Tentacullariid cestodes (Trypanorhyncha) from the Muséum national d'Histoire naturelle, Paris

Harry W. PALM
Institut für Zoomorphologie, Zellbiologie und Parasitologie,
Heinrich-Heine-Universität Düsseldorf,
Universitätsstraße 1, D-40225 Düsseldorf (Germany)
hpalm@gmx.net

Thorsten WALTER
Abteilung Fischereibiologie, Marine Pathologie,
Institut für Meereskunde an der Universität Kiel,
Düsternbrooker Weg 20, D-24105 Kiel (Germany)

Palm H. W. & Walter T. 2000. — Tentacullariid cestodes (Trypanorhyncha) from the Muséum national d'Histoire naturelle, Paris. *Zoosystema* 22 (4) : 641-666.

ABSTRACT
The present study was carried out to examine unidentified and identified specimens of *Nybelinia*, *Heteronybelinia*, *Mixonybelinia* and *Kotorella* deposited at the Muséum national d'Histoire naturelle, Paris. A total of 17 different species including type specimens was found: *Nybelinia africana* Dollfus, 1960; *N. erythraea* Dollfus, 1960; *N. goreensis* Dollfus, 1960; *N. lingualis* (Cuvier, 1817); *Nybelinia* cf. *lingualis* (Cuvier, 1817); *N. riseri* Dollfus, 1960; *N. scoliodoni* (Vijayalakshmi, Vijayalakshmi & Gangadharam, 1996); *N. strongyla* Dollfus, 1960; *N. surmenicola* Okada, 1929; *N. thyrsites* Korotaeva, 1971; *Heteronybelinia estigmena* (Dollfus, 1960); *H. eureia* (Dollfus, 1960); *H. minima* Palm, 1999; *H. nipponica* (Yamaguti, 1952); *H. robusta* (Dollfus, 1960); *H. yamagutii* (Dollfus, 1960); *Mixonybelinia edwinlintoni* (Dollfus, 1960) n. comb.; *Kotorella pronosoma* (Stossich, 1901). *M. edwinlintoni* is re-described. *Nybelinia oodes* Dollfus, 1960, *H. alloiotica* (Dollfus, 1960), *H. cadenati* (Dollfus, 1960), and *H. senegalensis* (Dollfus, 1960) are considered synonymous with *H. estigmena* (Dollfus, 1960). *H. punctatissima* (Dollfus, 1960) is considered synonymous with *Nybelinia lingualis*, and specimens of *H. punctatissima* as described *in* Dollfus (1960) are considered synonymous with *H. estigmena*. *H. rougetcampanae* (Dollfus, 1960) is considered synonymous with *H. nipponica*, and *N. rhynchobatus*

KEY WORDS
Cestoda,
Heteronybelinia,
host-specificity,
Kotorella,
Mixonybelinia,
Nybelinia,
taxonomy,
Tentaculariidae,
Trypanorhyncha,
zoogeography.

Yang, Lin, Liu & Peng 1995 synonymous with *Kotorella pronosoma*. Five new localities and 12 new host records were established. The adults of *Mixonybelinia edwinlintoni* n. comb. and *N. strongyla* are reported for the first time. A high degree of morphological variability within the same species was observed, with postlarvae having the potential to reach a larger size than adults. Most of the studied species exhibit a wide host range and distribution. List of valid species are given for the five genera within the family Tentacullariidae: *Nybelinia* (24 species), *Heteronybelinia* (10), *Mixonybelinia* (3), *Kotorella* (1), and *Tentacularia* (1).

MOTS CLÉS
Cestoda,
Heteronybelinia,
spécificité parasitaire,
Kotorella,
Mixonybelinia,
Nybelinia,
taxonomie,
Tentacullariidae,
Trypanorhyncha,
zoogéographie.

RÉSUMÉ

Cestodes Tentacullariidae (Trypanorhyncha) du Muséum national d'Histoire naturelle, Paris.

Cette étude a été entreprise pour examiner les spécimens identifiés et non identifiés de *Nybelinia, Heteronybelinia, Mixonybelinia* et *Kotorella* déposés au Muséum national d'Histoire naturelle, Paris. Dix-sept espèces ont été trouvées, y compris des spécimens-types : *Nybelinia africana* Dollfus, 1960 ; *N. erythraea* Dollfus, 1960 ; *N. goreensis* Dollfus, 1960 ; *N. lingualis* (Cuvier, 1817) ; *Nybelinia* cf. *lingualis* (Cuvier, 1817) ; *N. riseri* Dollfus, 1960 ; *N. scoliodoni* (Vijayalakshmi, Vijayalakshmi & Gangadharam, 1996) ; *N. strongyla* Dollfus, 1960 ; *N. surmenicola* Okada, 1929 ; *N. thyrsites* Korotaeva, 1971 ; *Heteronybelinia estigmena* (Dollfus, 1960); *H. eureia* (Dollfus, 1960) ; *H. minima* Palm, 1999 ; *H. nipponica* (Yamaguti, 1952) ; *H. robusta* (Dollfus, 1960) ; *H. yamagutii* (Dollfus, 1960) ; *Mixonybelinia edwinlintoni* (Dollfus, 1960) n. comb. ; *Kotorella pronosoma* (Stossich, 1901). *M. edwinlintoni* est redécrite. *Nybelinia oodes* Dollfus, 1960, *H. alloiotica* (Dollfus, 1960), *H. cadenati* (Dollfus, 1960) et *H. senegalensis* (Dollfus, 1960) sont considérées synonymes de *H. estigmena* (Dollfus, 1960). *H. punctatissima* (Dollfus, 1960) est considérée synonyme de *Nybelinia lingualis,* et des spécimens de *H. punctatissima* décrits par Dollfus (1960) sont considérés synonymes de *H. estigmena*. *H. rougetcampanae* (Dollfus, 1960) est considérée synonyme de *H. nipponica* et *N. rhynchobatus* Yang, Lin, Liu & Peng, 1995 est considérée synonyme de *Kotorella pronosoma*. Cinq nouvelles localités et 12 nouvelles mentions d'hôtes ont été trouvées. Les adultes de *M. edwinlintoni* n. comb. et de *N. strongyla* sont signalés pour la première fois. Un haut niveau de variabilité morphologique intra-spécifique a été observé, avec des post-larves qui ont la possibilité d'atteindre une taille supérieure à l'adulte. La plupart des espèces étudiées ont des hôtes nombreux et une large distribution. Une liste des espèces valides est donnée pour les cinq genres de la famille Tentacullariidae : *Nybelinia* (24 espèces), *Heteronybelinia* (10), *Mixonybelinia* (3), *Kotorella* (1) et *Tentacularia* (1).

