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

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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 aquadentata (Shipley & Hornell, 1906); N. africana Dollfus, 1960; N. javapadazariata Reimer, 1980; N. linguidis (Cuvier, 1817); N. riseri Dollfus, 1960; N. sakanarai sp. nov.; N. schmidt sp. nov.; N. scoliodoni (Vijayalakshmi, 1996) comb. nov.; Nybelinia sp.; Heteronybelinia elongata (Shah & Bligees, 1979) comb. nov.; H. estigmata (Dollfus, 1960) comb. nov.; H. heteromoerphi sp. nov.; H. minima sp. nov.; H. robusta (Linton, 1896) comb. nov.; H. yamaguti (Dollfus, 1960) comb. nov.; Mixonybelinia brevidigeti (Palm, Walter, Schwerdtfeger & Reimer, 1997) comb. nov. and M. southwelli (Palm & Walter, 1998) comb. nov. Tentacularia scoliodoni is transferred to the genus Nybelinia. Nine new locality and 15 new host records were established. The adults of Heteronybelinia estigmata and H. yamaguti 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 worldwide distribution pattern and a low host specificity, both in their fish second intermediate/paratenic hosts and in their final hosts.

INTRODUCTION

Trypanorhynchas 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, Sakarari & 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. herdmanni (Shipley & Hornell, 1906) with N. perideraeus (Shipley & Hornell, 1906) and Kioirella 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., 1969, 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).

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 scolecites 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-
RESULTS

A total of 17 species was identified, and 4 new species are described. Nine new localities 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)


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 tentaculat armature of the present specimen is given in Figs 1–2. Measurements: SL=3400; SW=1700; pbo=1510; pbv=1890; ppb=813; ppb=57; vell=550; app=585; BL=780 (756–813); BW=237 (227–265); BR=3.31; SP=1.9; 2.31; 1. TW metastasis=54–58, TW apical=46–51. A basal tentacular sheath 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 homeocanthous, homeomorphous, and a characteristic basal armature is absent. The massive hooks of the metasbals 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 metasbals 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. edwintoni* and *N. gorensis*. *N. edwintoni* 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 (Dollius, 1960). *N. gorensis* 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, Dollius (1960) remarked on the uniformity of the hooks, Two species with a similar tentacular armature, *N. anantararamorum* and *N. sygnes*, were placed in subgroup IAB by Palm et al., 1997, with hooks of similar size in the basal and metasbals part of the tentacles. *N. anantararamorum* 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. anantararamorum*. *N. sygnes* 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, Dollius, 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 Dollius, 1960
(Fig. 3)

MATERIAL EXAMINED. BMNH 1982.4.6.37–45, R. van der Elt 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 Elt leg., 11.05.1984, 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 Elt leg., 2.4.81, from the stomach of *Carcharhinus 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 Dollius (1960, see figures 9–19) and Palm et al. (1997). Measurements: SL=536, 440; SW=420, 485; pbo=327, 337, pp=205, 122; pb=178, 150; vell=210, 164; BL=174 (168–178), 133 (120–150); BW=73 (70–75), 70 (60–78); BR=2.4:1, 1.9:1, SP=1.8:1–1.1:1, 2.2:0.8:1; Short tentacles, about 200 long, with TW basal=28, 27; TW metastasis=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 metasbals 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
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 x 370–530 wide), the next enlarge in size towards 400–500 x 940–1030. The last 20 proglottids are a bit wider than long 1050–1200 x 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 x 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 x 160. Uterine ducts coiled before they enter the saciform 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 2.10:9:1–2.3:1.4:1 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 x 370–530 vs 11 x 290) and last (1050–1200 x 1250–1450, a bit wider than long vs 1100 x 900, a bit longer than wide) proglottids, the follicular ovary, and similarly 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 jayapaulzariahi* from *Harpodon nehereus*. Scolex. Scale bar=50 μm.

Fig. 5  *N. jayapaulzariahi*. Homeomorphic metasomal armature with slender hooks, metasomal hook as given in Reimer (1980), figure 4 (arrow). Scale bar=10 μm.
3. *Nybelinia javapaulzariati* 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; SL=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 homeoanthous, homeomorphous, and a characteristic basal armature is absent. The size of the slender, regularly curved hooks increases slightly towards the metasomal part of the tentacle: L=9.6–11.2; B=5.6–7.2 (metasomal) and L=5.6–7.2; B=5.6–7.2 (basal); hsr=6.

