slightly towards the apical end of the tentacles. The hook size in the metabasal armature was L=33–38, B=13–17; hsr=8.

REMARKS. The present specimen is similar to the type material, having a large scolex and pbo and slender tentacular hooks with a long shaft and a rounded base. The tentacular hooks of the type specimen are similarly shaped along the tentacle and diminish in size towards the tip and at the base (compare with Pintner 1927, p. 562). Additionally, both specimens were found in the same region, off the Indian coast. However, the present specimen also shows some differences to those described by Shipley & Hornell (1906) and Pintner (1927). The scolex measurements of the type (4500–5000, SW=2000) as well as the hook sizes (L=up to 48) are larger. Similarly, the scolex proportions of the two specimens differ (type: BR=4.3:1 and SP=1:1.7:1). In both cases, the descriptions are based on a single specimen only, and no data on the morphological variability within *N. aequidentata* are available.

The present specimen belongs to subgroup IAa of Palm *et al.* (1997) and due to the characteristically shaped slender hooks with a rounded base, slender shaft and strongly re-curved tip, it has similarities with *N. edwinlintoni* and *N. goreensis*. *N. edwinlintoni* is smaller, has a different bulb ratio (2.5:1) and scolex proportion (2.4:1.6:1) as well as a larger TW, TSW and smaller (L=18–20, B=10) hooks (Dollfus, 1960). *N. goreensis* is also smaller (SL=1235–1325), has a slightly different bulb proportion (2.5–3:1), a larger TW, TSW and smaller hooks. In addition, Dollfus (1960) remarked on the uniformity of the hooks. Two species with a similar tentacular armature, *N. anantaramanorum* and *N. syngenes*, were placed in subgroup IAb by Palm *et al.*, 1997, with hooks of similar size in the basal and metabasal part of the tentacles. *N. anantaramanorum* from the Gulf of Bengal differs in having smaller hooks and a smaller scolex (Reimer, 1980). However, there is a close relationship between *N. aequidentata* and *N. anantaramanorum*. *N. syngenes* resembles the present specimen in having similar tentacular hooks. However, it clearly differs by having a distinctly smaller scolex and larger hooks (L=68; Pintner, 1929, Dollfus, 1942). Thus, the present specimen is identified as *N. aequidentata*, and represents a new host record. However, the similarities between these species have to be kept in mind.

2. *Nybelinia africana* Dollfus, 1960 (Fig. 3)

MATERIAL EXAMINED. BMNH 1982.4.6.37–45, R. van der Elst *leg.*, 11.05.1984, 1 adult from the lower gut/upper intestine of *Carcharhinus obscurus*, South Africa; BMNH 1985.11.8.63–64, R. van der Elst *leg.*, 11.5.1984, 1 adult from *Carcharhinus leucas*, Richards Bay, South Africa. Other material: BMNH 1982.4.6.18–22, R. Bray *leg.*, from the lower stomach of *Carcharhinus obscurus*, Durban, South Africa; BMNH 1985.11.8.53–54, R. van der Elst *leg.*, 2.4.81, from the stomach of *Carcharhinas leucas*; BMNH 1985.11.8.55–56, R. Bray *leg.*, from the stomach of *Mustelus canis* (=*M. canis* or *M. queketti*), stomach, Durban, Natal.

DESCRIPTION. *Nybelinia africana* was described in detail by Dollfus (1960, see figures 9–19) and Palm et. al. (1997). Measurements: SL=536, 440; SW=420, 485; pbo=327, 337; pv=205, 122; pb=178, 150; vel=210, 164; BL= 174 (168–178), 133 (120–150); BW=73 (70–75), 70 (60–78); BR=2.4:1, 1.9:1, SP=1.8:1.1:1, 2.2:0.8:1; Short tentacles, about 200 long, with TW basal=28, 27; TW metabasal 23, 24; The tentacle sheaths are sinuous or spirally coiled, TSW=18–23, 17–20. The characteristic tentacular armature is homeomorphous with a basal armature of about 6 rows with rose-thorn-shaped hooks. The metabasal armature consists of slender hooks with a strongly re-curved tip (L=13.5–15.2, 12.5–14.8; B=5.6–7.2, 4.0–5.5). The tentacular hooks of the basal armature were

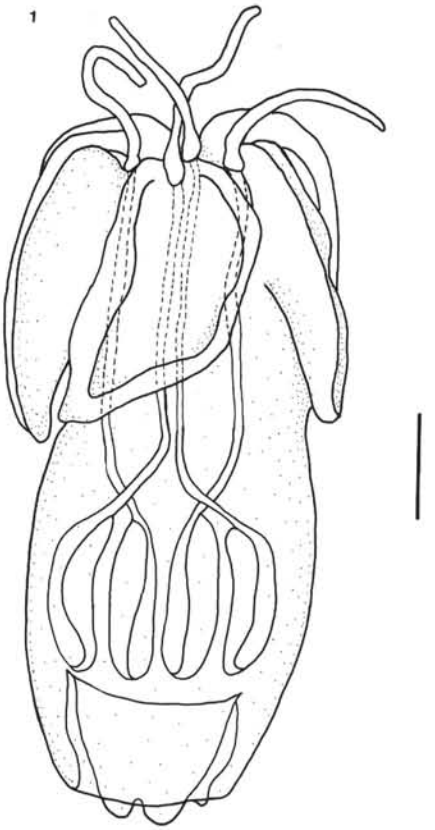


Fig. 1 *Nybelinia aequidentata* isolated from *Lepturacanthus savala*. Scolex. Scale bar=500 μm.

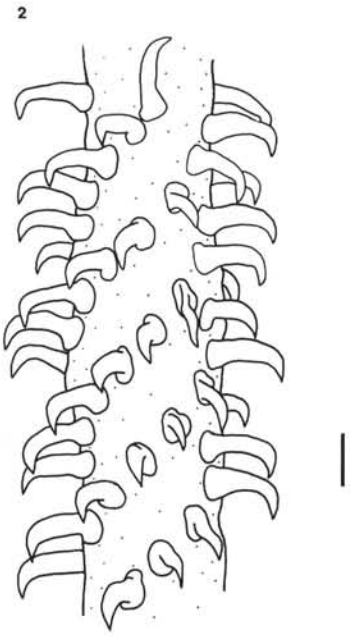


Fig. 2 *N. aequidentata*. Homeomorphous metabasal armature. Scale bar=25 μm.

rose-thorn shaped (L=9.6–12.0, 8.8–12.0; B=7.2–8.8, 7.2–8.8); hsr=7–8.

The strobila is acraspedote, with about 240 segments, last proglottid with rounded proximal end. The first 70 proglottids are very short (10–50 long × 370–530 wide), the next enlarge in size towards 400–500 × 940–1030. The last 20 proglottids are a bit wider than long 1050–1200 × 1250–1450. In mature proglottids (Fig. 3), genital atrium ventro-submarginal, in anterior half of the segment; genital pores alternate irregularly. Cirrus sac elongate and slender, 80 × 450 in size, directed anteromedially, sac thin-walled; cirrus unarmed and coiled within sac, internal and external seminal vesicle not seen; vas deferens coils medially to mid-line, then posteriorly towards genital complex. Testes of different shape, often ovoid, 70–95 in diameter (55–70 in proglottids 71–160), arranged in a single layer; testes number 80–90 per proglottis, encircle female genital complex and occupy entire medulla except for region of female genital complex and anterior of it. Ovary centrally, follicular, x-shaped with 2 major branches, each 95 × 160. Uterine ducts coiled before they enter the sacciform uterus. Vitelline follicles 25–35 in diameter.

REMARKS. Dollfus (1960) described larvae of *N. africana* from the body cavity of *Galeoides polydactylus*, *Mullus barbatus*, *Pagellus* sp. *Serranus cabrilla*, and *Trigla* sp.. The 3 scoleces measured by Dollfus were variable in size, ranging for example between 750–1100 (SL), 397–540 (pbo) and 19–35 (TW). The BR and SP were between 2.6:1–3.4:1 and 2.1:0.9:1–2.3:1.4:1 respectively and the hook size in the metabasal armature was between 14–17. The measurements for the present specimens were smaller and only the SP of the specimen from *Carcharhinus leucas* directly corresponds to specimen in tube 465 described by Dollfus (1960). However, the similar form and size of the basal and metabasal hooks together with a similar TW lead to the identification proposed. Palm *et al.* (1997) reported specimens of *N. africana* from the Mozambique coast which were larger in scolex and hook sizes than the above material. However, the form of the hooks along the tentacle as well as the BR, SP and TW were similar to those described by Dollfus (1960). Thus, it seems that *N. africana* has a variable scolex size, and, depending on this, a different hook size. However, the characteristic hook forms along the tentacle remain the same. Palm & Walter (1999) recognised adults of *N. africana* from *Carcharhinus melanopterus* from the Gulf of Suez, Egypt (named as *N. perideraeus* in Dollfus, 1942) on bases of the scolex size and the tentacular armature, and the present description of adult *N. africana* supports this synonymy. The strobila characters of the present specimens correspond with that of Dollfus's description in a similar size and shape of the first (10–50 × 370–530 vs 11 × 290) and last (1050–1200 × 1250–1450, a bit wider than long vs 1100 × 900, a bit longer than wide) proglottids, the follicular ovary, and similar sized vitellaria (25–35 vs 26–31). The present study records specimens from two further carcharhinid shark species and from *Mustelus canis* from South Africa. They represent new host and locality records, which indicates a circum-African distribution and a low host specificity of adult *N. africana*, as was earlier proposed for the postlarvae by Palm *et al.* (1997).

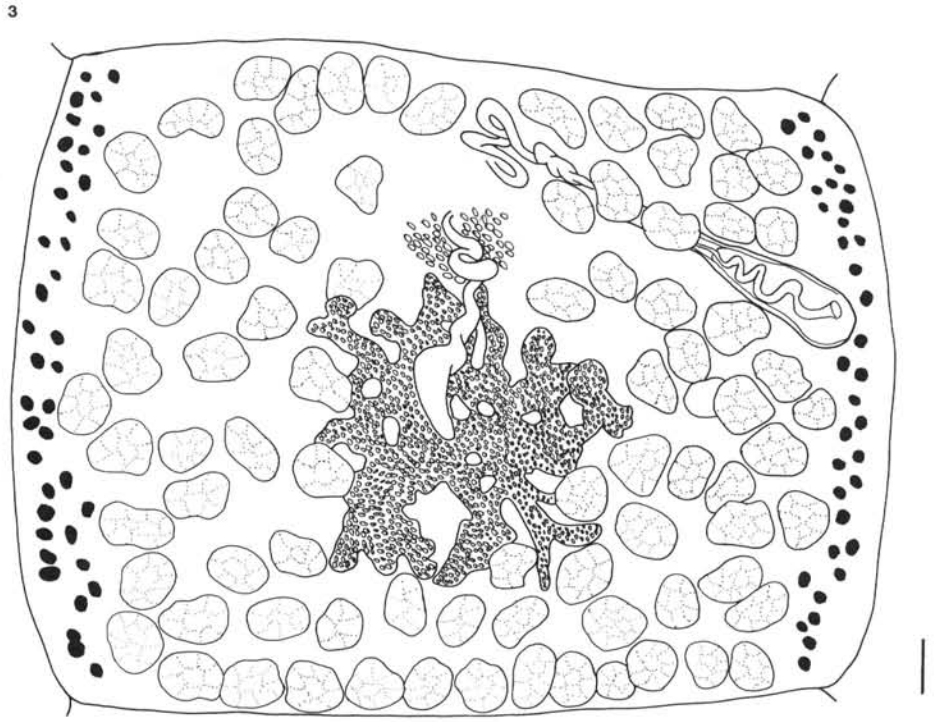


Fig. 3 *N. africana*. Mature segment. Scale bar=60 µm.

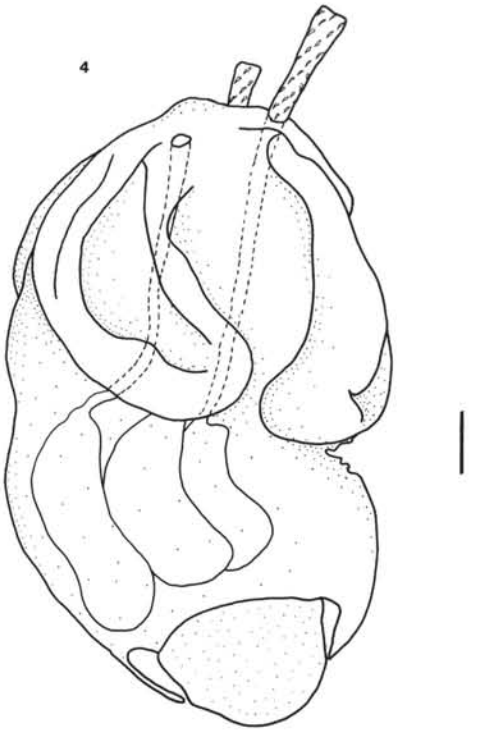


Fig. 4 *Nybelinia jayapaulazariahi* from *Harpodon nehereus*. Scolex. Scale bar=50µm.

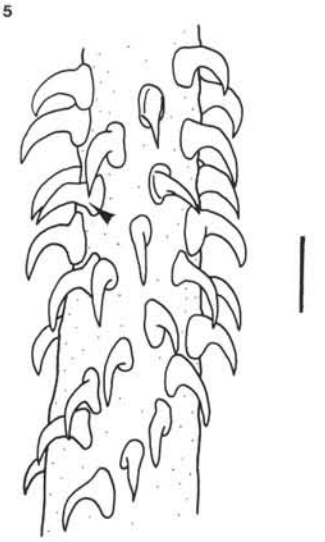


Fig. 5 *N. jayapaulazariahi*. Homeomorphous metabasal armature with slender hooks, metabasal hook as given in Reimer (1980), figure 4 (arrow). Scale bar=10 µm.