INTRODUCTION

As a part of a revision of the trypanorhynch genus *Nybelinia*, Palm *et al.* (1997), Palm & Walter (1999) and Palm (1999) described or re-described 17 species deposited in the British Museum (Natural History), London, and from the Natural History Museum, Vienna (Palm & Walter 1999). Palm (1999) erected two new genera, *Heteronybelinia* and *Mixonybelinia*, leav-

ing 31 species within the genus *Nybelinia* Poche, 1926. To date a total of 48 species of *Nybelinia*, *Heteronybelinia* and *Mixonybelinia* are considered valid (Palm 1999).

Dollfus (1960) described 16 different *Nybelinia* species from the coast of north-west Africa, and distinguished several species on the basis of minor differences in scolex ratios or sizes of the tentacular hooks. Palm *et al.* (1997) and Palm (1999) demonstrated that characters such as absolute values for tentacle diameter and bulb length do not invariably distinguish among species of *Nybelinia* and *Heteronybelinia*. These characters exhibit a higher level of intraspecific morphological variation than considered earlier. For example, the *Heteronybelinia estigmena* complex (see subgroup IIAa *in* Palm *et al.* 1997) might represent a single species, which could explain the current taxonomic problems within this subgroup. Thus, the original material described by Dollfus (1960) and additional specimens deposited in the Muséum national d'Histoire naturelle, Paris (MNHN), needs to be re-examined to clarify the true status of many species.

The present study was carried out to re-examine identified and unidentified trypanorhynchs belonging to the Tentaculariidae Poche, 1926, deposited at the MNHN. Besides the establishment of new host and locality records, species identification provides further insight into the zoogeographical distribution and allows comments to be made on the level of intraspecific morphological variability within tentaculariid species, which have not yet been considered in this context. Together with the study of deposited tentaculariids from other collections (Palm 1999; Palm & Overstreet 2000; Palm & Walter 1999), the present study summarises the current taxonomic status of all tentaculariid genera.

MATERIAL AND METHODS

Standard measurements and drawings of the scoleces of *Nybelinia* specimens deposited in the MNHN were made using a Leitz Wetzlar Dialux 20 microscope with an ocular micrometer. Special attention was given to unidentified specimens deposited as *Nybelinia* sp., other deposited and identified material was also examined for comparison. The type material of *Nybelinia anantaramanorum* Reimer, 1980 and *N. bengalensis* Reimer, 1980 was borrowed from the collection of Prof. Dr L. W. Reimer.

The following measurements were made: Scolex length (sl), scolex width at level of pars bothridialis (sw), length of pars bothridialis (pbo), length of pars vaginalis (pv), length of pars bulbosa (pb), length of 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 (tl) was estimated. In addition, 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 listed under the subheading *Material examined*. If more than three measurements were taken from a species out of a single host species, the mean is given with the range in parentheses. Illustrations are provided if useful for future species identification; otherwise the reader is referred to illustrations given by other authors. *Supplemental data* adds further characters which are useful for better species identification. The classification follows that of Palm (1995, 1997a), and the orientation of the tentacular surfaces follows that of Campbell & Beveridge (1994). The host identity was confirmed using Roper *et al.* (1984) and FishBase 1998 (Froese & Pauly 1998).

RESULTS

A total of 17 species was identified; five new locality and 12 new host records were established.

Detailed 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

Nybelinia africana Dollfus, 1960

Nibelinia perideraeus Shipley & Hornell, 1906 of Dollfus (1942). New synonym.

MATERIAL EXAMINED. — MNHN 653-660 HF (described *in* Dollfus 1960):
Dakar. Senegal, syntypes of *N. africana* from *Galeoides decadactylus* (Bloch, 1795) (junior synonym *G. polydactylus* [Vahl, 1798]).
Algiers. Algeria, *Mullus barbatus* Linnaeus, 1758; *Serranus cabrilla* (Linnaeus, 1758).
Gorée. Senegal, *Pagellus* sp.; *Trigla* sp.

ADDITIONAL MATERIAL. — **Ghardaqa.** Egypt, 22.XII.1938, leg. P. Budker, 2 adults of *N. africana* from the stomach of *Carcharhinus melanopterus* (Quoy & Gaimard, 1824), 1 specimen described and figured as *N. perideraeus in* Dollfus (1942: figs 97-100) (MNHN 661-672 HF, 749 HF).

SUPPLEMENTAL DATA. — The tentacular armature of the type specimens obtained from *Galeoides decadactylus* (Bloch, 1795) (junior synonym *Galeoides polydactylus* [Vahl, 1798]) and *Trigla* sp. with nearly completely everted tentacles shows slightly decreasing hook sizes towards the apical part of the tentacles.

DESCRIPTION
Measurements of basal hooks from *G. decadactylus* and *Trigla* sp. respectively, l = 10.7-13.5, 9.0-11.4; b = 5.5-6.9, 6.2-6.9; metabasal hooks: l = 16.5-17.0, 16.8-17.2; b = 6.9-7.2, 6.6-6.9; apical hooks: l = 13.6-13.9, 13.1-13.8; b = 6.2-6.9, 6.1-6.3.

REMARKS
Palm & Walter (1999) and Palm (1999) proposed the possible synonymy of the specimen of *N. perideraeus* described by Dollfus (1942) with *N. africana* on basis of the tentacular hooks and strobila characters, respectively. Re-examination of the deposited material in the MNHN confirms this synonymy.

The tentacular armature of *N. africana* diminishes in size towards the apical part of the tentacle, which has not been recorded before for this species. However, most of the specimens of *N. africana* studied had incompletely evaginated tentacles. A similar change in hook size along the tentacles has been earlier described for *Nybelinia aequidentata* by Pintner (1927).
Nybelinia africana has a circum-African distribution (Palm *et al.* 1997), and the present material confirms its occurrence in the Mediterranean Sea. Palm *et al.* (1997) and Palm (2000) recorded the species from the West and East Indian Ocean. *Nybelinia africana* is a frequent and widely distributed trypanorhynch, occurring in several teleost intermediate hosts (Palm *et al.* 1997) and elasmobranch final hosts (*Carcharhinus leucas* [Müller & Henle, 1839], *C. melanopterus* [Quoy & Gaimard, 1824], *C. obscurus* [Lesueur, 1818], *Mustelus canis* [Mitchill, 1815]).

Nybelinia erythraea Dollfus, 1960
(Fig. 1)

MATERIAL EXAMINED. — **Gulf of Suez.** Described *in* Dollfus (1960), holotype and paratype from *Cynoglossus sinusarabici* (Chabanaud, 1931) (MNHN 673 HF).

SUPPLEMENTAL DATA. — A muscular ring around the tentacle sheaths is visible in the type specimens. The tentacular armature is homeoacanthous and homeomorphous (Fig. 1). The size of the hooks on the partly everted tentacles varies between l = 14.5-16.1 and b = 13.1-15.1. It appears that the first basal hooks are larger than the hooks towards the metabasal part of the tentacle.