**Remarks.** The present specimen corresponds with those described by Dollius (1942). Although the scolices as well as hook sizes are smaller than those given by Dollius (1942), the scolices form as well as the form and arrangement of the tentacular hooks correspond with drawings of *N. lingualis* found in *Septia fillitouxi*, *S. officinalis* and *Mullus barbatus* (see Dollius, 1942, Figs 88–91). According to Dollius (1942), the bulbs are typically short (about 300–400 μm long), with a BR of about 2.2–2.5:1. Additionally, Dollius (1942) demonstrated a high degree of morphological variability within the species with a scolices 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 filliform microtriches on the distal boethridial surface and hook-like microtriches on the boethridial borders corresponds to those described for *Tentacularia coryphaenae*, *N. alliotiota*, *N. edirwintoni*, *N. queenslandensis* and *N. c.f. senegalensis* (Palm, 1995, Jones & Beveridge, 1998).

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

**Material examined.** BMNH 1987.3.2.19, R. Bray leg., 1 postlarva from the gut of *Tonguiusgenus pleurogramma*, Adelaide, South Australia; BMNH 1987.4.23.11–12, R. Bray leg., 03.12.1986, 2 postlarvae from the gastric chamber of *Arinoglossus imerialis*, Ciroana 76–78 m, 49°50'55"S, 3°44'3"W; BMNH 1987.4.23.18–32, R. Bray leg., 03.12.1986, 1 postlarva from the intestinal wall of *Pagusa lascaris*, Ciroana, English Channel, 49°50'55"S, 3°44'3"W, 76–78 m.

**Description.** *Nybelinia lingualis* was described in detail by Dollius (1942). The scolices 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, 510, 491, mm; BL=365 (326–397), 313 (303–322), 292 (289–294), 314; BW=138 (130–140), 128 (117–140), 114 (112–117), 114; BR=2.6:1, 2.6:1, 3.7:1, 3.4:3:1. The tentacles are long and slender and diminish in diameter towards the tip; TW=39, 42, 46, 46, TW=32=32, 33, 33, 38; TW distal=24, mm, mm, mm. 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 homeoanthous, 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, 7.2–9.6, 7.2–9.6, 7.2–9.6) than in the metasomal armature (L=14.5–16.7, 16.0–18.4, 16.0–18.4; B=9.3–13.0, 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 Dollius (1942). Although the scolices measurements as well as hook sizes are smaller than those given by Dollius (1942), the scolices form as well as the form and arrangement of the tentacular hooks correspond with drawings of *N. lingualis* found in *Septia fillitouxi*, *S. officinalis* and *Mullus barbatus* (see Dollius, 1942, Figs 88–91). According to Dollius (1942), the bulbs are typically short (about 300–400 μm long), with a BR of about 2.2–2.5:1. Additionally, Dollius (1942) demonstrated a high degree of morphological variability within the species with a scolices 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 filliform microtriches on the distal boethridial surface and hook-like microtriches on the boethridial borders corresponds to those described for *Tentacularia coryphaenae*, *N. alliotiota*, *N. edirwintoni*, *N. queenslandensis* and *N. c.f. senegalensis* (Palm, 1995, Jones & Beveridge, 1998).

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

**Material examined.** BMNH 1985.11.8.65, G. Ross leg., 30.11.1979, 3 postlarvae from *Trachyrus 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}; 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 homeoanthous, 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 scolices form as well as a homeoanthous, homeomorphous tentacular armature such as described for the present specimens. *N. riseri* is characterised by the champion-shaped scolices (see Dollius, 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 scolices proportions as described for specimens of *N. lingualis* taken from *Trachyrus felicipes* (see Dollius, 1942). However, the general scolices form with the small banana-shaped bulbs of *Nybelinia lingualis* (see Dollius, 1942) clearly differs to the present specimens. Thus, they are
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 *Xiphius 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; pb=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. Prebular 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; pb=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, prebular 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 strongylia* 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.
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 schmidtii* sp. nov.  (Figs 14–15)