3. *Nybelinia jayapaulazariahi* Reimer, 1980 (Figs 4–5)

MATERIAL EXAMINED. BMNH 1980.12.2.1, A. Roy *leg.*, 14.9.79, 1 postlarva from *Harpodon nehereus*, Houghly estuary, India (Figs 4–5).

DESCRIPTION. Measurements: SL=530; SW=326; pbo=298; pv=285; pb=165; app=114; vel=96; BL=157 (150–165); BW=54; BR=2.9:1; SP=1.8:1.7:1; TW=16–18.5; TSW=12.5–15.5; a basal tentacle swelling is absent; the tentacle sheaths are straight; Prebulbar organs and muscular rings around the basal part of the tentacle sheaths are absent. The retractor muscles originate at the basal part of the bulbs.

The tentacular armature is homeoacanthous, homeomorphous, and a characteristic basal armature is absent. The size of the slender, regularly curved hooks increases slightly towards the metabasal part of the tentacle; L=9.6–11.2; B=5.6–7.2 (metabasal) and L=5.6–7.2; B=5.6–7.2 (basal); hsr=6.

REMARKS. The present specimen from *Harpodon nehereus* corresponds closely with that of the original description by Reimer (1980) from *Cynoglossus* sp.. Beside a similar scolex form (Fig. 7 in Reimer, 1980) and similar scolex and bulb ratios (SP 1.9:–:1 and BR 3:1), the hook size is identical and the hook form (as given in Reimer, 1980, Fig. 8) resembles that given in Fig. 5 (see arrow). The hook form with its slender, regularly curved shaft is distinct from the robust rose-thorn shaped hooks of many other *Nybelinia* species. The values of the TW extracted from Fig. 7 of Reimer are slightly higher (ca. 20–25 µm) than those of the present specimen. Both specimens were found in the same part of the Indian Ocean, Houghly estuary, India, and the Bay of Bengal, India. *Harpodon nehereus* represents a new host for *Nybelinia jayapaulazariahi.*

4. *Nybelinia lingualis* (Cuvier, 1817) (Figs 6–9)

MATERIAL EXAMINED. BMNH 1987.3.2.19, R. Bray *leg.*, 1 postlarva from the gut of *Torquigener pleurogramma*, Adelaide, South Australia; BMNH 1987.4.23.11–12, R. Bray *leg.*, 03.12.1986, 2 postlarvae from the branchial chamber of *Arnoglossus imperialis*, Cirolana 76–78 m, 49°50'5"N, 3°44'3"W; BMNH 1987.4.23.18–32, R. Bray *leg.*, 03.12.1996, 1 postlarva from the intestinal wall of *Pagusa lascaris*, Cirolana, English Channel, 49°50'5"N, 3°44'3"W, 76–78 m.

DESCRIPTION. *Nybelinia lingualis* was described in detail by Dollfus (1942). The scolex of the specimen from *T. pleurogramma* is shown in Fig. 6. Measurements: SL=1606, 1720, 1700, 2040; SW=718, 982, 907, 1172; pbo=700, 1096, 1096, 1172; pv=642, 907, 907, 1171; pb=397, 321, 298, 341; ppb=75, 0, 0, 10; app=490, 510, 491, nm; BL=365 (326–397), 313 (303–322), 292 (289–294), 341; BW=138 (130–140), 128 (117–140), 114 (112–117), nm; BR=2.6:1, 2.4:1, 2.6:1, nm; SP=1.8:1.6:1, 3.4:2.8:1, 3.7:3:1, 3.4:3.4:1. The tentacles are long and slender and diminish in diameter towards the tip; TW basal=39, 42, 46, 46, TW metabasal=32, 33, 33, 38; TW distal=24, nm, nm, nm. A basal tentacular swelling is not present. The tentacle sheaths are coiled in 1 to 2 spirals near the bulbs; TSW= 36, 46, 42, 40. Prebulbar organs and muscular rings around the basal part of the tentacle sheaths are absent. The retractor muscles originate in the basal part of the bulbs.

The armature is homeoacanthous, homeomorphous, and a characteristic basal armature is present (Figs 7–9). The tentacular hook form changes towards the apical part of the tentacle from compact, rounded rose-thorn (Fig. 7), lacking an posterior extension of the basal plate, to more slender rose-thorn shaped hooks (Figs 8–9). The hooks in the basal part of the tentacle are smaller (L=11.0–13.0, 11.6–13.6, 11.6–13.6, 11.6–13.6; B=9.3–11.2, 7.2–9.6, 7.2–9.6, 7.2–9.6) than in the metabasal armature (L=14.5–16.7, 16.0–18.4, 16.0–18.4, 16.0–18.4; B=9.3–13.0, 12.0–13.5, 12.0–13.5, 12.0–13.5). The number of hooks per half spiral diminish towards the apical part of the tentacle; hsr=6–7 (basal), hsr=5–6 (apical).

REMARKS. The present specimens correspond with those described by Dollfus (1942). Although the scolex measurements as well as hook sizes are smaller than those given by Dollfus (1942), the scolex form as well as the form and arrangement of the tentacular hooks correspond with drawings of *N. lingualis* found in *Sepia filliouxi*, *S. officinalis* and *Mullus barbatus* (see Dollfus, 1942, Figs 88–91). According to Dollfus (1942), the bulbs are typically short (about 300–400 µm long), with a BR of about 2.2–2.5:1. Additionally, Dollfus (1942) demonstrated a high degree of morphological variability within the species with a scolex size between 1.2–3.2 mm. As with *Tentacularia coryphaenae*, *Nybelinia lingualis* has a wide zoogeographical distribution and a low host specificity. The present findings with the exception of specimens in *Pagusa lascaris* are new host records and extend the known range of distribution for the species to Australian waters. Palm (1995) examined specimens of the same species (BMNH 1987.4.23.18–32 from *P. lascaris*) and tentatively identified them as *N. lingualis*. The present finding confirms this identification. Thus, the surface morphology of *Nybelinia lingualis* with filiform microtriches on the distal bothridial surface and hook-like microtriches on the bothridial borders corresponds to those as described for *Tentacularia coryphaenae*, *N. alloiotica*, *N. edwinlintoni*, *N. queenslandensis* and *N.* c.f. *senegalensis* (Palm, 1995, Jones & Beveridge, 1998).

5. *Nybelinia riseri* Dollfus, 1960 (Figs 10–11)

MATERIAL EXAMINED. BMNH 1985.11.8.65, G. Ross *leg.*, 30.11.1979, 3 postlarvae from *Trachyurus felicipes* (Figs 10–11), stomach wall, East Cape, South Africa.

DESCRIPTION. Measurements: SL=1455 (1380–1587); SW (pbo)=580 (510–680); SW (pv)=400 (300–454); pbo=630 (585–662); pv=636 (567–700); pb=294 (280–303); ppb=204 (151–233); app=331 (312–360); BL=284 (270–303); BW=100 (84–117); BR=2.8:1 (2.7:1–3.2:1); SP=2.1:2.2:1. The tentacles are not completely evaginated, a basal tentacle swelling is absent. TW=51–56. The tentacle sheaths are straight and the TSW without invaginated tentacles is nearly half as small (TSW=23–28) than with invaginated tentacles (TSW=42–46). Prebulbar organs and muscular rings around the basal part of the tentacle sheaths are absent. The retractor muscles originate in the basal part of the bulbs.

The tentacular armature is homeoacanthous, homeomorphous, and consists of compact rose-thorn-shaped tentacular hooks (upper basal armature, L=14–19; B=12–15). The hooks are in tight spirals (Fig. 11) and the hooks diminish in size towards the basal part of the tentacles (L=12–14; B=9–12); hsr=6–7.

REMARKS. Only two species, *N. riseri* and *N. lingualis*, have been described as having a similar champion-shaped scolex form as well as a homeoacanthous, homeomorphous tentacular armature such as described for the present specimens. *N. riseri* is characterised by the champion-shaped scolex (see Dollfus, 1960), however, the hooks in the basal part of the tentacle (L=11–12, B=11–12) are smaller than observed for the present specimens. *N. lingualis* corresponds with a similar basal armature (see above) and scolex proportions as described for specimens of *N. lingualis* taken from *Trachyurus felicipes* (see Dollfus, 1942). However, the general scolex form with the small banana-shaped bulbs of *Nybelinia lingualis* (see Dollfus, 1942) clearly differs to the present specimens. Thus, they are

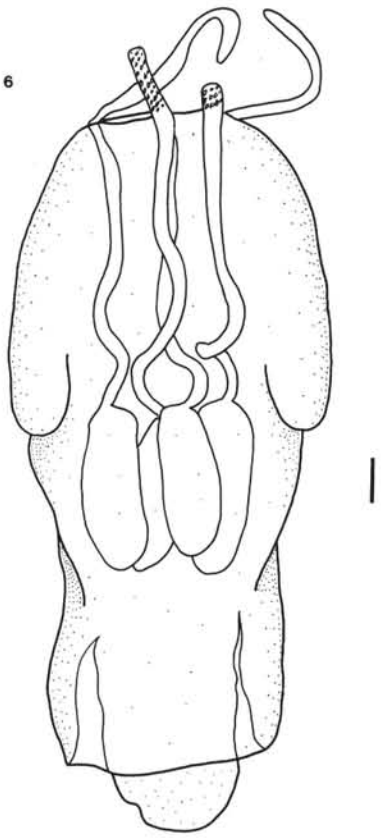


Fig. 6 *Nybelinia lingualis* from *Torquigener pleurogramma*. Scolex. Scale bar=100 µm.

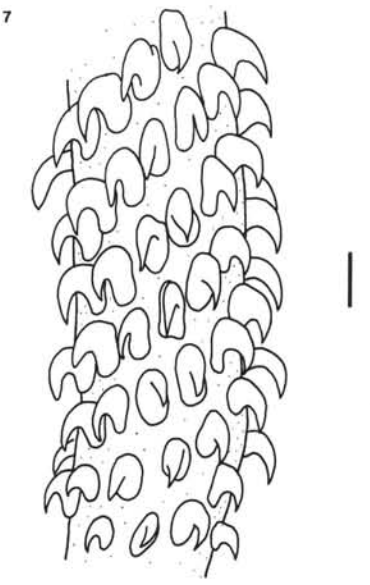


Fig. 7 *N. lingualis* from *T. pleurogramma*. Homeomorphous basal armature consisting of rounded hooks without anterior extension of the basal plate. Scale bar=10 µm.

identified as belonging to *Nybelinia riseri* on basis of the characteristic scolex form. It has to be kept in mind that the tentacles of the present specimens were not completely evaginated. The present finding represents a new host and locality record.

6. *Nybelinia sakanariae* sp. nov. (Figs 12–13)

MATERIAL EXAMINED. Holotype and paratype, BMNH 1976.1.7.9, Hecht *leg.*, 2 postlarvae from the stomach of *Xiphiurus capensis*, South Africa. Additional material: BMNH 1976.1.7.7–8, Hecht *leg.*, 1 postlarva from the testes of *Trachurus trachurus*, Algoa Bay, South Africa.

DESCRIPTION (Fig. 12). Measurements: SL=1512, 1507; SW=775, 747; pbo=700, 700; pv=680, 647; pb=397, 386; ppb=94, 100; vel=360, 335; app=360, 335; BL=387, 335; BW=116, 113; BR=3.3:1, 3:1; SP=1.8:1.7:1, 1.8:1.7:1. A basal tentacle swelling is absent. TW=51–56. The tentacle sheaths are short, little coiled with a TSW=51–56. Prebulbar organs and muscular rings around the basal part of the tentacle sheaths are absent. The retractor muscles originate in the basal part of the bulbs.

The armature is homeoacanthous, homeomorphous, and consists of compact rose-thorn-shaped tentacular hooks (Fig. 13); upper basal and metabasal armature, L=16–22; B=13.5–17.0). Characteristic basal hooks are absent. However, the hooks diminish in size towards the basal part of the tentacles (L=12–14; B=11–13); hsr=6–7.

ADDITIONAL MATERIAL. SL=3270; SW=1020; pbo=1134; pv=1172; pb=605; ppb=567; vel=756; app=740; BL=580; BW=147; BR=3.9:1; SP=2:2:1. The tentacles are short and a basal tentacle swelling is absent. TW=56–61. The tentacle sheaths are straight, prebulbar organs and muscular rings around the basal part of the tentacle sheaths are absent. The retractor muscles originate in the basal part of the bulbs. Metabasal armature, L=21–23; B=15–17. A characteristic basal armature is absent, the hooks diminish in size towards the basal part of the tentacles (L=11–13; B=11–13); hsr=7.

REMARKS. The present specimens correspond with *Nybelinia strongyla* in having a similar scolex, SP, BR, TW and a similar hook size. However, the scolex size is smaller than indicated by Dollfus (1960) and the type material deposited at the MNHN Paris revealed a different hook shape. The material also resembles *N. riseri* as described by Dollfus (1960) with corresponding values of SL, BL, BW, BR, ppb and a similar basal hook size. The hook form of *N. riseri* appears massive with a broad base, and hooks are tightly packed along the tentacle. However, the hooks of the armature of *N. riseri* of about 11–12 µm are distinctly smaller than in the present specimens, and the characteristic scolex form of *N. riseri* (see above) was not present. The specimens also have some similarities with *Nybelinia queenslandensis* Jones & Beveridge, 1998 with a similar hook form. However, the specimens clearly differ in having the hooks more tightly spaced and different values for SL, TW, BR and SP. Thus, the present specimens represent a new species, *Nybelinia sakanariae* sp. nov. Interestingly, the additional material obtained from another host had a much larger scolex than observed

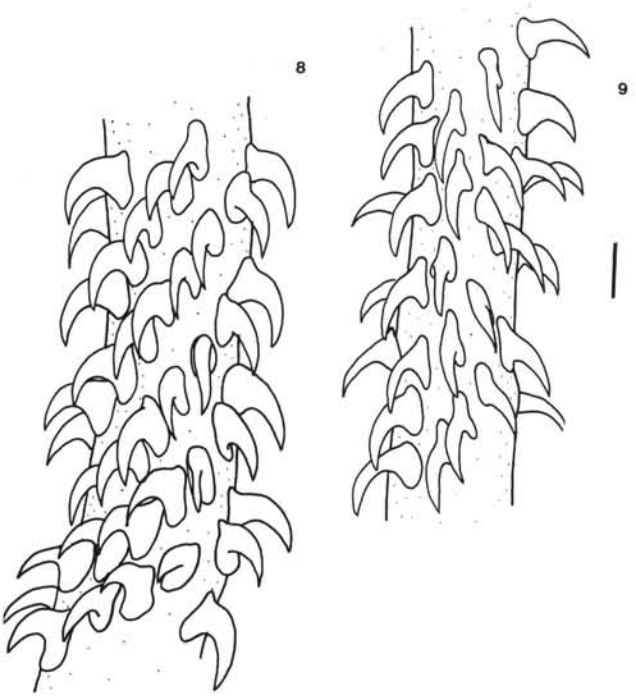


Fig. 8 *N. lingualis* from *T. pleurogramma*. Homeomorphous metabasal armature. Scale bar=10 μm.