REMARKS
Nybelinia erythraea resembles *N. basimegacantha* Carvajal, Campbell & Cornford, 1976 by its characteristic homeomorphous tentacular armature and the elongated bulbs. In both species, the first basal hooks are larger than the hooks of the metabasal armature. However, the species are difficult to compare due to the contracted condition of the type specimens of *N. erythraea* and their largely invaginated tentacles. The scolex of *N. basimegacantha* as described by Carvajal *et al.* (1976) is

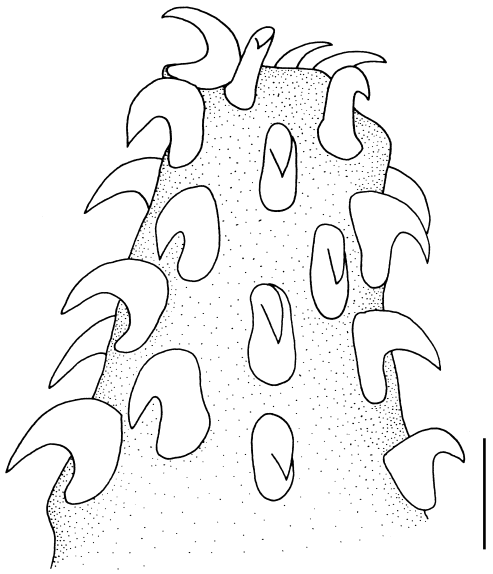

FIG. 1. — *Nybelinia erythraea* (type) isolated from *Cynoglossus sinusarabici*, basal armature. Scale bar: 15 µm.

larger than that of *N. erythraea*. Until further material of *N. erythraea* with evaginated tentacles becomes available, both species are considered valid. *N. erythraea* changes its position to subgroup 1Ac of Palm *et al.* (1997).

Nybelinia goreensis Dollfus, 1960
(Fig. 2)

MATERIAL EXAMINED. — **Gorée.** Senegal, described by Dollfus (1960), holotype and paratype from *Sphyrna lewini* (Griffith & Smith, 1834) (junior synonym *Sphyrna diplana* Springer, 1941) (MNHN 674-677 HF).

ADDITIONAL MATERIAL. — **Gorée.** Senegal, 21.V.1951, leg. Y. Rouget-Campana, paratype 1 adult from the stomach/intestine of *Sphyrna lewini* (MNHN 750 HF).

SUPPLEMENTAL DATA OF HOLOTYPE. — Scolex measurements: pbo = 655; pv = 630; pb = 452; sp = 1.4:1.4:1. The tentacular armature of *N. goreensis* consists of homeomorphous hooks (Fig. 2). The slender, falciform hooks increase in size towards the metabasal part of the tentacle. Basal hooks: l = 17.1-24.2; b = 6.1-7.9; metabasal hooks: l = 31.0; b = 10.0. Towards the tip of the tentacle the hooks decrease in size (apical hooks: l = 21.0-24.0; b = 7-8).

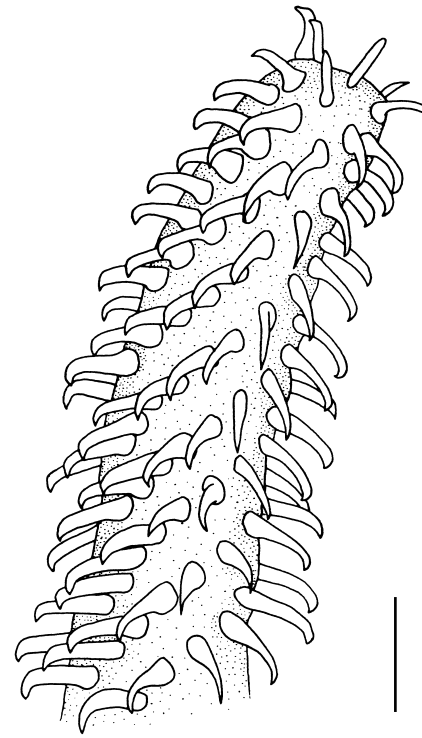

FIG. 2. — *Nybelinia goreensis* from *Sphyrna lewini*, homeomorphous metabasal and apical armature. Scale bar: 30 µm.

REMARKS

Nybelinia goreensis is characterised by a medium-sized scolex (1235-1325) with a tentacular armature consisting of slender falciform hooks. The latter character resembles *N. aequidentata* (Shipley & Hornell, 1906) which has a similar hook form along the tentacle. However, the species clearly differ by having craspedote (*N. goreensis*) or acraspedote (*N. aequidentata*) strobilae. They can be further distinguished by scolex size. Other similar species are *Mixonybelinia edwinlintoni* (Dollfus, 1960) n. comb., *N. syngenes* (Pintner, 1929), *N. anantaramanorum* Reimer, 1980 (see Palm 1999) and *N. bengalensis* Reimer, 1980. The metabasal armature of *M. edwinlintoni* is heteromorphous (see below) and *Nybelinia syngenes* has a larger scolex, different bulb ratio and larger metabasal hooks. However, *N. syngenes* was incompletely described and re-examination of the type material is necessary to confirm its

validity. Both species, *N. goreensis* (see above) and *N. syngenes* (Pintner, 1929), were collected from hammerhead sharks. A comparison with the type material of *Nybelinia anantaramanorum* Reimer, 1980 revealed no significant difference in the basal tentacular armature between the two species. The tentacles of the type material of *N. anantaramanorum* are only partly evaginated, thus, a comparison of the metabasal armatures is not possible. The scolex measurements lie between those of *N. aequidentata* and *N. goreensis.* As the entire tentacular armature is an essential feature to distinguish between these species, we consider *N. anantaramanorum* as *species inquirendae. N. bengalensis* also resembles *N. goreensis,* however, it clearly differs in having short, oval bulbs, a small tw and smaller hooks.
Nybelinia goreensis has been described only from *Sphyrna lewini* from the coast of Northwest Africa.

Nybelinia lingualis (Cuvier, 1817)

Tetrarhynchus lingualis Cuvier, 1817.

Nybelinia punctatissima Dollfus, 1960. New synonym.

MATERIAL EXAMINED. — 30.III.1957, postlarva from the body cavity of *Thunnus thynnus* (Linnaeus, 1758), fish market, Paris (MNHN 679 HF).