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. Prebular 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 homeocanthous, 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 acarespedote, 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

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

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

**Fig. 10** *Nybelinia riseri*. Scolex from *Trachysurus feliceps*. 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.
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 1Aa of
Palm et al. (1997) and resembles, with a rose-thorn-shaped basal and
metabasal tentacular armature, *N. antichorum, N. palliata, N.
strongyla, N. riseri, N. sphyrnae* and *N. thysites*. A comparison with
the type material of *N. antichorum* and *N. palliata*, deposited at the
U.S. National Parasite Collection, Beltsville, revealed differences in
oncosty. *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 (Dolfls, 1960). *N. sphyrnae* and *N.
thysites* also differ in hook and scolex form/size (see Beveridge &
Campbell, 1996). Thus, the present specimen represents a new
species, *Nybelinia schmidtii* sp. nov.

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

8. *Nybelinia scoliodoni* (Vijayalakshmi, Vijayalakshmi &
Gangadham, 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 (Figs. 16–17). Measurements: SL=667; SW=320;
pho=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 homeoanchothous, homeomorphous,
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 metabalusal hooks (L=22–26) with a small base (B=7.7–10.5); hsr basal=6–7, hsr metabalusal=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 & Gangadharan, 1996) as a species of uncertain status due to an incomplete 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 specimens 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 metabalusal hooks, with a size between L=8–11 in the basal and L=30, B=3 in the metabalusal armature as given by Vijayalakshmi et al. (1996), is unique within the genus. As with the scolex size, the hooks of the present specimens 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 *Carearhinus limbatis* 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 incomplete strobila was found. The scolex size and tentacular armature corresponds to the material deposited at the BMNH. Thus, *Glyptis 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 larger pph, 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 metabalusal hooks (Fig. 18, figure 17 in Palm, 1992) in *Pseudapenaeus maculatus* from the North-East Brazilian coast and described the specimens as *N. indica* with a homeomorphous metabalusal 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).
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 homoecanthous, 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. oode (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. oode. 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 oode 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 Tentacularidae 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 the bulbs, retractor muscle originates at base of bulbs. 4 proxobases of variable length and width, armed with hooks; metasomal tentacular armature homeoanchoan with heteromorphic hooks on different tentacle surfaces. Basal hooks heteromorphic, characteristic basale armature absent or present. Cirrus unarmed, cirrus sac alternates irregularly.

**TYPE SPECIES:** *Heteronybelinia estigmens* (Dollfus, 1960).


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

10. _Heteronybelinia elongata_ (Shah & Bilquees, 1979) comb. nov.

(Figs 19–25)


**DESCRIPTION.** The scolex morphology of the type material of _H. elongata_ (Shah & Bilquees, 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; pt=556, 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, 4.1; Sp=1.8, 1.9. 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 homeoanchoan, 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=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; pt=397; ppb=61; app=257; vel=233; BL=387 (377–397), BW=91 (89–94); BR=4.2; 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=4.5–6.2; 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 homeoanchoan, 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 subgroup IAB to II Aa 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 II Aa, all having a similar armature with similar sized tentacular hooks. It is recommended that the type material of species in subgroup II Aa 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 estigmens_ (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 _Caracharhinus limbus_us, South Africa; BMNH 1985.11.8.63–64, R. van der Elst leg.; 11.03.1984, 1 adult from _Caracharhinus leucas_, Richards Bay, South Africa; BMNH
Fig. 19  *Heteromybeliunia 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.

DESCRIPTION. The scolex of a specimen from *C. limbatis* 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; vcl=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; 1.9:1.4:1; 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 metasbacial 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 ant bothridial=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, (ant bothridial); hsr=6–7.

The slightly stained scolex of the specimen from *Carcharhinus limbatis* consists of about 190 acraspedode 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 acraspedode proglottids of the specimen from *Carcharhinus leucas* vary in size,

![Fig. 26 Heterophylenia estigmata. Scolex from Carcharhinus limbatis. Scale bar=100 μm.](image-url)
depending on contraction (anterior segments: 80 x 330–20 x 520), final segments 300–370 x 860–880; testes 33–55 in diameter.