Fig. 9 *N. lingualis* from *T. pleurogramma*. Homeomorphous apical armature. Scale bar=10 μm.

for the type material but the same kind of tentacular armature. The size should be considered as a case of intraspecific morphological variability within the species.

ETYMOLOGY. The new species is named after J.A. Sakanari, in honour to her work on the life cycle of trypanorhynch cestodes.

7. *Nybelinia schmidti* sp. nov. (Figs 14–15)

MATERIAL EXAMINED. Holotype BMNH 1982.12.3.1, G. Ross *leg*., 23.07.1978, 1 adult from the stomach of *Isurus glaucus*, Algoa Bay, South Africa.

DESCRIPTION (Figs 14–15). Measurements: SL=1172; SW=832; pbo=794; pv=473; pb=289; ppb= 46; vel=373; BL=289; BW=104 (94–117); BR=2.8:1; SP=2.7:2.6:1. The tentacles are long and slender; TW=18.4–23.5; and a basal swelling is absent. The tentacle sheaths are spirally coiled; TSW=46–51. Prebulbar organs and muscular rings around the basal part of the tentacle sheaths are absent. The retractor muscles originate at the basal part of the bulbs.

The tentacular armature is homeoacanthous, homeomorphous, and a characteristic basal armature is absent. The massive and rose-thorn shaped hooks increase in size towards the metabasal part of the tentacle, L=13.5–15.0; B=11.7–13.3 (metabasal) and L=9.0–10.3; B=8.3–9.0 (basal); the hooks in the metabasal part of the tentacle are slightly more slender than in the basal part; hsr=5–6.

The strobilar is acraspedote, with about 240 very large segments, wider than long. The proglottids in the anterior part of strobila are 140–155 long × 1400–1540 wide, the final proglottids enlarge in size towards 450–560 × 2800–3080. In mature proglottids, genital

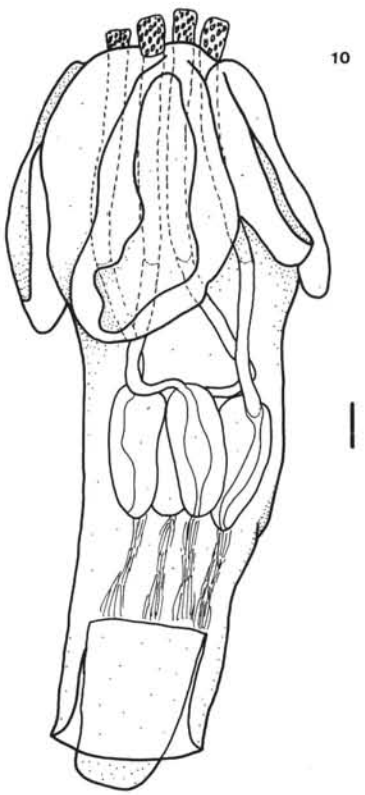


Fig. 10 *Nybelinia riseri*. Scolex from *Trachyurus felicipes*. Scale bar=100 μm.

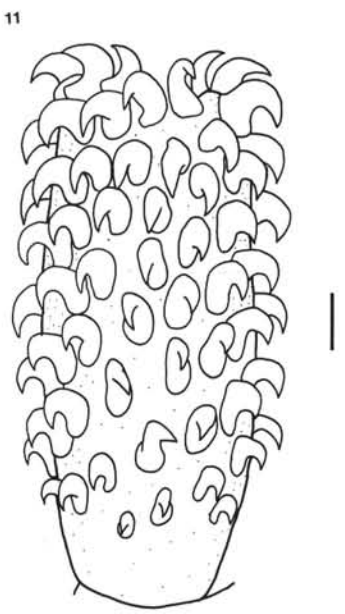


Fig. 11 *N. riseri*. Homeomorphous basal armature consisting of rounded hooks without anterior extension of the basal plate. Scale bar=15 μm.

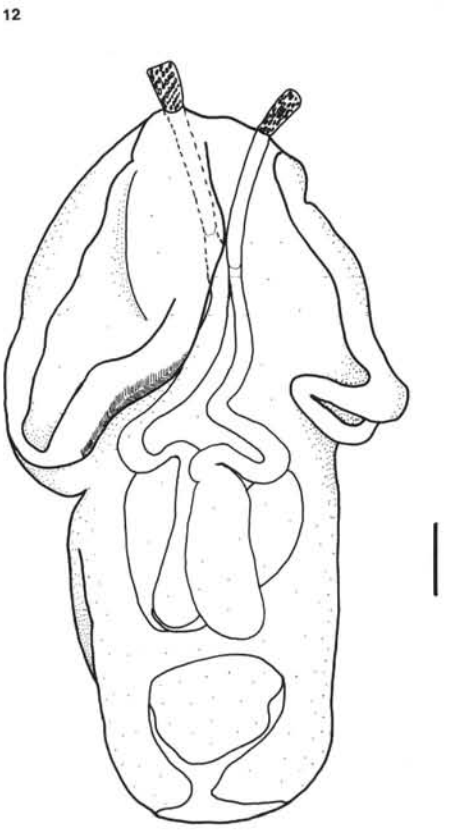


Fig. 12 *Nybelinia sakanariae* sp. nov. Scolex from *Xiphiurus capensis*. Scale bar=150 μm.

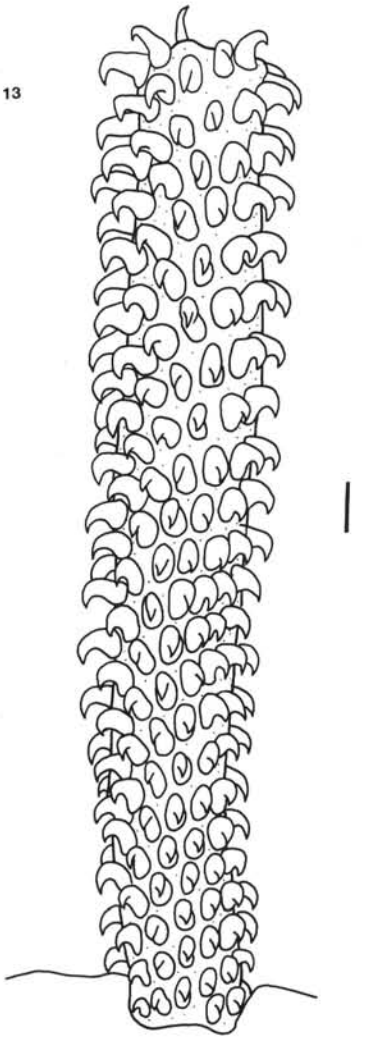


Fig. 13 *N. sakanariae* sp. nov. from *X. capensis* Homeomorphous basal and metabasal armature. Scale bar=20 μm.

atrium ventro-submarginal, in anterior third of the segment; genital pores alternate irregularly. Cirrus sac elongate and slender, in final segments 55–90 × 1200–1330 in size, directed anteromedially, parallel to anterior end of the proglottids; sac thin-walled; cirrus unarmed and coiled within sac. Other internal structures not seen.

REMARKS. The present specimen belongs to subgroup IAa of Palm *et al.* (1997) and resembles, with a rose-thorn-shaped basal and metabasal tentacular armature, *N. anthicosum, N. palliata, N. strongyla, N. riseri, N. sphyrnae* and *N. thyrsites*. A comparison with the type material of *N. anthicosum* and *N. palliata*, deposited at the U.S. National Parasite Collection, Beltsville, revealed differences in oncotaxy. *N. strongyla* has a much larger TW=55 and SL=2300 and larger hooks, and *N. riseri* has smaller hooks together with a larger TW and a different scolex form (Dollfus, 1960). *N. sphyrnae* and *N. thyrsites* also differ in hook and scolex form/size (see Beveridge & Campbell, 1996). Thus, the present specimen represents a new species, *Nybelinia schmidti* sp. nov.

ETYMOLOGY. The new species is named after the parasitologist G. D. Schmidt.

8. *Nybelinia scoliodoni* (Vijayalakshmi, Vijayalakshmi & Gangadharam, 1996) comb. nov. (*Tentacularia scoliodoni*) (Figs 16–17)

MATERIAL EXAMINED. BMNH 1976.11.5.42–43, R. van der Elst *leg.*, 1 adult from the gut of *Carcharhinus limbatus*, South Africa. Additional material: NHMV 2111, A.E. Shipley *leg.*, 1 adult from *Glyphis gangeticus* (=*Carcharhinus gangeticus*), India.

DESCRIPTION (Fig. 16–17). Measurements: SL=667; SW=320; pbo=267; pv=227; pb=144; vel=267; BL=133 (125–144); BW=59 (56–64); BR=2.2:1; SP=1.9:1.6:1. The tentacles are 173–200 long and a basal tentacle swelling is absent. The TW varies along the tentacle; at the most proximal part of the basal armature, TW=14–17; at the basal armature, TW=23–25; at the apical armature, TW=12–13. The tentacle sheaths are straight (TSW=18–21), prebulbar organs and muscular rings around the basal part of the tentacle sheaths are absent. The retractor muscles originate in the basal part of the bulbs.

The metabasal armature is homeoacanthous, homeomorphous,

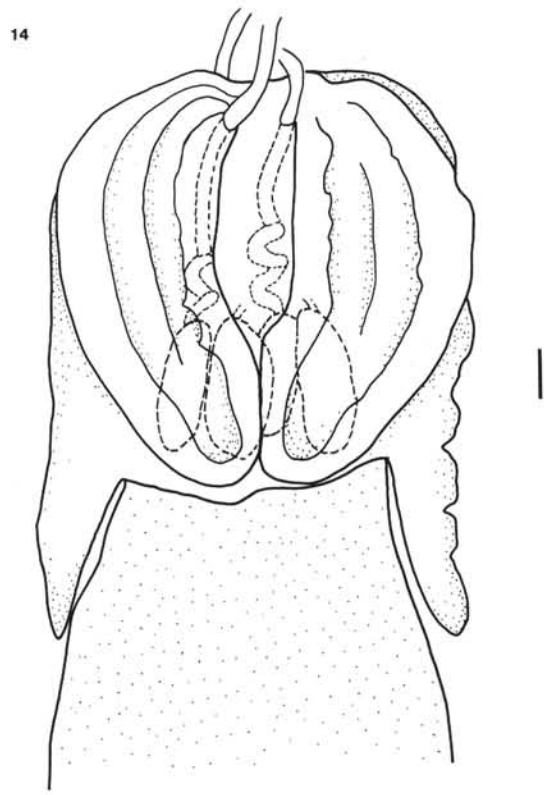


Fig. 14 *Nybelinia schmidti* sp. nov. Scolex from *Isurus glaucus*. Scale bar=100 μm.

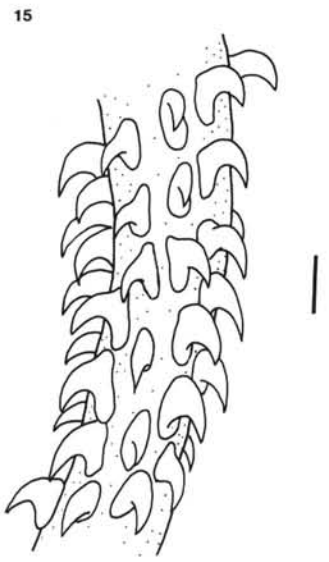


Fig. 15 *N. schmidti* sp. nov. Homeomorphous basal and metabasal armature. Scale bar=10 μm.

and a distinctive basal armature is present (Fig. 17). The basal armature consists of about 11 rows with compact rose-thorn-shaped hooks, increasing in size (row 1–5: L=3.5–5.6, B=3.5–4.9, and row 6–11: L=7–9.8, B=5.6–8.4). From rows 12–14, the hook form changes to long, spiniform metabasal hooks (L=22–26) with a small base (B=7.7–10.5); hsr basal=6–7, hsr metabasal=4–5.

No complete strobila is present. The first acraspedote proglottids are wider than long (330 × 50) and slightly increasing in size (490 × 205). Other internal structures were not seen.

REMARKS. Palm & Walter (1999) considered *Nybelinia* (*Tentacularia*) *scoliodoni* (Vijayalakshmi, Vijayalakshmi & Gangadharam, 1996) as a species of uncertain status due to an uncomplete original description and a strong similarity to *Nybelinia indica* Chandra, 1986. However, the present specimen confirms the validity of *Tentacularia scoliodoni*, and assigns the species to the genus *Nybelinia* Poche, 1926. Though the scolex measurements of the present specimen are smaller and the scolex and bulb ratios show differences to those given in the original description, the tentacular armature corresponds in detail with *N. scoliodoni*. The drastic change in form from rose-thorn shaped basal to spiniform metabasal hooks, with a size between L=8–11 in the basal and L=30, B=3 in the metabasal armature as given by Vijayalakshmi *et al.* (1996), is unique within the genus. As with the scolex size, the hooks of the present specimen are slightly smaller than those of the original description. However, Vijayalakshmi *et al.* (1996, figure 8) demonstrated minute hooks on the basal part of the tentacle, similar to those in rows 1–5 of the present specimen, and also indicated the characteristic change in TW along the tentacles (figure 7). The known range of distribution is extended to South Africa, and *Carcharhinus limbatus* is a new host for *N. scoliodoni*. Under the co-type material of *Nybelinia perideraeus* (Shipley & Hornell, 1906), slide No. 12f, an adult *N. scoliodoni* with an uncomplete strobila was found. The scolex size and tentacular armature corresponds to the material deposited at the BMNH. Thus, *Glyphis gangeticus* represents a new host for *N. scoliodoni*, and this finding supports its occurrence in Indian Ocean waters.