ADDITIONAL MATERIAL. — **Vanneau.** France, 29.VI.1923, 2 postlarvae from *Raja* sp. (MNHN 761-762 HF); 20.VI.1924, 3 postlarvae from the gills of *Chelidonichthys lucerna* (Linnaeus, 1758) (MNHN 764-766 HF).
Cap Cautin. Morocco, 15.IX.1932, leg. V. Bernard, 2 postlarvae from the mesentery of *Trigla lyra* Linnaeus, 1758 (MNHN 756-757 HF).
Monacco. 08.IV.1938, leg. H. Nouvel, postlarva from *Eledone cirrhosa* (Lamarck, 1798) (junior synonym *Eledone aldrovandii* MacGillivray, 1843) (MNHN 763 HF).
Agadir. Morocco, 04.VIII.1945, 2 postlarvae from the stomach and the musculature of *Trigla bicarinata* (unrecognisable binomen) (MNHN 751-752 HF).
Ajaccio. Corsica, IV.1948, leg. E. Houdemer, 3 postlarvae from between the tunica of the stomach wall of *Scomber scombrus* Linnaeus, 1758 (MNHN 693 HF, 758 HF); 12.VI.1952, leg. G. Houdemer, 2 postlarvae from the mesentery of *Mullus surmuletus* Linnaeus, 1758 (MNHN 759-760 HF).
Arcachon. Gironde, France, 1949, 3 postlarvae from *Chelidonichthys gurnardus* (Linnaeus, 1758) (MNHN 753-755 HF).
Sète. France, 07.I.1950, 23.I.1952, leg. L. Euzet, 3 adults from *Hexanchus griseus* (Bonaterre, 1788) (MNHN 687-688 HF); 07.X.1953, 30.X.1953, 25.XI.1953, leg. L. Euzet, 3 adults from *Dasyatis violacea* (Bonaparte, 1832) (MNHN 689-691 HF); 29.IX.1951, leg. L. Euzet, 4 adults from *Isurus oxyrhynchus* Rafinesque, 1810 (MNHN 680-686 HF).

DESCRIPTION
sl = 2700; sw = 1620; pbo = 1755; pv = 1350; pb = 462; ppb = 238; vel = 672; app = 924; bl = 392 (378-420); bw = 131 (121-138); br = 3.0:1; sp = 3.8:2.9:1; tw metabasal = 38-41. A basal tentacular swelling is absent. The tentacle sheaths are straight; tsw = 31-34. 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 present. The hooks change continuously from compact, rounded rose-thorn-shaped (basal armature), lacking an anterior extension of the basal plate, to more slender rose-thorn-shaped hooks with anterior extension (metabasal hooks). The hooks in the basal part of the tentacle are smaller (l = 6.9-11.0; b = 6.2-8.6) than in the metabasal (l = 15.5-16.2; b = 10.0-11.0) and apical armature (l = 16.9-17.2; b = 8.6-9.3). The number of hooks per half spiral diminishes towards the apical part of the tentacle; hsr = 6-7 (basal); hsr = 5-6 (apical).

REMARKS
N. lingualis is a widely distributed species and has been recorded from the Atlantic (Dollfus 1942) and from South Australia (Palm 1999). Several elasmobranchs including *Carcharhinus leucas*, *C. melanopterus* and *C. obscurus* (Dollfus 1942; Bates 1990; Palm 1999) have been recorded as final hosts for this common trypanorhynch. *Dasyatis violacea*, *Hexanchus griseus*, *Isurus oxyrhynchus*, and *Thunnus thynnus* represent new host records for *N. lingualis*. With the exception of *T. thynnus*, the specimens reported here were recorded as *Nybelinia* sp. by Dollfus (1969).

A specimen labelled as holotype of *Heteronybelinia punctatissima* (Dollfus, 1960) could be re-identified as *N. lingualis* (see above). Thus, *N. punctatissima* becomes a junior synonym of *N. lingualis*. As Dollfus did not use the holotype for his original description of *N. punctatissima in* Dollfus (1960), but described specimens which were re-identified as *Heteronybelinia estigmena* within the present study, specimens of *N. punctatissima* as described by Dollfus (1960: 837-842, figs 54-59) are synonymous with *Heteronybelinia estigmena* (see below).

Nybelinia cf. *lingualis* (Cuvier, 1817)

MATERIAL EXAMINED. — **Arcachon.** Gironde, France, 1949, leg. H. Nouvel, 2 postlarvae from *Chelidonichthys lucerna* (Linnaeus, 1758) (*Trigla lucerna*) (MNHN 767-768 HF).

DESCRIPTION

sl = 1620, 1100; sw = 765, 672; pbo = 966, 616; pv = 714, nm; pb = 392, 336; ppb = 252, nm; app = 470, 182; vel = 266, 308; bl = 364 (350-378), 299 (294-308); bw = 118 (107-127), 110 (98-119); br = 3.1:1, 2.7:1; sp = 2.5:1.8:1, nm. The tentacle sheaths are coiled, tsw = 35-40, 38-41. Prebulbar organs and muscular rings around the basal part of the tentacle sheaths not visible. The retractor muscles originate in the basal part of the bulbs. The tentacles are not completely evaginated, a basal tentacular swelling is absent, tw basal = 44, 40. The basal tentacular armature is homeoacanthous, homeomorphous and consists of compact rose-thorn-shaped hooks diminishing in size towards the basal part of the tentacles (l = 7.6-10.0, 6.9-10.0; b = 6.8-9.1, 6.2-9.0); hsr = nm, 6-7.

REMARKS

The tentacles of the present specimens were not completely evaginated, which would enable a definitive identification as *N. lingualis* or *N. riseri*. However, the scolex-form is similar to *N. lingualis*, as illustrated by Dollfus (1942). The specimens are therefore identified as *N.* cf. *lingualis.*

Nybelinia riseri Dollfus, 1960
(Fig. 3)

MATERIAL EXAMINED. — **Monterey.** USA, 21.V.1948, leg. N. W. Riser, holotype and 1 paratype, postlarvae from the stomach contents of *Raja binoculata* Girard, 1855 (MNHN 694 HF).
Concarneau. France, 02.VII.1951, leg. R. Legendre, 4 postlarvae from the body cavity of *Mullus surmuletus* Linnaeus, 1758 (MNHN 695 HF, 769-770 HF).

SUPPLEMENTAL DATA. — The holotype was adequately described by Dollfus (1960). The basal and metabasal tentacular armature of the paratype and the apical armature of a specimen from *Mullus surmuletus* are shown in Fig. 3.

DESCRIPTION

Measurements of the paratype and four specimens from *M. surmuletus*, sl = 1665, 1716 (1465-1890); sw = 600, 928 (630-980); pbo = 826, 938 (770-1005); pv = 630, 1000 (798-1150); pb = 378, 294 (252-350); ppb = 21, 8 (5-10); vel = 245, 448 (336-532); app = 623, nm, nm, 434, nm; bl = 362 (350-371), 256 (238-280), 259 (252-266), 226 (214-234), nm; bw = 121 (116-131), 112 (98-126), 130 (126-140), 127 (124-134), nm; br = 3.0:1, 2.3:1, 2.0:1, 1.8:1, nm; sp = 2.2:0.6:1, 2.9:3.0:1, 3.5:4.0:1, 3.1:3.2:1, nm; tw basal = 52-55, 38-41, 38-41, 38-41, 52-55; tw metabasal = 31-34, 31-34, 31-34, 34-36, 45-48; tw apical = 24-25 (paratype). A basal tentacular swelling is absent. The tentacle sheaths are straight; tsw = 30-40, 34-35, 31-35, 40-44, nm. 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 present, consisting of about 10 rows. The tentacular hook form changes towards the metabasal part of the tentacle from compact, rounded rose-thorn-shaped (Fig. 3A), lacking an anterior extension of the basal plate (uncinate), to more slender rose-thorn-shaped hooks with a slight anterior extension (Fig. 3B, C). The hooks in the basal part of the tentacle are smaller (l = 7.0-11.1, 10.0-14.2, 10.0-14.2, 10.1-15.2, 10.2-14.1; b = 8.0-12.1, 7.0-10.1, 6.9-14.1, 8.9-14.1, 7.0-10.2) than in