REMARKS. The present specimens are most similar to *H. alliotica*, *H. punctatissima* and *H. estigmene*, which were considered as belonging to subgroup II Aa 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. estigmene*, *H. punctatissima*, *H. senegalensis*, *H. alliotica* 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 metascleral 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 x 0.96–1.00 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. alliotica* and *H. cadenati* also have a bulb ratio of about 4, and *H. punctatissima* differs from *H. estigmene* 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. alliotica* (Figs 29–30), which was re-described by Palm (1995) from *Carcharhinus limbus* 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. estigmene*.

This and a previous study (Palm & Walter, 1999) demonstrate wide intraspecific variability in scolex morphology within several species of *Nybelinia* (see also *H. africana*) and *Heteronybelinia*, similar to that described earlier for other tentaculariid genera *Tentacularia* and *Hepatoxyylon* (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 species. The identification of the present specimens as *Heteronybelinia estigmene* 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. estigmene** (Dollfus, 1960) comb. nov.

**Material examined.** BMNH 1989.1.18.2, R. Bray leg., 14.01.1971, Cirolana, Atlantic Ocean off Morocco, 33°43′3N, 8°38′W, 222–236 m. 1 postlarva from *Scomber scomas*.

**REMARKS.** Due to its scolex morphology and the homeocanthous, 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. estigmene*. However, the partly invaginated metascleral 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)

DESCRIPTION (Figs 31–33). With the characters of the genus *Heteronybelinia*. Measurements: SL=1367, 1300, 1367, 1467; SW=833, 934, 800, 800; pb=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), mm; TW basal=53–60, 53–60, 48–50, 52–54; TW apical=75–80, 65–70, 58–61, mm; 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); above 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; bsr=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
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 Dolfus (1960). Though the morphometrical data correspond, the drawings of the tentacular armature of *H. eureia* as given by Dolfus (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 Dolfus, 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. strongylus* (see Jones & Beveridge, 1998, Dolfus, 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. 34** *Heteronybelinia minima* sp. nov., Scolex from *Harpodon nehereus*. Scale bar=50 μm.

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

**Fig. 36** *H. minima* sp. nov. from *P. paradiseus*. Heteromorphous metasomal 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.

**DESCRIPTION.** With the characters of the genus *Heteronybelina*. The scelax of the holotype as well as the scelax and basal and metabasal tentacular armature of a specimen from *P. paradiseus* are shown in Figs 34 and 35–38 respectively. The scelax is small, differing in size and shape between specimens. Measurements (from types 1980.12.2.1): SL = 706, SW = 366, PH = 247, 454; PV = 267, 397; PB = 200, 252; app = 280, 250; vel = 84, 186; BL = 191 (187–200), 237 (226–252); BW = 54 (43–66), 83 (74–89); BR = 3.5, 2.9; SP = 2.1, 1.3; 1.8, 1.6; 1.1. 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 homeoananchous, 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 changes 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=20–24; B=15.2–16.8 (bothridial) and L=24–27.2; B=8.6–7.2 (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 scelax size and the characteristic tentacular armature. The present specimens from *Harpodon neheurus*, *Polyneus paradiseus* and *Polyneus* sp. clearly demonstrate a heteromorphous armature, where the hook form changes from rose-thorn shaped to falcate hooks, giving the tentacles a homeoanchous 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. Heteronybelina robusta** (Linton, 1890) (Figs 39–41)

**MATERIAL EXAMINED.** BMNH 1976.11.5.42–43, R. van der Elst leg., 1 adult from the stomach of *Sphyraena luewini*, South Africa.

**DESCRIPTION.** *Nybelina yamaguti* was described in detail by Dolfus (1960, see figures 1–5) and *Palm et al.* (1997). The following measurements were taken: SL = 2646; SW = 1080; Pho = 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 diminish in size along the tentacle; TW metascler = 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 homeoanchous, heteromorphous, and a characteristic basal armature with bill-hooks is present. The hooks of the metabasal armature are different in shape and size on both bothridial and antibothridial tentacle surfaces. The form of the hooks is described in detail in Dolfus (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 strobila 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.
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 *Sphyraena levini* from South Africa. A world-wide distribution for the species has been proposed by Palm et al. (1997).