N. scoliodoni has similarities with *N. indica* Chandra, 1986, which was also described from the Indian Ocean. *N. indica* differs due to its larger size, a large ppb, a larger TW in the basal part of the tentacle and a more gradual change in hook form along the tentacles (Chandra, 1986). In contrast to this, the form of the hooks as well as their size show similarities to both *N. scoliodoni* and the present specimen. The real identity of *N. indica* and a possible synonymy with *N. scoliodoni* cannot be decided until a re-examination of the type material is undertaken. Therefore, both species remain valid, and on the basis of the above described characters, the present specimen is identified as *N. scoliodoni*. The present specimen was obtained from a carcharhinid shark from South Africa, which further extends the distribution of the species from the Indian to the South African coast.

Palm (1997b) found similar small *Nybelinia* specimens (SL=640, SP=3.6:2:1) with a similar tentacular armature (L=5–24, rose-thorn shaped basal and spiniform metabasal hooks (Fig. 18; figure 17 in Palm, 1992) in *Pseudupenaeus maculatus* from the North-East Brazilian coast and described the specimens as *N. indica* with a homeomorphous metabasal armature. The drawing of the tentacular armature of one of the specimens as given in Palm (1992) shows similar hooks as demonstrated for the present specimens. However, its affinities with *N. indica* or *N. scoliodoni* cannot be decided at present (see above).

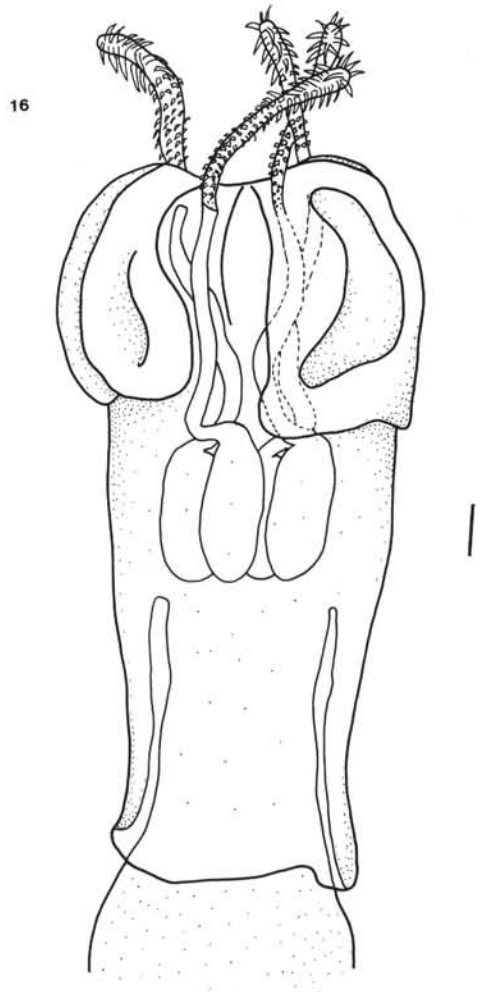


Fig. 16 *Nybelinia scoliodoni*. Scolex from *Carcharhinus limbatus*. Scale bar=50 µm.

Fig. 17 *N. scoliodoni*. Homeomorphous basal and metabasal armature consisting of rose-thorn shaped and falcate hooks. Scale bar=20 µm.

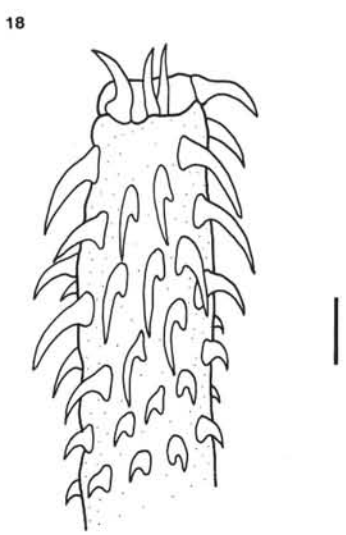


Fig. 18 *N. indica*. Homeomorphous basal and metabasal armature (Palm 1992). Scale bar=20 µm.

9. *Nybelinia* sp.

MATERIAL EXAMINED. BMNH 1979.9.13.94, *leg.* R. van der Elst, 2 postlarvae from the kidney of *Coryphaena hippurus*, Cape Vidal, South Africa.

DESCRIPTION. The following measurements were taken: SL=1172, 1228; SW=775, 907; pbo=888, 850; pv=624, 548; pb=252, 257; ppb= 33, 38; app=364, 294; vel= 186; 150; BL=246 (234–247), 251 (224–266); BW=99 (84–112), 114 (112–117); BR=2.5:1, 2.2:1; SP=3.5:2.5:1, 3.3:2.1:1. The tentacles are long, TL=586–606, 583 and slender, TW=32.8–35.2, 32.8–35.2 and a basal swelling is absent. The tentacle sheaths are sinuous; TSW=32.8–37.6, 32.8–37.6. Prebulbar organs and muscular rings around the basal part of the tentacle sheaths are absent. The retractor muscles originate at the basal part of the bulbs.

The tentacular armature is homeoacanthous, homeomorphous and a characteristic basal armature is absent. The small and rose-thorn shaped hooks are of the same size along the tentacle, L=8.0–10.4, 8.0–10.4; B=8.8–11.0, 8.8–11.0; hsr=6.

REMARKS. The present specimens resemble *N. oodes* and *N. riseri* as described by Dollfus (1960), both species having small rose-thorn shaped homeomorphous hooks along the tentacle. *N. riseri* has a

different scolex form (see above), larger TW and TSW and the tentacular hooks are larger. In contrast, the morphological measurements SL, TL, TW, TSW and the small size and form of the hooks are similar to *N. oodes* (SL=920, TL=400–500, TW=24–27, TSW=40–48, B=9.3–10.6) as described by Dollfus (1960). Examination of the type material revealed a slightly heteromorphous tentacular armature for *N. oodes*. This neither corresponds to the original description (see Dollfus, 1960, Figs 36–37) nor to the present specimens. Thus, the present postlarvae should not be assigned to *Nybelinia oodes* and might represent a new *Nybelinia* species. This needs to be decided after re-description of the *Nybelinia* type material deposited at the MNHN Paris.

Heteronybelinia gen. nov.

Trypanorhynchs with the characters of the Tentacullariidae Poche, 1926. Scolex compact, 4 triangular bothridia, with hook-like microtriches along the bothridial borders and filamentous microtriches on the rest of the bothridia and the scolex. 4 tentacles emerging from bulbs, retractor muscle originates at base of bulbs. 4 proboscis of variable length and width, armed with hooks; metabasal tentacular armature homeoacanthous with heteromorphous hooks on different tentacle surfaces. Basal hooks heteromorphous, characteristic basal armature absent or present. Cirrus unarmed, cirrus sac alternates irregularly.

TYPE SPECIES. *Heteronybelinia estigmena* (Dollfus, 1960).

OTHER SPECIES. *H. alloiotica* (Dollfus, 1960), *H. cadenati* (Dollfus, 1960), *H. elongata* (Shah & Bilquees, 1979), *H. eureia* (Dollfus, 1960), *H. heteromorphi* sp. nov., *H. karachii* (Khurshid & Bilqees, 1988), *H. minima* sp. nov., *H. nipponica* (Yamaguti, 1952), *H. perideraeus* (Shipley & Hornell, 1906), *H. punctatissima* (Dollfus, 1960), *H. robusta* (Linton, 1890), *H. rougetcampanae* (Dollfus, 1960), *H. senegalensis* (Dollfus, 1960), *H. yamagutii* (Dollfus, 1960), all formerly belonging to the genus *Nybelinia* Poche, 1926.

COMMENT. This new genus comprises subgroup II in Palm *et al.* (1997).

10. *Heteronybelinia elongata* (Shah & Bilqees, 1979) comb. nov. (Figs 19–25)

MATERIAL EXAMINED. Types BMNH 1989.5.18.5, Shah & Bilqees *leg.*, 1979, 2 postlarvae from *Pellona elongata*, Pakistan; BMNH 1980.6.23.13, A. Roy *leg.*, 1 postlarva from the gonads of *Lepturacanthus savala*, Hooghly estuary, India. Other material not measured: BMNH 1992.7.1.193–196, A. Roy *leg.*, postlarva from *Lepturacanthus savala*, Sugar Island, Bay of Bengal.

DESCRIPTION. The scolex morphology of the type material of *H. elongata* (Shah & Bilqees, 1979) from *Pellona elongata*, together with the scoleces and armature of specimens from *Lepturacanthus savala*, are given in Figs 19–25. The type material is re-described as follows (Fig. 19): The scolex is about 2 mm large, but is variable in size, SL=2173, 2362 (a third specimen on the same slide: 1740); SW=1000, 1021; pbo=982, 964; pv=1021, 1021; pb=536, 548; ppb= 227, 252; app=605, 624; vel=302, 300; BL=514 (490–536), 525 (510–548); BW=130 (125–135), 128 (112–144.8); BR=3.9:1, 4.1:1; SP= 1.8:1.9:1. The tentacles are long and slender with a TW metabasal =15.2–17.6; TW basal= 17.6–20.8, diminishing slightly towards the metabasal part of the tentacle. A basal tentacular swelling is absent. Prebulbar organs were absent, muscular rings around the basal part of the tentacle sheaths were visible in some specimens (see also Fig. 22). Tentacle sheaths straight; retractor muscles originate at the basal part of the bulbs.

The tentacular armature is homeoacanthous, heteromorphous, and a characteristic basal armature is absent (see Figs 23–24). The form of the hooks is rose-thorn shaped. The hook size in the metabasal region (see Fig. 25) ranged between L=11.2–12.8; B=9.2–11.2, 11.2–12.8 (bothridial) and L=9.2–11.2, 8.8–11.2; B=5.6–7.2, 7.2–9.2 (antibothridial), and the hook size in the basal region of the tentacle was between L=9.2–11.2; B=9.2–11.2 (bothridial) and L=5.6–7.2; B=4–5.6, 5.6–7.2 (antibothridial); the hook size increases only on the antibothridial tentacle surface; hsr=6–7.

Postlarvae from *Lepturacanthus savala* (Fig. 20): Measurements: SL=1360; SW=642; pbo=662; pv=605; pb=397; ppb=61; app=257; vel=233; BL=387 (377–397), BW=91 (89–94); BR=4.2:1; SP= 1.7:1.5:1. The tentacles are long and slender with a TW metabasal =20.8–24; TW basal= 24–27.2. A basal tentacular swelling is absent. Prebulbar organs are absent and muscular rings around the basal part of the tentacle sheaths are present; TSW= 32.8–36, straight; retractor muscles originate at the basal part of the bulbs.

The hook size in the metabasal armature ranged between L=9.6–11.2; B=9.2–11.2 (bothridial) and L=8.0–9.2; B=5.6–7.2 (antibothridial), and the hook size in the basal part of the tentacle was between L=7.2–9.2; B=7.2–9.6 (bothridial) and L=4–5.6; B= 5.6–7.2 (antibothridial); The hook size increases mainly on the antibothridial tentacle surface towards the metabasal part of the tentacle; hsr=6–7.

Scoleces, muscular ring and the tentacular armature of specimens BMNH 1992.7.1.193–196 are shown in Figs 21–25.

REMARKS. The type material of *N. elongata* from *Pellona elongata* is re-described, as well as additional material of the same species collected from *Lepturacanthus savala*. Though the material differs in absolute morphometrical values, BR, SP and the tentacular armature are very similar. Recently, Palm & Walter (1999) examined the type material of *N. perideraeus* from the Natural History Museum Vienna and re-described the species as having a homeoacanthous, heteromorphous tentacular armature. The authors considered *N. dakari* to be synonymous with *N. perideraeus*, characterised by tentacular hooks of similar size in the basal and metabasal part of the tentacle. The present material of *N. elongata* also has very similar scolex measurements as well as similar tentacular hooks to those of *N. perideraeus*. However, the hook size increases on the antibothridial tentacle surface towards the metabasal part of the tentacle. Thus, until further material becomes available, both species are considered valid. The position of *N. elongata* changes from subgoup IAb to IIAa in Palm *et al.* (1997).

N. elongata appears to have a high degree of scolex variability, e.g. the SL ranges between 1739 and 2362 in 3 different specimens on the same slide. As well as similarities between *N. elongata* and *N. perideraeus*, a close relationship can be seen to other species from subgroup IIAa, all having a similar armature with similar sized tentacular hooks. It is recommended that the type material of species in subgroup IIAa described by Dollfus (1960) be compared with *N. perideraeus* and *N. elongata* to clarify the species identity within this subgroup (also see below).