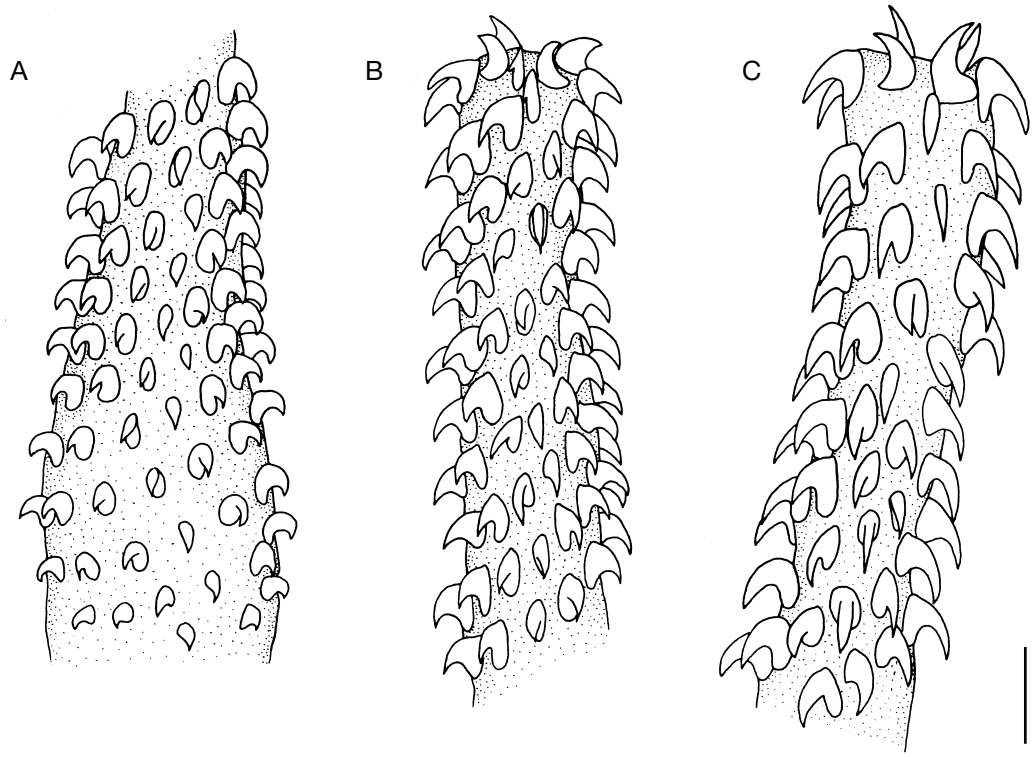

FIG. 3. — *Nybelinia riseri*; **A**, **B**, from *Raja binoculata*; **A**, basal armature; **B**, metabasal armature; **C**, from *Mullus surmuletus*, apical armature. Scale bar: 25 µm.

the metabasal armature (l = 13.2-17.1, 16.1-17.2, 19.1-21.3, 18.9-21.1, 17.0-19.1; b = 12.1-13.2, 12.0-13.3, 12.1-16.2, 14.1-14.9, 13.0-14.1), the apical hooks increase slightly in size. The number of hooks per half spiral diminishes towards the apical part of the tentacle; hsr = 7-8, 6-7, 7-8, 6-7, 7-8 (basal), hsr paratype = 4-5 (apical).

REMARKS

Dollfus (1960) described a specimen of *Nybelinia riseri* with incompletely evaginated tentacles. On the slide with the holotype, a second specimen with nearly completely evaginated tentacles reveals a characteristic armature consisting of compact, rounded rose-thorn-shaped basal hooks, lacking an anterior extension of the basal plate, and more slender rose-thorn-shaped metabasal hooks. However, in contrast to *N. lingualis*, the apical hook form remains similar to that seen on the metabasal part of the tentacle, and the hooks increase slightly in size. Together with the characteristic mushroom shaped scolex, this character distinguishes *Nybelinia riseri* from *N. lingualis*. Both species are closely related, and *N. riseri* changes its position from subgroup 1Aa to subgroup 1Ba *in* Palm *et al.* (1997).

Palm (1999) identified *Nybelinia* specimens from *Trachyurus felicipes* (unrecognisable binomen) from the South African coast as *Nybelinia riseri*, indicating however, that only the first part of the tentacle was evaginated. The confirmation of the validity of *Nybelinia riseri* with its characteristic scolex form supports the assignment of these specimens to *N. riseri*. The present finding extends the distribution of *N. riseri* to the Mediterranean and South Africa and represents two new host records.

Nybelinia scoliodoni (Vijayalakshmi, Vijayalakshmi & Gangadharam, 1996)

Tentacularia scoliodoni Vijayalakshmi, Vijayalakshmi & Gangadharam, 1996.

MATERIAL EXAMINED. — **Concarneau.** France, leg. R. Legendre, 3 postlarvae from *Balistes carolinensis* Gmelin, 1789 (junior synonym *Balistes capriscus* Gmelin, 1789) (MNHN 696 HF, 771 HF).

DESCRIPTION

sl = 791, 770, 980; sw = 686, 686, 685; pbo = 462, 434, 560; pv = 252, 245, 294; pb = 228, 224, 226; vel = 392, 364, 630; app = 350, 364, 462; bl = 226 (224-228), 214 (207-221), 208 (190-224); bw = 83 (69-97), 91 (72-110), 84 (80-124); br = 2.7:1, 2.4:1, 2.5:1; sp = 2.1:1.1:1, 1.9:1.1:1, 2.5:1.3:1. The tentacles are not completely evaginated, a basal tentacle swelling is absent; tw basal = 29-31, 31-34, 29-31; tw metabasal = 32-34, 33-34, 33-34. The tentacle sheaths are sinuous (tsw = 29-31, 31-34, nm), prebulbar organs and muscular rings around the basal part of the tentacle sheaths are not visible. The retractor muscles originate in the basal part of the bulbs.