*Mixonbybelinia* 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 probosicides of various length and width, armed with massive hooks; metabasal tentacular armature homeocamphous with heteromorphous hooks on different tentacle surfaces. Characteristic basal armature consisting of homeomorphous hooks present. Cirrus unarmed, cirrus sac alternates irregularly.


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


**MATERIAL EXAMINED.** The Natural History Museum London:

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 subgroups as proposed by Palm et al. (1997) can be consistently separated on the basis of their characteristic basal 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 superfamilial 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 *Calitetrarhynchus*, *Lacistorhynchus*, *Mixodigma*, *Poeiilococanthurum* and *Pseudolacistorhynchus* (other examples see Campbell & Beveridge, 1994, Palm, 1995). This simplifies further studies of tentacularid trypanorhynchs of the *Nybelinia* type.

The present study again demonstrates how level of morphological variation within different species of *Nybelinia* and *Heteronybelinia*. *Nybelinia africana* and *Heteronybelinia yamaguti* 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 tentacularid trypanorhynchs, such as *Tentacularia coryphaenae*, evidenced by the numerous synonyms 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 IIa (Heteronybelinia estigmata species complex) and in the *Nybelinia aequidensata* 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 tentacularids 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 estigmata*, *H. robusta*) and 2 species (*Nybelinia africana*, *Heteronybelinia estigmata*) 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 coriceps* 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 tentacularid genera and most of the species are

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**Discussion**

Of the material deposited at the British Museum Natural History, 17 different trypanorhynchs, 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 homeocanthous, homeomorphous (*Nybelinia*) from those having a heteroecanthous, heteromorphous metatabal armature with heteromorphous basal hooks (*Heteronybelinia* gen. nov.) and from species with a heteromorphous metatabal and homeomorphous basal armature, which are assigned to *Mixonybelinia* gen. nov. *Mixonybelinia* is a tentacularid genus in which different armature types occur along the tentacle. This has been described earlier for non-tentacularid trypanorhynchs, such as the mixodigmatid *Mixodigma*

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**Material examined.** The Natural History Museum London: BMNH 1997.11.4.7, 1977.11.4.8--9. *M. southwelli* was described in detail by Southwell (1929) and Palm & Walter (1999).
characterised by a cosmopolitan distribution pattern, which distinguish those trypanorhynch 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 tentacularid with a flexible, unspecialised life cycle pattern might be essential for these oceanic trypanorhyncs, 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 metabalas armatures, such as *H. scioliodoni* 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. aestividentata*, the hook size decreases towards the basal and apical part of the tentacle. It is evident that the tentacular armament 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 tentacularid genera.

**CLASSIFICATION**

The sub-groupings of Palm et al. (1997) remain a basis for further taxonomic work within tentacularid 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 tentacularid 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 metabalas hooks:

   b. Size of basal hooks equal or metabalas hooks

   c. Size of basal hooks larger than metabalas hooks
      *N. basseumcantha* Carvajal, Campbell & Cornford, 1976

   B. Species with characteristic basal armature
   
   a. Size of basal hooks smaller than or equal to metabalas hooks

   b. Size of basal hooks larger than metabalas hooks
      *N. gopala* 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 metabalas hooks

   b. Size of basal hooks equal to or larger than metabalas hooks
      *H. perideraes* (Shipley & Hornell, 1906)

   B. With characteristic basal armature
   
   a. Size of basal hooks smaller or equal than metabalas hooks

4. *Mixonybelinia* gen. nov.
   (type species: *Mixonybelinia beveridgei* (Palm, Walter, Schwerdtfeger & Reimer, 1997))


   (type and only species: *Koorella pronosa* (Stossich, 1901))

   *Nybelinia lingualis* has been considered as belonging to subgroup Aa 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 tentacularid 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 *Mixonbybelinia* species. Beveridge et al. (1999) suggested that the transition in armature types from homeoanconths to heteroanconths has occurred once and the transition from heteroanconths to poeciloanconths types has occurred several times within trypanorhynch evolution. However, it has to be considered that the development of heteromorphs 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 Tentaculartidae.

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