11. *Heteronybelinia estigmena* (Dollfus, 1960) comb. nov. (Figs 26–28)

MATERIAL EXAMINED. BMNH 1976.11.5.42–43, R. van der Elst *leg.*, 1 adult from the gut of *Carcharhinus limbatus*, South Africa; BMNH 1985.11.8.63–64,. R. van der Elst *leg*; 11.05.1984, 1 adult from *Carcharhinus leucas*, Richards Bay, South Africa; BMNH

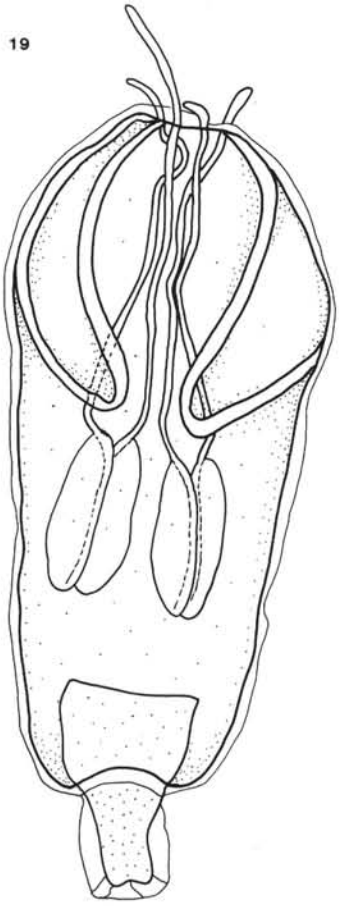


Fig. 19 *Heteronybelinia elongata*. Scolex from *Pellona elongata*. Scale bar=200 µm.

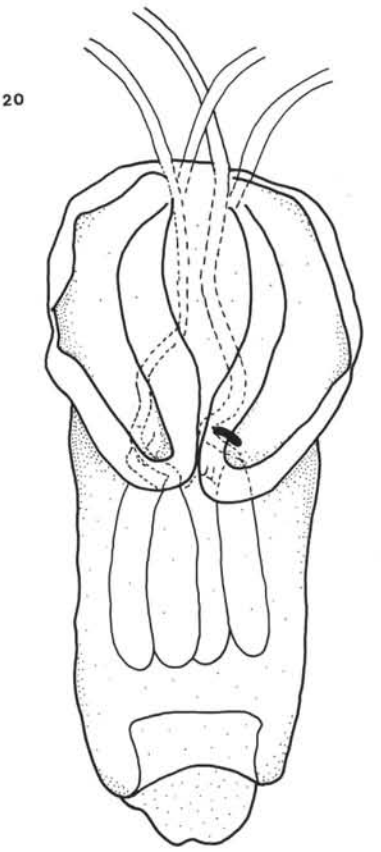


Fig. 20 *H. elongata*. Scolex from *Lepturacanthus savala*. Scale bar=100 µm.

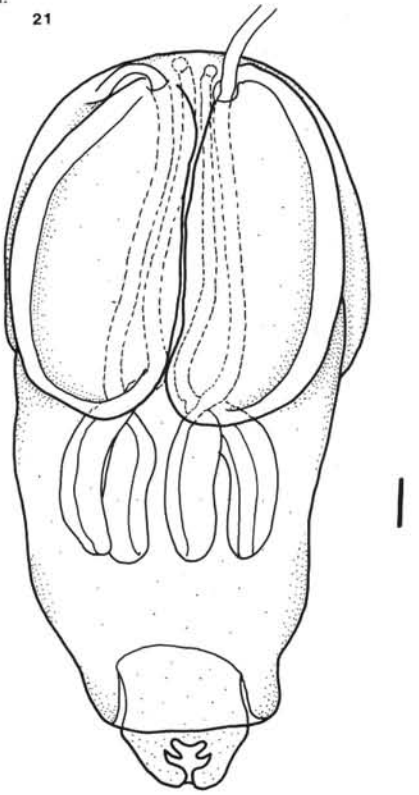


Fig. 21 *H. elongata*. Scolex from *L. savala*. Scale bar=100 µm.

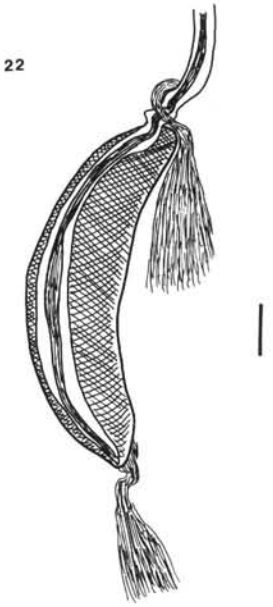


Fig. 22 *H. elongata* from *L. savala*.. Muscular ring around tentacle sheath. Scale bar=50 µm.

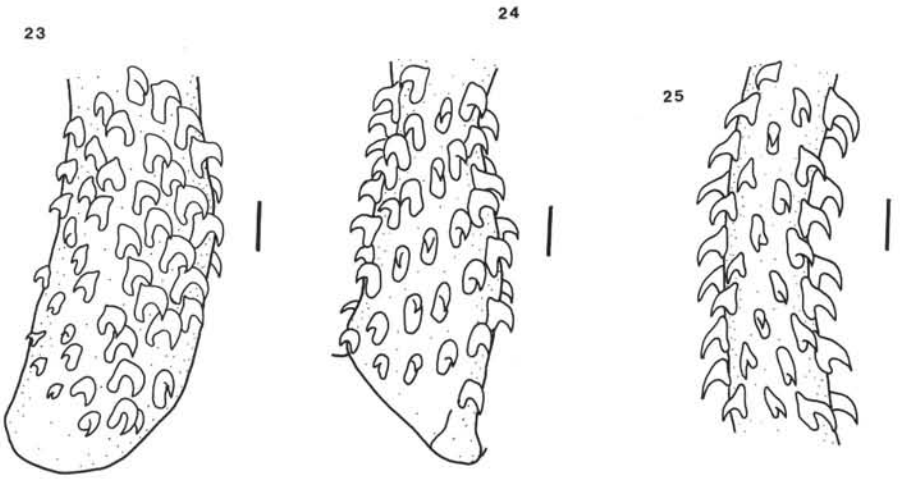


Fig. 23 *H. elongata* from *L. savala*. Heteromorphous basal armature, external surface. Scale bar=10 μm.
Fig. 24 *H. elongata* from *L. savala*. Heteromorphous basal armature, bothridial surface, external face on left hand side. Scale bar=10 μm.
Fig. 25 *H. elongata* from *L. savala*. Heteromorphous metabasal armature, external surface. Scale bar=10 μm.

1996.8.19.1–3, D.T.J. Littlewood *leg.*, Aug. 1995, 1 postlarva from the stomach of a kingfish, Port Royal, Kingston, Jamaica.

DESCRIPTION. The scolex of a specimen from *C. limbatus* is shown in Fig. 26. Measurements: SL=1210, 1134, 1000; SW=700, nm, 493; pbo=700, 642; 500; pv=510, 473, 500; pb=448, 330; 307; ppb=95, 75, 27; vel=170, 232, 160; BL=442 (428–448), 326 (312–331), 287 (280–294); BW=128 (126–130), 104 (84–107), 81 (75–92); BR=3.5:1, 3.2:1; 3.5:1; SP=1.6:1.1:1, 1.9:1.4:1, 1.6:1.6:1. The tentacles are long and slender, with TW=27–30; 23–28, 20–22; TSW increases in size towards the base of the tentacles (24–27, 22–28, 29–32), a basal tentacular swelling is absent. Prebulbar organs are absent and muscular rings around the basal part of the tentacle sheaths are present in specimens from *Carcharhinus* spp. The retractor muscles originate at the base of the bulbs.

The tentacular armature is homeoacanthous, heteromorphous, and a characteristic basal armature is absent (Figs 27–28). The hooks diminish in size towards the basal part of the tentacle, the hooks are rose-thorn shaped on both sides of the tentacles. The single hook sizes of the three specimens in the metabasal armature were L=9.2–11.2, B=9.2–11.2; L=10.4–12, B=10.4–12; L=9.2–10.5, B=9.3–10.5 (mean L bothridial=10.4) and L=7.2–9.6, B=7.2–9.6; L=9.6–10.4, B=10.4–12; L=7.4–8, B=7.4–8 (mean L antibothridial=8.7), and in the basal part of the tentacle L=7.2–9.2, B=7.2–9.2; L=7.2–8.8, B=7.2–8.8; L=7.2–8, B=7.2–8 (bothridial) and L=5.6–7.2, B=5.6–7.2; L=5.6–7.2, B=4.8–5.6; L=5–6, B=5–6, (antibothridial); hsr=6–7.

The slightly stained strobila of the specimen from *Carcharhinus limbatus* consists of about 190 acraspedote proglottids. Proglottids wider than long and increasing in size (about 50th proglottid: 55–60 × 475–485; 100th: 185–210 × 560–585; 150th: 360–420 × 755–780; 190th: 670–730 × 840–900). 80–90 testes in a single layer, 33–55 (between 100th and 150th segments) and 50–65 (final segments) in diameter. Genital pores ventro-lateral, in the anterior half near the middle of the proglottids, alternate irregularly; cirrus sac elongate, directed anteromedially, reaching the anterior end of the proglottids; increasing in size, from 50–60 × 290–350 until 85–90 × 345–365 in last segments. Other internal structures not seen. The acraspedote proglottids of the specimen from *Carcharhinus leucas* vary in size,

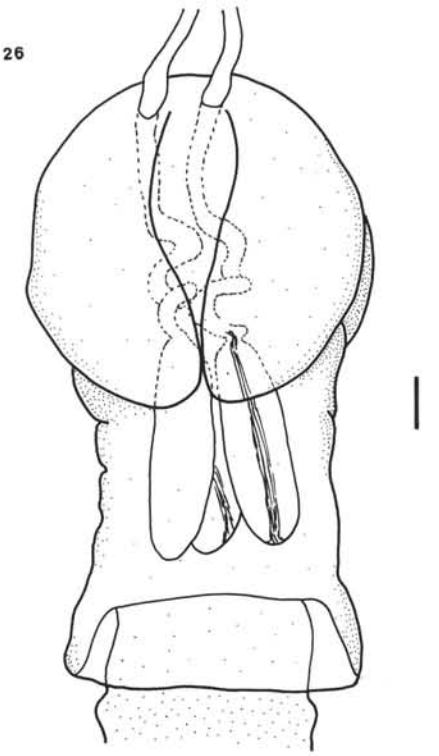


Fig. 26 *Heteronybelinia estigmena*. Scolex from *Carcharhinus limbatus*. Scale bar=100 μm.

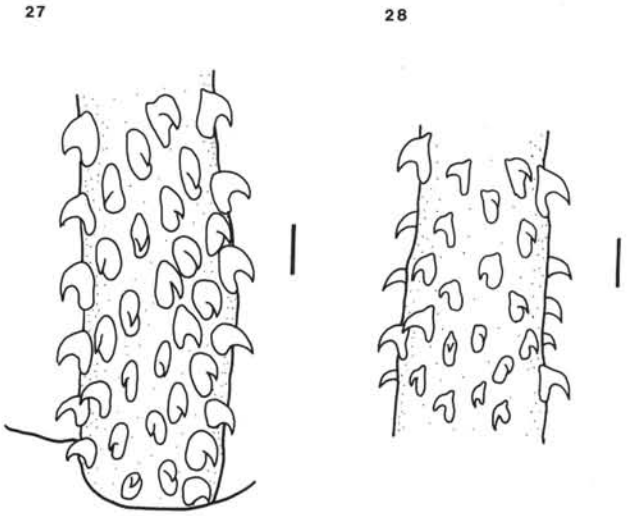


Fig. 27 *H. estigmena* from *C. limbatus*. Heteromorphous basal armature, bothridial surface. Scale bar=10 µm.

Fig. 28 *H. estigmena* from *C. limbatus*. Heteromorphous metabasal armature, antibothridial surface. Scale bar=10 µm.

depending on contraction (anterior segments: 80 × 330–20 × 520), final segments 300–370 × 860–880; testes 33–55 in diameter.

REMARKS. The present specimens are most similar to *H. alloiotica*, *H. punctatissima* and *H. estigmena*, which were considered as belonging to subgroup IIAa by Palm *et al.* (1997), comprising species having a heteromorphous tentacular armature with hooks diminishing in size towards the basal part of the tentacle, and no characteristic basal armature. Dollfus (1960) described 6 species, *H. dakari, H. estigmena, H. punctatissima, H. senegalensis, H. alloiotica* and *H. cadenati*, with a heteromorphous tentacular armature and small hooks of about 10–11 µm (bothridial) and 8 µm (antibothridial). All these species have a very similar scolex and hook morphology, mainly differing from each other by a different bulb ratio and different scolex proportions. Palm & Walter (1999) proposed the synonymy of *Nybelinia dakari* Dollfus, 1960 with *H. perideraeus*, differing from the other species in having a basal armature of similar size to the metabasal armature. Though Dollfus (1960) stated that the bulb ratio of *H. dakari* was small (about 2.5:1), his drawing (figure 43) indicates a ratio of about 4. His bulb measurements of 0.380–0.386 × 0.96–0.100 mm are faulty (0.96 might stand for 0.096), which would also indicate a bulb ratio of about 3.9, thus, corresponding to the ratio of *H. perideraeus* (see Palm & Walter, 1999). *H. senegalensis, H. alloiotica* and *H. cadenati* also have a bulb ratio of about 4, and *H. punctatissima* differs from *H. estigmena* by having a slightly different bulb ratio and different scolex dimensions (2.1:1.6:1 vs 1.5:1:1). However, these two species appear to be very similar, and the tentacular armature of *H. alloiotica* (Figs 29–30), which was re-described by Palm (1995) from *Carcharhinus limbatus* from the Gulf of Mexico, also corresponds with that of the present material. The present finding represent 3 new host and locality records for *H. estigmena*.