The metabasal armature is homeoacanthous, homeomorphous and a distinctive basal armature is present. The basal armature consists of about 11 rows with compact rose-thorn-shaped hooks, increasing in size (rows 1-5: l = 3.4-6.9, 3.4-6.9, 4.1-7.2; b = 3.4-4.1, 3.4-6.6, 3.8-6.2; and rows 6-11: l = 7.5-13.8, 7.2-13.8, 7.8-14.2; b = 6.9-8.6, 6.9-10.3, 7.2-11.2). From rows 12-14, the hook form changes. The last hooks measure l = 20.7, 24.1, nm, with a small base b = 11.0, 10.3, nm; hsr basal = 6-7, decreasing in size towards the metabasal part.

REMARKS

Palm (1999) described in detail the morphology and tentacular armature of *Nybelinia scoliodoni*. Though the tentacles of the present specimens were not completely evaginated, the scolex form, hook sizes and the change in the hook form correspond to the material described by Palm (1999). The size and bulb ratio for the present specimens differ slightly from those of the adults obtained from *Carcharhinus limbatus* (Müller & Henle, 1839), *Glyphis gangeticus* (Müller & Henle, 1839), and *Scoliodon palasorrah* (Cuvier) (Palm 1999; Vijayalakshmi *et al.* 1996). This is a further example of intraspecific variability within the genus *Nybelinia*. The present finding is the first report of *N. scoliodoni* from the Mediterranean and represents a new host record.

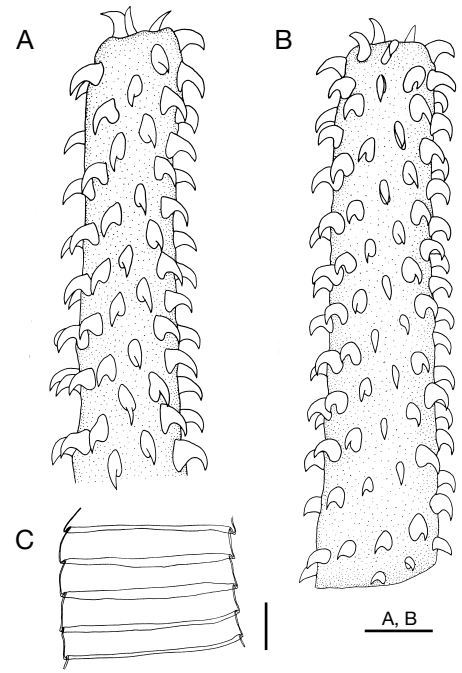

FIG. 4. — *Nybelinia strongyla*; **A**, from *Sphoeroides pachygaster*, metabasal armature; **B**, **C**, from *Sphyrna tudes*; **B**, basal and metabasal armature; **C**, craspedote strobila. Scale bars: A, B, 30 µm; C, 300 µm.

Nybelinia strongyla Dollfus, 1960 (Fig. 4)

MATERIAL EXAMINED. — **Dakar.** Senegal, adequately described *in* Dollfus (1960), holotype from *Sphoeroides pachygaster* (Müller & Troschel, 1848) (junior synonym *Liosaccus cutaneus* [Günther, 1870]) (MNHN 697 HF).

SUPPLEMENTAL DATA. — The tentacular armature of the holotype is re-drawn in Fig. 4A. The tentacles have slender rose-thorn-shaped hooks of similar shape along the tentacle, diminishing slightly in size towards the base.

ADDITIONAL MATERIAL. — **Dakar.** Senegal, 17.III.1949, leg. J. Cadenat, 1 adult from *Sphyrna tudes* (Valenciennes, 1822) (MNHN 806-807 HF).

DESCRIPTION

sl = 1920; sw = 1100; pbo = 845; pv = 503; pb = 585; vel = 832; bl = 553 (533-572); bw = 198 (182-208); br = 2.8:1; sp = 1.4:1:1. The tentacles are not completely evaginated, a basal tentacular swelling is absent; tw basal = 62; tw metabasal = 59. The tentacle sheaths are coiled (tsw = 50-53), prebulbar organs and muscular rings around the basal part of the tentacle sheaths are not visible. The retractor muscles originate in the basal part of the bulbs.

The tentacle armature is homeoacanthous, homeomorphous (Fig. 4A, B) and a distinctive basal armature is absent. The hooks are slender rose-thorn-shaped and increase slightly in size from the base towards the metabasal part of the tentacle (Fig. 4B). Basal hooks: l = 15-17; b = 12-13; metabasal: l = 18-20; b = 14-16; hsr = 6-7.

The strobila is craspedote (Fig. 4C), with about 220 segments behind velum, continuously increasing in size posteriorly. Last proglottid with a rounded posterior end. The first 50 proglottids are 30-80 long × 530-600 wide, the next 130 proglottids enlarge in size to 490 long × 1 535 wide. The final 40 proglottids are between 500-515 long and 1 680-1 735 wide. With the exception of the vitelline follicles (20-40 in diameter), no further details of the internal structure of the contracted and thick proglottids were visible.

REMARKS

Nybelinia strongyla is a large tentaculariid and can be characterised by the presence of large rose-thorn-shaped hooks, increase slightly in size from the basal towards the metabasal part of the tentacle. The species resembles other *Nybelinia* species having rose-thorn-shaped metabasal hooks, such as *N. schmidti* Palm, 1999, *N. thyrsites* Korotaeva, 1971, and *N. queenslandensis* Jones & Beveridge, 1998. *N. schmidti* is smaller and has smaller hooks, tightly spaced along the tentacle. *N. thyrsites* differs in its acraspedote strobila and nearly eight hooks per half spiral row, and *N. queenslandensis* differs in its small scolex with an acraspedote strobila and tightly spaced hooks. Other similar species are *N. anthicosum* Heinz & Dailey, 1974 and *N. lingualis*. However, the former differs with larger hooks and an acraspedote strobila, and the latter differs in its characteristic basal armature.

Nybelinia strongyla has only been recorded from the African coast (Dollfus 1960). The present finding represents a new host record and the first description of an adult specimen. *N. strongyla* changes its position to subgroup 1Aa of Palm *et al.* (1997).

Nybelinia surmenicola Okada, 1929 (Fig. 5)

MATERIAL EXAMINED. — **Victoria.** British Columbia, Canada, 1941, 2 postlarvae from *Gurnardus fabrici* (host not listed *in* Froese & Pauly 1998) (MNHN 775-776 HF).

Departure Bay. Canada, 06.VIII.1946, leg. E. Kuitune, 2 postlarvae from the stomach of *Ophiodon elongatus* Girard, 1854 (MNHN 772-773 HF).

Monterey Bay. California, USA, 04.VI.1948, leg. N. W. Riser, postlarva from *Moroteuthis robusta* (Verill, 1876) (MNHN 774 HF).

DESCRIPTION

sl = 4725, 5670, 4500, 6930, 4770; sw = 1890, 1980, 1575, 2115, 2430; pbo = nm, 2295, 1980, 2565, nm; pv = nm, 1980, 1980, 2565, nm; pb = nm, 945, 700, 1035, nm; ppb not present; vel = nm, 2025, 2030, 2925, 2250; app = 2025, 2610, 1890, 3420, 1500; bl = nm, nm, 672 (630-728), 961 (952-966), nm; bw = nm, nm, 280 (266-294), 324 (308-336), nm; sp = nm, 2.4:2.4:1, 2.8:2.8:1, 2.5:2.5:1, nm; br = nm, nm, 2.4:1, 3.0:1, nm; a basal tentacle swelling is absent. tw basal = 110, 111, 80, 83, 120; tw metabasal = 103, 103, 70, 70, 107; tw in the apical region = nm, nm, nm, 57, nm. The tentacle sheaths are straight (tsw = nm, nm, 75, 70, nm), one specimen with nearly completely evaginated tentacles, tl = 1400; prebulbar organs are absent, muscular rings around the basal part of the tentacle sheaths are visible in some specimens. The retractor muscles originate in the basal part of the bulbs.

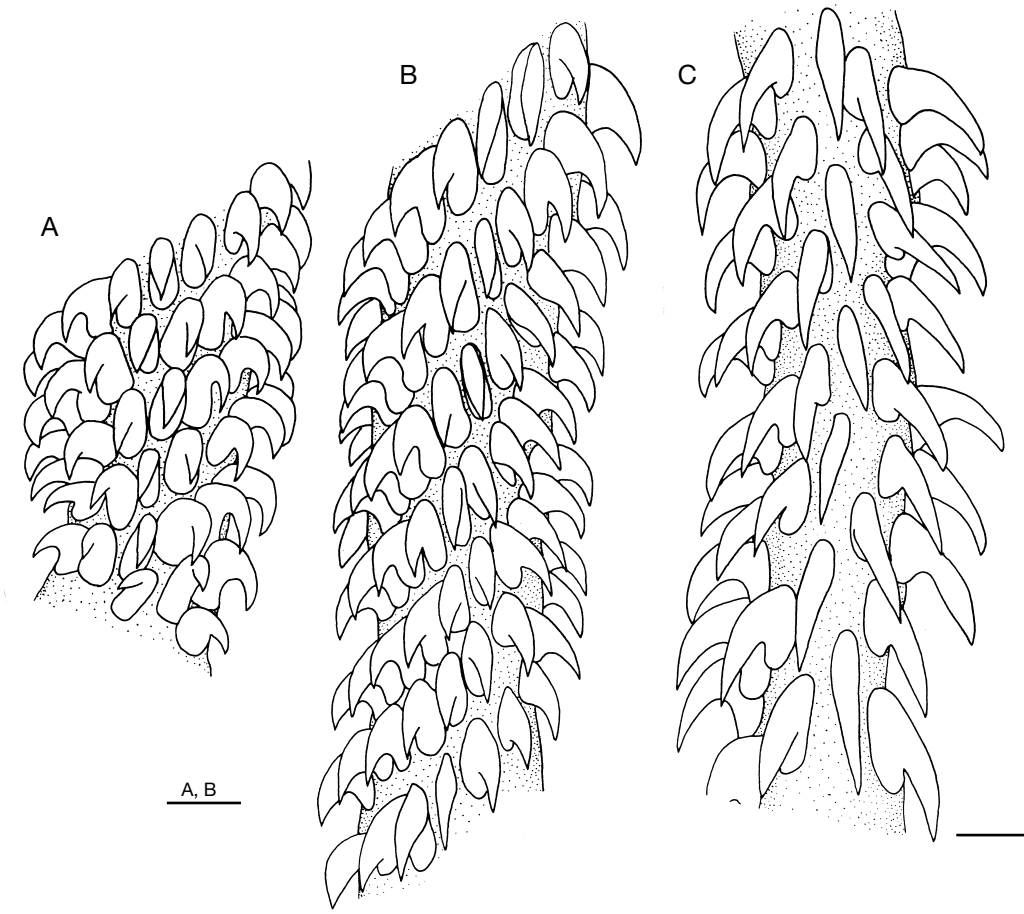

FIG. 5. — *Nybelinia surmenicola* from *Ophiodon elongatus*; **A**, basal armature; **B**, metabasal armature; **C**, apical armature. Scale bars: 30 µm.

The armature is homeoacanthous, homeomorphous. The basal and metabasal armature consists of compact rose-thorn-shaped tentacular hooks (Fig. 5A, B), lacking an anterior extension of the base; basal: l = 28.1-34.2, 30.1-34.1, 22.3-28.2, 21.9-27.8, 24.1-28.3; b = 22.1-24.8, 28.1-30.1, 21.2-27.3, 22.3-26.7, 21.0-25.0; metabasal: l = 38.1-38.9, 38.2-39.0, 34.1-38.0, 34.1-38.9, 30.1-40.8; b = 30.1-33.5, 34.2-35.1, 27.8-32.0, 28.2-34.2, 26.7-33.0; the hooks in the apical part of the tentacles are more slender with a short base (Fig. 5C); apical: l = nm, nm, 40.0-41.1, 40.1-48.2, nm; b = nm, nm, 24.1-26.0, 23.9-26.1, nm. The basal and metabasal hooks are tightly spaced along the tentacle, being more widely spaced in the apical armature. Characteristic basal hooks absent; hsr basal = 7-8; hsr metabasal = 7-8; hsr apical = 6-7.

REMARKS

Nybelinia surmenicola is a large tentacullariid trypanorhynch, resembling *N. lingualis* and *N. riseri* with its rose-thorn-shaped hooks without anterior extension of the base. However, the two latter species have rose-thorn-shaped hook with an anterior extension of the base in the metabasal and apical part of the tentacle. The character combination of the large scolex size and the

compact hook arrangement along the tentacle is unique within *Nybelinia*. As the hook size increases slightly towards the metabasal part of the tentacle, *N. surmenicola* changes its position from subgroup IAb to IAa *in* Palm *et al.* (1997). *Nybelinia surmenicola* has been recorded and described (as the adult) from *Lamna ditropis* Hubbs & Follett, 1947 (Shimazu 1975). Illustrations of the scolex and the metabasal armature resemble the present specimens in detail. However, the apical and basal armature was not described. In the original description, Okada (*in* Dollfus 1929) illustrated a strongly contracted postlarva from the squid *Todarodes pacificus* (Steenstrup, 1880), drawing, however, only the basal part of the tentacles. *N. surmenicola* has been described from various intermediate teleost and cephalopod hosts from the North (Bates 1990; Kinne 1990) and also South Pacific (Oliva *et al.* 1996). The present finding in *Moroteuthis robusta* represents a new host record, as N. W. Riser collected the present specimen in 1948 and recorded *Nybelinia* sp. from *M. robusta* in his thesis (Kinne 1990).

Nybelinia thyrsites Korotaeva, 1971

MATERIAL EXAMINED. — **New Zealand.** 1829, leg. Quoy & Gaimard, 2 postlarvae from the intestine of *Squalus* sp. (MNHN 777-778 HF). Material from the same origin was described by Dollfus (1942) and Beveridge & Campbell (1996) as 2 specimens from unknown host and locality (MNHN A_2R 1140).