This and a previous study (Palm & Walter, 1999) demonstrate wide intraspecific variability in scolex morphology within several species of *Nybelina* (see also *H. africana*) and *Heteronybelinia*, similar to that described earlier for other tentacullariid genera *Tentacularia* and *Hepatoxylon* (Palm, 1995). Additionally, Palm *et al.* (1997) pointed out the dubious value of the 2 characters tentacle width and bulb ratio, which Dollfus used to distinguish the above 6

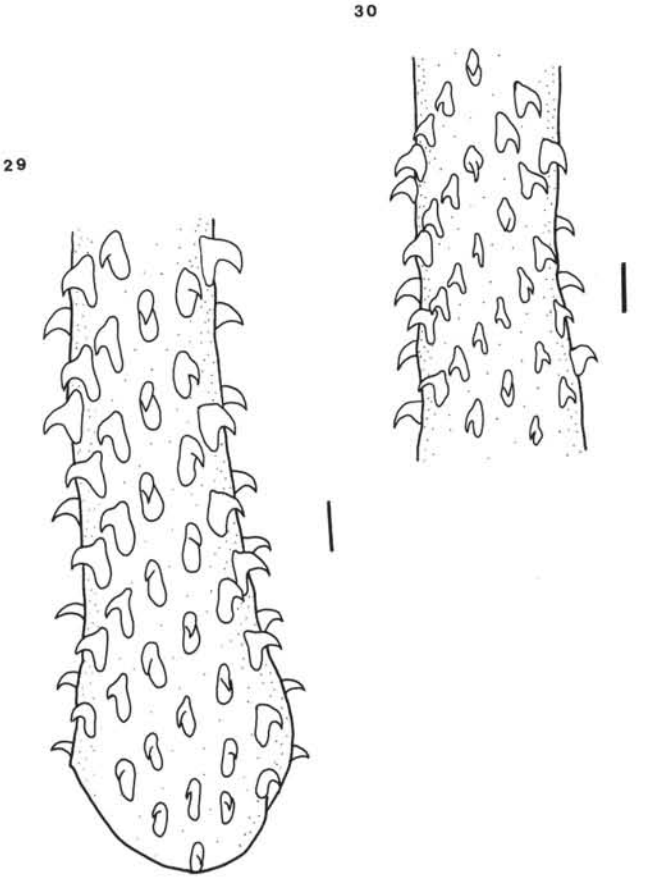


Fig. 29 *Heteronybelinia alloiotica* from *Carcharhinus limbatus*. Heteromorphous basal armature, bothridial surface. Scale bar=10 µm.

Fig. 30 *H. alloiotica*. Heteromorphous metabasal armature, antibothridial surface. Scale bar=10 µm.

species. The identification of the present specimens as *Heteronybelinia estigmena* needs to be confirmed by re-examining the type material of the above mentioned species. The possibly synonymy of all these species has to be kept in mind.

Heteronybelinia cf. ***estigmena*** (Dollfus, 1960) comb. nov.

MATERIAL EXAMINED. BMNH 1989.1.18.2, R. Bray *leg.*, 14.01.1971, Cirolana, Atlantic Ocean off Morocco, 33°43'N, 8°38'W, 222–236 m. 1 postlarva from *Scomber scolias*.

REMARKS. Due to its scolex morphology and the homeoacanthous, heteromorphous tentacular armature with a basal hook size of L=8.8–10.4, B=8.8–10.4 (bothridial) and L=5.6–7.2, B=5.6–7.2 (antibothridial), the present specimen was tentatively identified as *H. estigmena*. However, the partly invaginated metabasal armature and the unusual form due to fixation prevent precise identification. The presence of a muscular ring around the tentacle sheaths could not be demonstrated to be of any taxonomic significance.

12. ***Heteronybelinia heteromorphi*** sp. nov. (Figs 31–33)

MATERIAL EXAMINED. Holotype and paratype, BMNH 1982.4.26.282–284, R. van der Elst *leg.*, 16.5.78, 2 adults from the stomach of *Sphyrna mokarran*, South Africa; Additional material: BMNH 1968.2.14.30–31, Gooding *leg.*, 2 adults from *Sphyrna blochii*, Singapore.

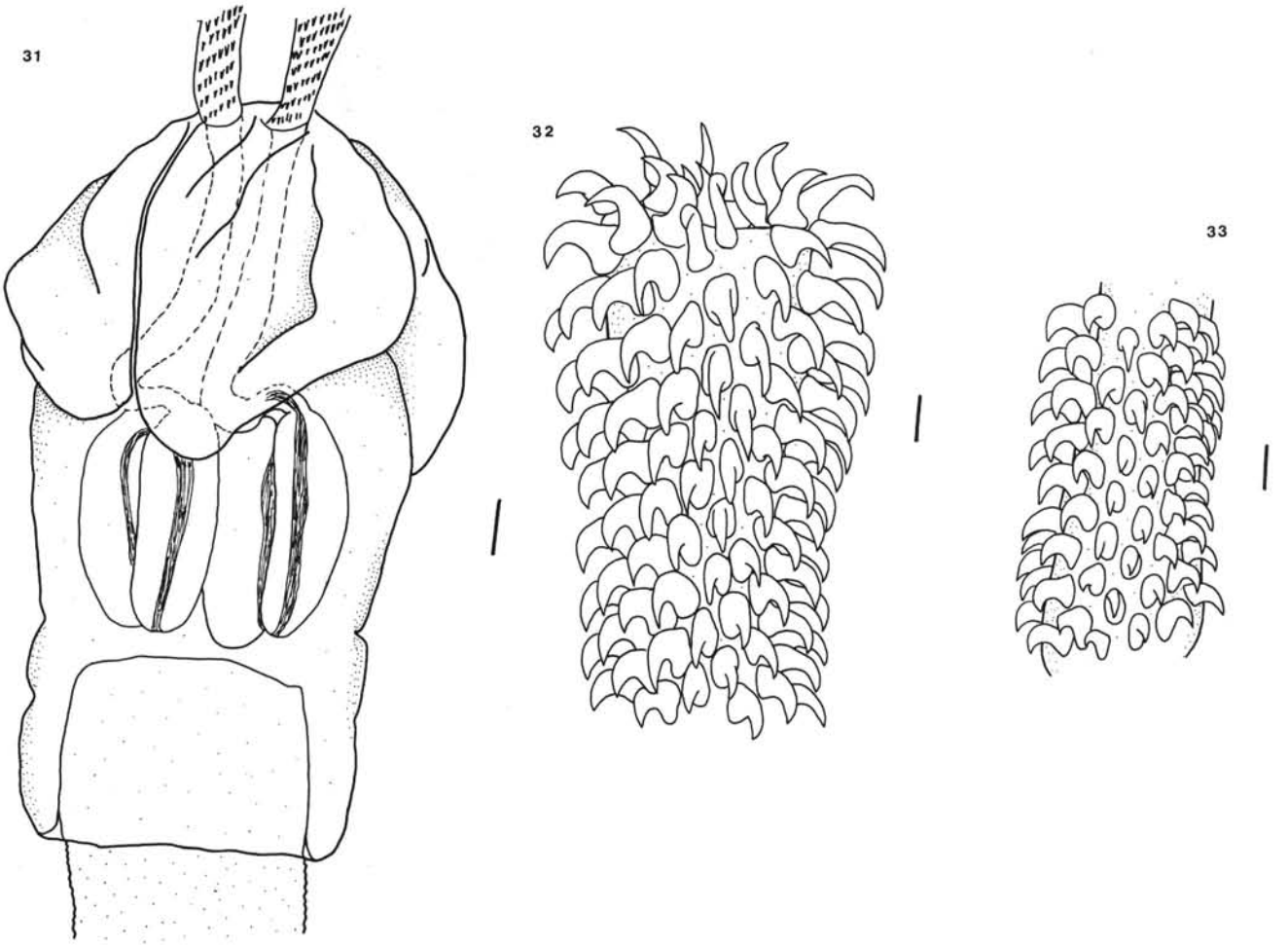


Fig. 31 *Heteronybelinia heteromorphi* sp. nov.. Scolex from *Sphyrna makorran*. Scale bar=100 µm.
Fig. 32 *H. heteromorphi* sp. nov. from *S. makorran*. Heteromorphous metabasal armature, bothridial (left hand side) and antibothridial (right hand side) surfaces. Scale bar=15 µm.
Fig. 33 *H. heteromorphi* sp. nov. from *S. makorran*. Heteromorphous basal armature, bothridial (left) and antibothridial (right) surfaces. Scale bar=15 µm.

DESCRIPTION (Figs 31–33). With the characters of the genus *Heteronybelinia*. Measurements: SL=1367, 1300, 1367, 1467; SW=833, 934, 800, 800; pbo=767, 734, 734, 867; pv=534, 500, 567, 506; pb=500, 447, 334, 427; ppb=20, 40, 105, 160; vel=333, 340, 317, 300; BL=437 (414–454), 404 (387–414), 327 (308–334), 405 (368–427); BW=154 (134–163), 181 (174–187), 158 (137–175), 176 (173–179); BR=2.8:1, 2.2:1, 2.1:1, 2.3:1; SP=1.5:1.1:1, 1.6:1.1:1, 2.2:1.7:1, 2.0:1.2:1. The tentacles are long, robust and increase in diameter towards the tip of the tentacle; TL=540 (27 rows of hooks), 480 (23 rows), 560 (25 rows), nm; TW basal=53–60, 53–60, 48–50, 52–54; TW apical=75–80, 65–70, 58–61, nm; a basal swelling is absent. The tentacle sheaths are straight; TSW=53–66, 45–54, 68–70, 69–74. Prebulbar organs and muscular rings around the basal part of the tentacle sheaths are absent. A thickening, encircling more than half of the tentacle sheath near the entrance to the bulbs, is present. The retractor muscles originate at the basal part of the bulbs.

The tentacular armature is homeoacanthous, heteromorphous, and a characteristic basal armature is absent. The form of the hooks is rose-thorn shaped becoming more slender towards the tip of the tentacle (Fig. 32). Similarly, the form changes from the bothridial to the antibothridial surface. The hook sizes of the metabasal tentacular armature for BMNH 1982.4.26.282–284 and 1968.2.14.30–31 are as follows: above 22th row, L=24–28, B=19–21; L=25–28, B=15–17 (bothridial) and L=28–32, B=12–15; L=30–32, B=12–15 (antibothridial); about 14th row, L=22–25, B=16–17; L=21–23, B=16–17 (bothridial) and L=25–28, B=11–15; L=30–32, B=12–15 (antibothridial); The basal hooks (Fig. 33) ranged between L=16–18 and B=10–12; hsr=7–8.

The strobila of the largest specimen of BMNH 1982.4.26.282–284 consists of about 350 acraspedote proglottids. The proglottids are uniform in measurements, much wider (934–1034) than long (50–134). Proglottids of smaller specimens measured about 600 in width and 100 in length. The genital pores alternate irregularly; cirrus sac 35–40 × 140–160. Small testes (25–40 in diameter) and vitellaria (10–15); other internal structures not seen.

REMARKS. The present specimens belong to subgroup IIAa (Palm *et al.*, 1997), with a heteromorphous armature and hooks increasing in size towards the metabasal part of the tentacle. The large hook size

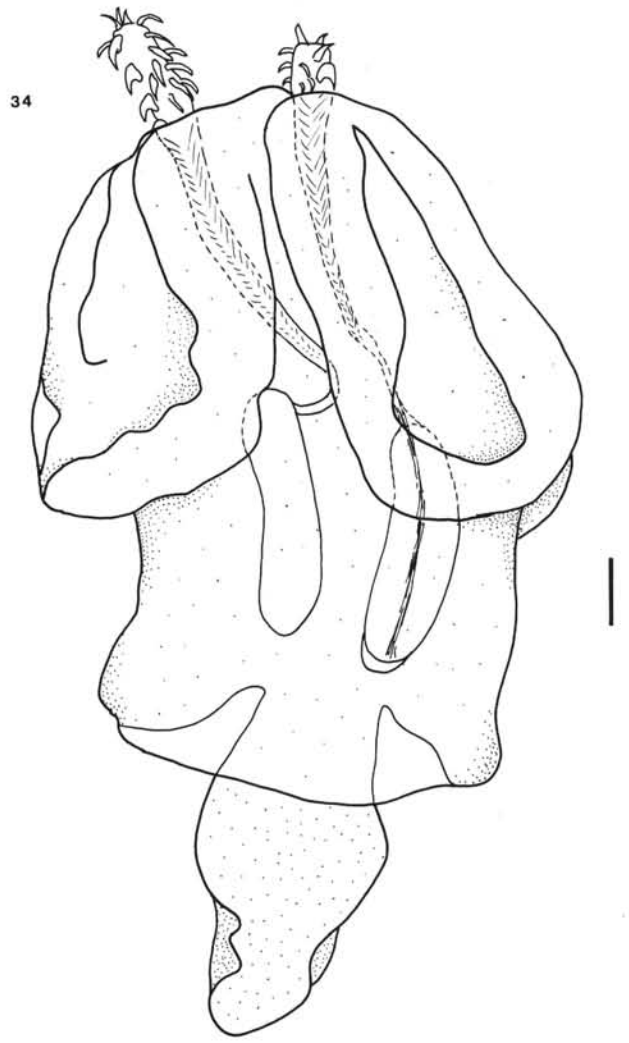


Fig. 34 *Heteronybelinia minima* sp. nov.. Scolex from *Harpodon nehereus*. Scale bar=50 µm.

and the tight arrangement of the hooks along the tentacle is characteristic for the specimens, and together with the heteromorphous armature, the character combination corresponds only with *Heteronybelinia eureia* as described by Dollfus (1960). Though the morphometrical data correspond, the drawings of the tentacular armature of *H. eureia* as given by Dollfus (1960, figures 33–35) indicate more widely spaced and more slender hooks than was observed in the present specimens. This was confirmed by examination of the type material at the MNHN Paris. Additionally, the description by Dollfus, based on postlarvae, precludes comparison of the strobilar characters. Thus, the present specimens represent a new species, *Heteronybelinia heteromorphi* sp. nov. Other similar species with a compact hook pattern are *Nybelinia queenslandensis* and *N. strongyla* (see Jones & Beveridge, 1998, Dollfus, 1960). However, these species have a homeomorphous tentacular armature.

ETYMOLOGY. The new species is named after the characteristic heteromorphous armature.

13. ***Heteronybelinia minima*** sp. nov. (Figs 34–38)

MATERIAL EXAMINED. Holotype and paratype, BMNH 1980.12.2.1, A. Roy *leg*., 14.09.79, 2 postlarvae from *Harpodon*

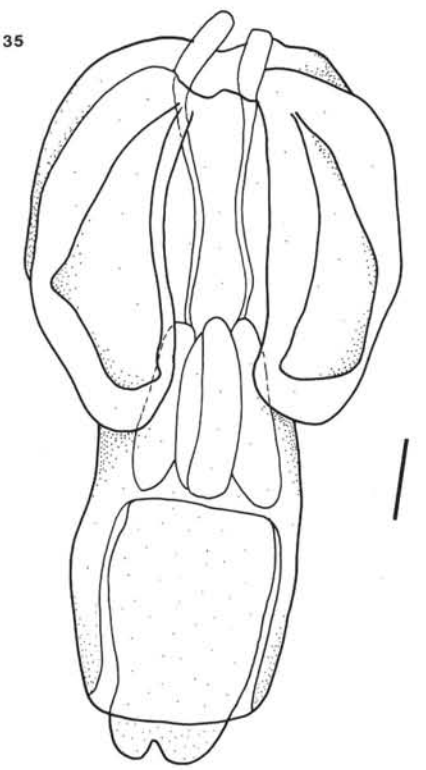


Fig. 35 *H. minima* sp. nov.. Scolex from *Polynemus paradiseus*. Scale bar=100 µm.

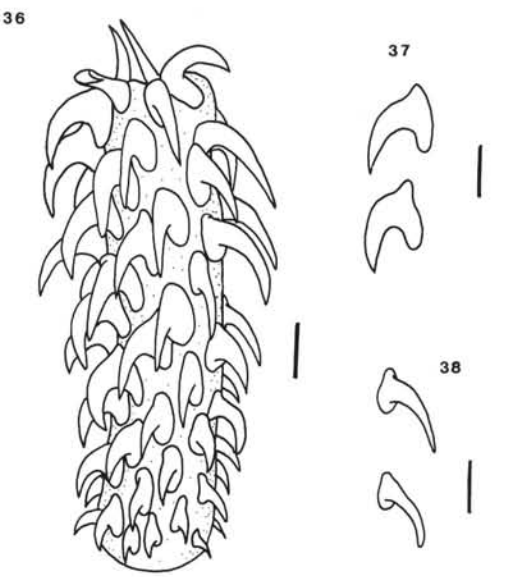


Fig. 36 *H. minima* sp. nov. from *P. paradiseus*. Heteromorphous metabasal armature, bothridial (left hand side) and antibothridial (right hand side) surfaces. Scale bar=15 µm.

Fig. 37 *H. minima* sp. nov., hooks on bothridial surface. Scale bar=15 µm.

Fig. 38 *H. minima* sp. nov., hooks on antibothridial surface. Scale bar=15 µm.

nehereus, Houghly estuary, India. Other postlarvae identified as *H. minima* sp. nov.: BMNH 1980.6.23.13 from *Polynemus* sp.; 1980.6.23.14, A. Roy *leg.*, *Polynemus* sp., Houghly estuary, India (4 postlarvae); 1992.7.1.189 from *Harpodon nehereus*; 1992.7.1.190–192, A. Roy *leg.*, *Polynemus paradiseus*, Sugar Island, Bay of Bengal (5 postlarvae).

DESCRIPTION. With the characters of the genus *Heteronybelinia*. The scolex of the holotype as well as the scolex and basal and metabasal tentacular armature of a specimen from *P. paradiscus* are shown in Figs 34 and 35–38 respectively. The scolex is small, differing in size and shape between specimens. Measurements (from types 1980.12.2.1): SL=706, 926; SW=386, 642; pbo=427, 454; pv=267, 397; pb=200, 252; app=280, 270; vel=84, 186; BL=191 (187–200), 237 (229–252); BW=54 (43–66), 83 (74–89); BR=3.5:1, 2.9:1; SP=2.1:1.3:1, 1.8:1.6:1. The tentacles are long, in inverted condition nearly reaching the apical end of the bulbs, with a TW=23–28; TW increases towards the tip of the tentacles, a basal tentacular swelling is absent. Prebulbar organs and muscular rings around the basal part of the tentacle sheaths are absent. The retractor muscles originate at the base of the bulbs (Fig. 34).

The tentacular armature is homeoacanthous, heteromorphous and a characteristic basal armature is absent (Figs 36–38). The hooks diminish in size towards the basal part of the tentacle, the form of the hooks differs from compact and rose-thorn shaped (bothridial) to falcate hooks with a stout base (antibothridial). The hook size in the metabasal armature ranged between L=20.8–24; B=15.2–16.8 (bothridial) and L=24–27.2; B=5.6–7.2 (antibothridial), and the hook size in the basal part of the tentacle was between L=12–17.6; B=7.2–12 (bothridial) and L=15.2–17.6; B=7.2–8.8 (antibothridial); hsr=6.

ETYMOLOGY. The new species is named for its small size.

REMARKS. *H. minima* sp. nov. is easily identifiable by its small scolex size and the characteristic tentacular armature. The present specimens from *Harpodon nehereus*, *Polynemus paradiseus* and *Polynemus* sp. clearly demonstrate a heteromorphous armature, where the hook form changes from rose-thorn shaped to falcate hooks, giving the tentacles a heteroacanthous appearance. However, the quincunx formation of the hooks is still recognisable. The absence of a characteristic basal armature places the species in subgroup IIAa of Palm *et al.* (1997).

14. *Heteronybelinia robusta* (Linton, 1890) (Figs 39–41)

MATERIAL EXAMINED. BMNH 1976.11.5.42–43, R. van der Elst *leg.*, 1 adult from the gut of *Carcharhinus limbatus*, South Africa. Additional material: USNPC 7727, E. Linton *leg.*, 3 adults from *Dasyatis centroura*, Woods Hole, USA.

DESCRIPTION (Figs 39–41). With the characters of the genus *Heteronybelinia*. Measurements: SL=1020; SW=699; pbo=510; pv=377; pb=257; vel=294; BL=246 (233–257); BW=82 (79–84); BR=3:1; SP=2:1.5:1. The tentacles are slender, and increase in width towards the metabasal and decrease towards the apical part of the tentacle; TW=24–30; a basal swelling is absent. The tentacle sheaths have two spiral coils; TSW=24–27. Prebulbar organs and muscular rings around the basal part of the tentacle sheaths are absent. The retractor muscles originate at the basal part of the bulbs.

The tentacular armature is homeoacanthous, heteromorphous and a characteristic basal armature is absent. The form of the hooks changes slightly from compact and rose-thorn shaped (bothridial) to more slender hooks with a stout base (antibothridial) (Fig. 40). The hook size in the metabasal armature ranged between L=11.7–12.5; B=7.2–9.2 (bothridial) and L=13.0–14.0; B=5.6–7.2 (antibothridial), and hooks of the basal part of the tentacle (Fig. 41) were minute, between L=5.6–7.2; B=5.6–7.2 (bothridial) and L=4–5.6; B=4–5.6 (antibothridial), continuously increasing towards the tip; hsr=6–7.

The strobila of the small specimen consists of 71 acraspedote proglottids. Measurements of the proglottids were as follows: proglottid 20: length=48, width=320; proglottid 48: length=140, width=400; proglottid 62: length=490, width=656; proglottid 70: length=610, width=746. Genital pores ventro-lateral, in the anterior third of the proglottids, alternate irregularly; cirrus sac elongate, directed anteromedially, reaching the anterior end of the proglottids. Other internal structures were not seen.

REMARKS. The present specimen corresponds to 3 specimens described as *N. robusta* by Linton (1924). Scolex measurements and the characteristic tentacular armature lie within the same range. Thus the present specimen is identified as belonging to the same species. However, as the type material of *N. robusta* is not available at the USNPC, the taxonomy of *N. robusta* still needs to be clarified.

There are several species which have rose-thorn-shaped heteromorphous hooks along the tentacle. *H. robusta* differs from all adequately described species due to the small scolex size with minute basal hooks, continuously increasing in size from 5 to 12.5 (bothridial) and 4 to 14 μm (antibothridial). The general hook form remains rose-thorn shaped along the tentacles. Thus, the present specimen belongs into subgroup IIAa of Palm *et al.* (1997).

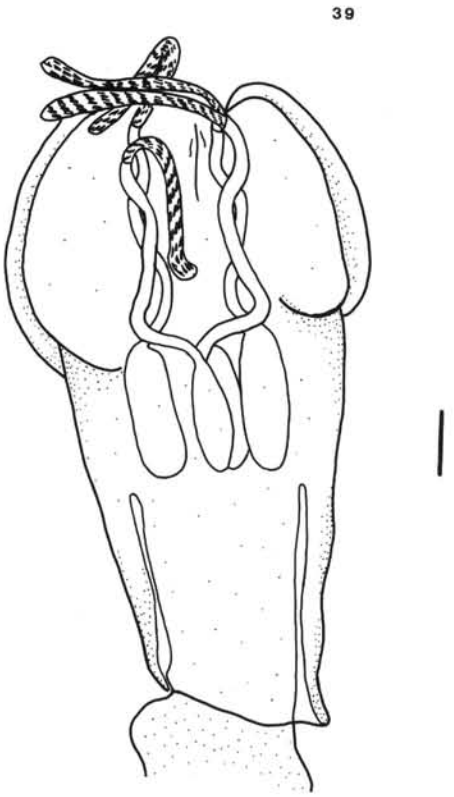
15. *Heteronybelinia yamagutii* (Dollfus, 1960) nov. comb. (Fig. 42–44)

MATERIAL EXAMINED. BMNH 1976.11.5.41, R. van der Elst *leg.*, 1 adult from the stomach of *Sphyrna lewini*, South Africa.

DESCRIPTION. *Nybelinia yamagutii* was described in detail by Dollfus (1960, see figures 1–5) and Palm *et al.* (1997). The following measurements were taken: SL=2646; SW=1080; pbo=1134; pv=1000; pb=1455; vel=140; BL= 1430 (1418–1455); BW= 236 (220–247); BR=6.1:1; SP=0.8:0.7:1. The tentacles are long and slender and deminish in size along the tentacle; TW metabasal=90–98, TW apical=66–75. A basal tentacular swelling is not present. The tentacle sheaths are sinuous; TSW=51–56. Prebulbar organs and muscular rings around the basal part of the tentacle sheaths are absent. The retractor muscles originate in the basal part of the bulbs.

The armature is homeoacanthous, heteromorphous, and a characteristic basal armature with bill-hooks is present. The hooks of the metabasal armature are different in shape and size on bothridial and antibothridial tentacle surfaces. The form of the hooks is described in detail in Dollfus (1960). The hook size in the metabasal armature was between L=69–75 (bothridial) and L=60–65 (antibothridial). The size of the basal hooks was between L=18–23. The bill-hooks were in rows 3–4 with a total length of 41–46.

The 12.5 cm long worm has a craspedote strobilar with several hundred segments increasing in size (Figs 42–44); last proglottid with rounded proximal end. The size varies in the first 2 cm of the strobila between 70–100 long and 300–420 wide, from 4–5 cm between 195–220 and 780–900 (Fig. 42), from 7–8 cm between 360–420 and 1260–1400 (Fig. 43), and at the final proglottids between 360–400 and 1680–1820 (Fig. 44). In mature proglottids, the elongate cirrus sac is directed anteromedially, and alternates irregularly (Fig. 42). Testes often ovoid, in double layer, often not in middle of segments. Testes number per proglottis (62–70 and 80–90), size (40–55 and 50–70 in diameter) and size of vitellaria (13–16 and 15–33 in diameter) increases between the first 3 cm and after 7 cm



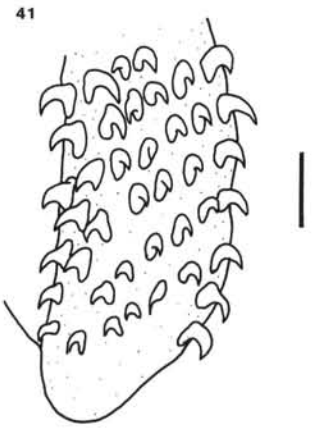


Fig. 39 *Heteronybelinia robusta*. Scolex from *Carcharhinus limbatus*. Scale bar=100 µm.
Fig. 40 *H. robusta* Heteromorphous metabasal armature, bothridial (right hand side) and antibothridial (left hand side) surfaces. Scale bar=10µm.
Fig. 41 *H. robusta*. Heteromorphous basal armature, antibothridial surface. Scale bar=10 µm.

of the strobila respectively. Ovary centally, follicular, with 2 major branches.

REMARKS. The scolex measurements as well as the form and size of the tentacular armature correspond with those in the original description (Dollfus, 1960) and those of specimens from the Mozambique coast (Palm et. al., 1997). A high variability in scolex morphology has been described from 20 specimens of 7 host species by Palm *et al.* (1997). However, *H. yamagutii* is easily distinguishable from all other *Heteronybelinia* species by its metabasal tentacular armature consisting of large claw-like hooks and its basal armature consisting of smaller hooks and characteristic bill hooks. Adult *H. yamagutii* is a large trypanorhynch with segments of different shape and size along the strobila. The testes number as well as the size of testes and vitellaria also vary along the strobila. The present finding is the first report of adult *H. yamagutii*, occurring in *Sphyrna lewini* from South Africa. A world-wide distribution for the species has been proposed by Palm *et al.* (1997).

Mixonybelinia gen. nov.

Trypanorhynchs with the characters of the Tentaculariidae Poche, 1926. Scolex compact, 4 triangular bothridia, with hook-like microtriches along the bothridial borders and filamentous microtriches on the rest of the bothridia and the scolex. 4 tentacles emerging from bulbs, the retractor muscle originates at the base of the bulbs. 4 proboscides of various length and width, armed with massive hooks; metabasal tentacular armature homeoacanthous with heteromorphous hooks on different tentacle surfaces. Characteristic basal armature consisting of homeomorphous hooks present. Cirrus unarmed, cirrus sac alternates irregularly.

TYPE SPECIES. *Mixonybelinia beveridgei* (Palm, Walter, Schwerdtfeger & Reimer, 1997) (subgroup II in Palm *et al.*, 1997).

OTHER SPECIES. *Mixonybelinia southwelli* (Palm & Walter, 1999)

16. *Mixonybelinia beveridgei* (Palm, Walter, Schwerdtfeger & Reimer, 1997) comb. nov.

MATERIAL EXAMINED. The Natural History Museum London:

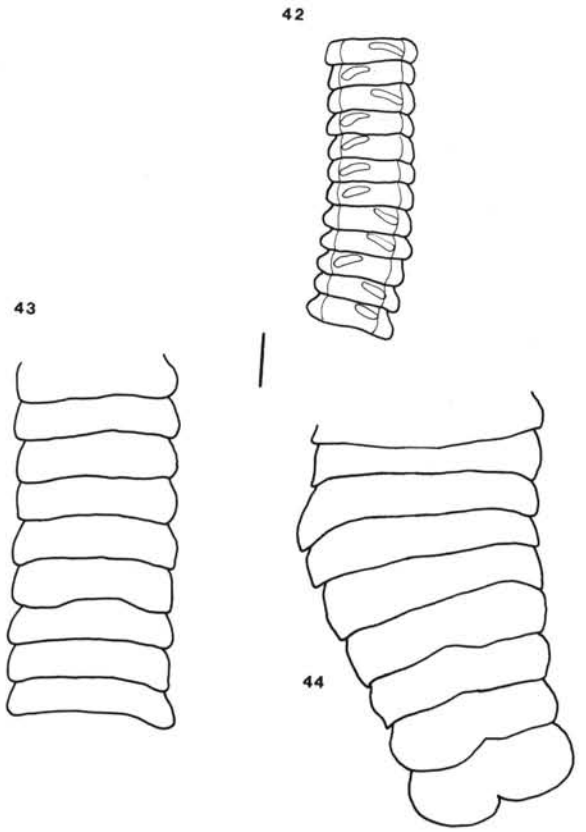


Fig. 42–44 *H. yamagutii*. Strobila 4–5 cm (42) and 7–8 cm (43) behind scolex, and last proglottids (44). Scale bar=500μm.

BMNH 1997.3.24.1, 1997.3.24.2, 1997.3.24.3–4, 1997.3.24.5. *M. beveridgei* was described in detail by Palm *et al.* (1997).

17. *Mixonybelinia southwelli* (Palm & Walter, 1999) comb. nov.

MATERIAL EXAMINED. The Natural History Museum London: BMNH 1977.11.4.7, 1977.11.4.8–9. *M. southwelli* was described in detail by Southwell (1929) and Palm & Walter (1999).

DISCUSSION

Of the material deposited at the British Museum Natural History, 17 different trypanorhynch species, formerly all belonging to the genus *Nybelinia* Poche, 1926, were identified. In addition, two new genera, *Heteronybelinia* gen. nov. and *Mixonybelinia* gen. nov., are erected, and 4 new species, *N. sakanariae* sp. nov., *N. schmidti* sp. nov., *H. heteromorphi* sp. nov., and *H. minima* sp. nov., are described. The new genera separate species with a homeoacanthous, homeomorphous (*Nybelinia*) from those having a homeoacanthous, heteromorphous metabasal armature with heteromorphous basal hooks (*Heteronybelinia* gen. nov.) and from species with a heteromophous metabasal and homeomorphous basal armature, which are assigned to *Mixonybelinia* gen. nov. *Mixonybelinia* is a tentacullariid genus in which two different armature types occur along the tentacle. This has been described earlier for non-tentacullariid trypanorhynchs, such as the mixodigmatid *Mixodigma leptaleum* Dailey & Vogelbein, 1982 and the lacistorhynchid *Dasyrhynchus talismani*, Dollfus, 1935 (Dailey & Vogelbein, 1982; Beveridge & Campbell, 1993)

After a first subdivision of the genus by Dollfus (1960), Palm *et al.* (1997) recently subdivided the different *Nybelinia* species on the basis of the tentacular armature and discussed the erection of subgenera. However, the authors did not split the genus into several genera or subgenera. The material in the Natural History Museum clearly demonstrates that the species of the subgroupings as proposed by Palm *et al.* (1997) can be consistently separated on the basis of their characteristic metabasal and basal tentacular armature. They can clearly be recognised, though there is a higher level of intraspecific variation associated with the scolex as well as hook sizes along the tentacles than previously indicated.

Following Campbell & Beveridge (1994) and Palm (1995), the erection of different genera on the basis of the tentacular armature is justified. In their most recent classification, Campbell & Beveridge (1994) used the tentacular armature at the superfamily level, and Palm (1995) at the generic level. In other families within the order, several genera can be distinguished mainly on basis of their characteristic tentacular armature, such as the genera *Callitetrarhynchus*, *Lacistorhynchus*, *Mixodigma*, *Poeciloacanthum* and *Pseudolacistorhynchus* (other examples see Campbell & Beveridge, 1994, Palm, 1995). This simplifies further studies of tentacullariid trypanorhynchs of the *Nybelinia* type.

The present study again demonstrates a high level of morphological variation within different species of *Nybelinia* and *Heteronybelinia*. *Nybelinia africana* and *Heteronybelinia yamagutii* have been re-described and do not correspond in every detail with the original descriptions of the type material. Similar morphological variation occurs in other tentacullariid trypanorhynchs, such as *Tentacularia coryphaenae*, evidenced by the numerous synonymies in the literature (see Dollfus, 1942, Palm, 1995). In comparing the detailed descriptions of 16 *Nybelinia* species recognised by Dollfus (1960), several of them are very similar and can be distinguished only on the basis of minor differences of the hooks, which lie within the limits of intraspecific variation for this character in more recently described species (see Palm & Walter, 1999). Additionally, Palm *et al.* (1997) demonstrated a low host specificity of several *Nybelinia* species, which leads to the suggestion that some of the material examined by Dollfus, which was mainly obtained from the same region off Dakar but from different host fish species, might belong to the same species. This is especially possible in subgroup IIAa (*Heteronybelinia estigmena* species complex) and in the *Nybelinia aequidentata* species complex (see remarks above). It is recommended that until the type material and more material from the Dakar region can be examined, the species described by Dollfus (1960) remain valid. However, several are possible synonyms.

Adult tentacullariids also can show a low level of host specificity and different shark species can harbour several *Nybelinia* and *Heteronybelinia* species. During the present study, *Carcharhinus limbatus* and *C. leucas* were found to be infested with 3 species (*Nybelinia scoliodoni*, *Heteronybelinia estigmena*, *H. robusta*) and 2 species (*Nybelinia africana*, *Heteronybelinia estigmena*) respectively. A similar wide host range has been also demonstrated for some other trypanorhynchs (Palm & Overstreet in press, Palm, 1997b) as well as other marine parasite species, such as Antarctic parasites infesting the rock cod *Notothenia coriiceps* from the South Shetland Islands (Palm *et al.*, 1998). This behaviour seems to be characteristic for cosmopolitan marine parasitic helminths, such as the nematodes *Contracaecum osculatum* and *Pseudoterranova decipiens*. In conclusion, it is postulated that the currently known tentacullariid genera and most of the species are

characterised by a cosmopolitan distribution pattern, which distinguishes those trypanorhynchs from species such as the eutetrarhynchids of endemic Australian and South American rays (see also Palm *et al.*, 1997, Rego & Dias, 1976). A low level of specialisation of tentaculariids with a flexible, unspecialised life cycle pattern might be essential for these oceanic trypanorhynchs, which would explain for example their occurrence in marine plankton (Dollfus, 1974) as well as the enigmatic infestation of humans (Fripp & Mason, 1983).

The present and previous studies demonstrate that several species exist which change their kind of tentacular armature continuously along the tentacle, such as *N. africana* and *N. lingualis*. Some species change more abrupt between a characteristic basal and metabasal armatures, such as *H. scoliodoni* and *M. southwelli*, while others retain their general hook shape but continuously increase the hook size, such as in *H. estigmena* and *H. robusta*. In *N. aequidentata*, the hook size decreases towards the basal and apical part of the tentacle. It is evident that the tentacular armature within the group is highly variable, making the description of completely evaginated tentacles essential for identification. However, these differences in hook type and size along the tentacles represent an ideal tool for future taxonomic work within these tentaculariid genera.

CLASSIFICATION

The subgroupings of Palm *et al.* (1997) remain a basis for further taxonomic work within tentaculariid trypanorhynchs. Together with the studies of Palm & Walter (1999) (*N. southwelli*) and Jones & Beveridge (1998) (*N. queenslandensis*), 48 species belong to the genera *Nybelinia* (31 species), *Heteronybelinia* (15) and *Mixonybelinia* (2). The current classification of tentaculariid cestodes is as follows:

1. Genus: *Tentacularia* Bosc, 1797

   (type and only species: *Tentacularia coryphaenae* Bosc, 1797)

2. Genus *Nybelinia* Poche, 1926 (subgroup I in Palm *et al.*, 1997)

   (type species: *Nybelinia lingualis* (Cuvier, 1817))

   A Species without characteristic basal armature

   a Size of basal hooks smaller than metabasal hooks:
   N. aequidentata (Shipley & Hornell, 1906), *N. anthicosum* Heinz & Dailey, 1974, *N. edwinlintoni* Dollfus, 1960, *N. goreensis* Dollfus, 1960, *N. jayapaulazariahi* Reimer, 1980, *N. palliata* (Linton, 1924), *N. queenslandensis* Jones & Beveridge, 1998, *N. riseri* Dollfus, 1960, *N. sakanariae* sp. nov., *N. schmidti* sp. nov., *N. sphyrnae* Yamaguti, 1952, *N. thyrsites* Korotaeva, 1971

   b Size of basal hooks equal to metabasal hooks
   N. anantaramanorum Reimer, 1980, *N. bengalensis* Reimer, 1980, *N. oodes* Dollfus, 1960, *N. pintneri* Yamaguti, 1934, *N. rhynchobatus* Yang Wenchuan, Lin Yuguang, Liu Gencheng & Peng Wenfeng, 1995, *N. strongyla* Dollfus, 1960, *N. surmenicola* Okada, 1929, *N. syngenes* (Pintner, 1929), *N. tenuis* (Linton, 1890), *Nybelinia* sp.

   c Size of basal hooks larger than metabasal hooks
   N. basimegacantha Carvajal, Campbell & Cornford, 1976

   B Species with characteristic basal armature

   a Size of basal hooks smaller than or equal to metabasal hooks
   N. africana Dollfus, 1960, *N. anguillae* Yamaguti, 1952, *N. bisulcata* (Linton, 1889), *N. erythraea* Dollfus, 1960, *N. indica* Chandra, 1986, *N. lingualis* (Cuvier, 1817), *N. manazo* Yamaguti, 1952, *N. scoliodoni* (Vijayalakshmi, Vijayalakshmi & Gangadharam, 1996)

   b Size of basal hooks larger than metabasal hooks
   N. gopalai Chandra & Hanumantha Rao, 1985

3. *Heteronybelinia* gen. nov. (subgroup II in Palm *et al.*, 1997)

   (type species: *Heteronybelinia estigmena* (Dollfus, 1960))

   A Without characteristic basal armature

   a Size of basal hooks smaller than metabasal hooks
   H. alloiotica (Dollfus, 1960), *H. cadenati* (Dollfus, 1960), *H. elongata* (Shah & Bilqees, 1979), *H. estigmena* (Dollfus, 1960), *H. eureia* (Dollfus, 1960), *H. heteromorphi* sp. nov., *H. karachii* (Khurshid & Bilqees, 1988), *H. minima* sp. nov., *H. punctatissima* (Dollfus, 1960), *H. robusta* (Linton, 1890), *H. senegalensis* (Dollfus, 1960)

   b Size of basal hooks equal to or larger than metabasal hooks

   H. perideraeus (Shipley & Hornell, 1906)

   B With characteristic basal armature

   a Size of basal hooks smaller or equal than metabasal hooks
   H. nipponica (Yamaguti, 1952), *H. rougetcampanae* (Dollfus, 1960), *H. yamagutii* (Dollfus, 1960)

4. *Mixonybelinia* gen. nov.

   (type species: *Mixonybelinia beveridgei* (Palm, Walter, Schwerdtfeger & Reimer, 1997))

   Mixonybelinia beveridgei (Palm, Walter, Schwerdtfeger & Reimer, 1997), *M. southwelli* (Palm & Walter, 1999)

5. *Kotorella* Euzet & Radujkovic, 1989

   (type and only species: *Kotorella pronosoma* (Stossich, 1901))

Nybelinia lingualis has been considered as belonging to subgroup IAa by Palm *et al.* (1997) and is assigned to subgroup Ba on basis of the gradual change of hook form along the tentacle (see Figs 7–9). The basal hooks without an anterior extension of the base easily distinguish the species from most *Nybelinia*, and therefore are interpreted as a characteristic basal armature. Some other species listed in this classification might change their position after re-examination of the type-material. However, classification as well as comparative discussions on species validity is simplified if using the presented scheme. How strobila morphology such as the shape of segments and structure of the genital complex can be incorporated into this classification will be an important task for future studies.

PHYLOGENY

The above classification most probably does not reflect the phylogeny within tentaculariid trypanorhynchs. Palm *et al.* (1997) failed with their cladistic analysis of the genus *Nybelinia* and the present study

describes in more detail the high morphological variability in hook patterns within the genera *Nybelinia* and *Heteronybelinia*. Although the armature types help in distinguishing between the different species within the group, the same hook forms and patterns are found within *Nybelinia*, *Heteronybelinia* and *Mixonybelinia* species. Beveridge *et al.* (1999) suggested that the transition in armature types from homeoacanthous to heteroacanthous has occurred once and the transition from heteroacanthous to poeciloacanthous types has occurred several times within trypanorhynch evolution. However, it has to be considered that the development of heteromorphous from homeomorphous hook patterns might also have occurred several times within different species, as proposed by Palm (1995). Methods other than morphology will be essential to clarify the phylogenetic situation within the Tentaculariidae

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