DESCRIPTION

sl = 1148, 1162; sw = 840, 938; pbo = 518, 518; pv = 364, 434; pb = 350, 350; ppb = 0, 10; app = 294, 322; vel = 340, 392; bl = 310 (294-322), 320 (308-336); bw = 129 (120-140), 143 (126-155); br = 2.4:1, 2.2:1; sp = 1.5:1:1, 1.5:1.2:1; tentacle sheaths are irregularly coiled, tsw = 51-55, 41-44; tw basal 48-52, 48-51; tw metabasal = 45-48, 45-48; a basal tentacular swelling is absent. Prebulbar organs and muscular rings around the basal part of the tentacle sheaths are not visible. The retractor muscles originate at the base of the bulbs.

The tentacular armature is homeoacanthous, homeomorphous and a characteristic basal armature is absent. The hooks in the basal part of the tentacle are smaller (l = 14.3-17.1, 12.9-16.7; b = 11.0-13.1, 10.2-13.0) than in the metabasal armature (l = 18.1-20.1, 17.8-21.0; b = 14.1-15.1, 13.4-15.1), and diminish in size towards the apical part; basal: hsr = 7-8; metabasal: hsr = 7-8.

REMARKS

Nybelinia thyrsites is adequately described in Beveridge & Campbell (1996). The present material was not labelled in the Dollfus collection but the similar scolex and hooks as given in Beveridge & Campbell (1996) enable a reliable identification. The present material (collected by Quoy & Gaimard in 1829) was interpreted by Beveridge & Campbell (1996) as belonging to *N. thyrsites*. The present description of two further specimens confirms this finding.

Heteronybelinia estigmena (Dollfus, 1960) (Fig. 6)

Nybelinia estigmena Dollfus, 1960.
Nybelinia alloiotica Dollfus, 1960. New synonym.
Nybelinia cadenati Dollfus, 1960. New synonym.
Nybelinia oodes Dollfus, 1960. New synonym.
Nybelinia punctatissima Dollfus, 1960. New synonym.
Nybelinia senegalensis Dollfus, 1960. New synonym.

TYPE MATERIAL. — Deposited under MNHN 704-708 HF, described *in* Dollfus (1960).
Gorée. Senegal, holotype and paratypes of *Heteronybelinia estigmena* from *Alectis alexandrinus* (Geoffroy St Hilaire, 1817) (junior synonym *Hynnis goreensis* Cuvier, 1833) and from *Boops boops* (Linnaeus, 1758).
Dakar. Senegal, paratypes from *Selene setapinnis* (Mitchill, 1815).

MATERIAL EXAMINED. — **Gorée.** Senegal, leg. J. Cadenat, 2 postlarvae from the branchial cavity of *Sphyraena guachancho* Cuvier, 1829 (MNHN 698-699 HF). — Postlarva from the branchial cavity of *Coryphaena equisetis* Linnaeus, 1758 (MNHN 700 HF). — Postlarva from the branchial cavity of *Epinephelus fasciatus* (Forsskål, 1775) (junior synonym *Epinephelus alexandrinus* [Valenciennes, 1828]) (MNHN 701). — Postlarva from the branchial cavity of *Fistularia tabacaria* Linnaeus, 1758 (MNHN 702 HF). — Postlarva from the branchial cavity of *Alectis alexandrinus* (Geoffroy St Hilaire, 1817) (MNHN 703 HF). — Postlarva from the gills

of *Pomadasys incisus* (Bowdich, 1825) (junior synonym *Pristipoma bennetti* Lowe, 1838) (MNHN 692 HF). — Postlarva from the gills of *Echeneis naucrates* Linnaeus, 1758 (MNHN 713 HF). — Postlarva from the branchial cavity of *Sphyraena guachancho* Cuvier, 1829 (MNHN 712 HF). — Postlarva from the branchial cavity of *Seriola dumerili* (Risso, 1810) (MNHN 715 HF). — Postlarva from the branchial cavity of *Alectis alexandrinus* (Geoffroy St Hilaire, 1817) (MNHN 714 HF). — Postlarva from the branchial cavity of *Alectis alexandrinus* (Geoffroy St Hilaire, 1817) (MNHN 717 HF). — Postlarva from the branchial cavity of *Caranx rhonchos* Geoffroy St Hilaire, 1817 (MNHN 718).
Joal. Dakar, Senegal, 16.III.1946, leg. J. Cadenat, 1 adult from the intestine of *Carcharinus obscurus* (LeSueur, 1818) (MNHN 811-812 HF).
Salerno. Florida, USA, 1948, leg. N. W. Riser, 2 adults from the spiral valve of *Carcharhinus leucas* (Valenciennes, 1839) (junior synonym *Eulamia platyodon* [Poey, 1861]), (MNHN 779-781 HF).

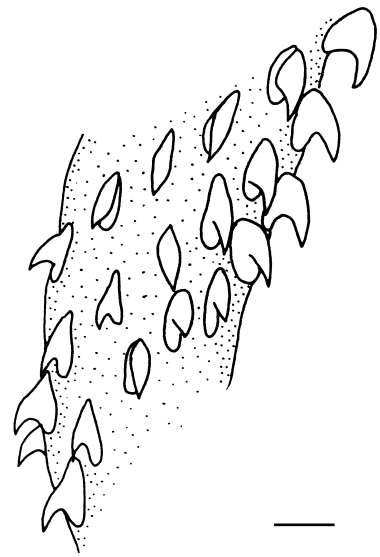

FIG. 6. — *Heteronybelinia estigmena* (= holotype *Nybelinia oodes)* from *Pomadasys incisus*, metabasal armature, external surface, bothridial face on right hand side. Scale bar: 10 µm.

REMARKS

Heteronybelinia estigmena was described by Dollfus (1960) from three different host species, *Boops boops* (Linnaeus, 1758), *Alectis alexandrinus* (Geoffroy St Hilaire, 1817) and *Selene setapinnis* (Mitchill, 1815). The same hosts also harboured specimens of *H. cadenati* and *H. senegalensis*. Similarly, *Sphyraena guachancho* harboured two of the *Heteronybelinia* species, *H. alloiotica* and *H. punctatissima*. Re-examination of the type material revealed only minor differences in scolex morphology and tentacular armature of the specimens described by Dollfus (1960), lying within the range of intraspecific morphological variability as described for other *Nybelinia* and *Heteronybelinia* species (Palm 1999; present study). Dollfus (1960) described *N. oodes* as a species with a homeomorphous tentacular armature. In contrast to the description given by Dollfus (1960), re-examination of the holotype deposited in the MNHN also reveals a heteromorphous tentacular armature (Fig. 6). The hook form changes slightly from the bothridial (basal: l = 6.6-8.5, b = 6.6-8.5; metabasal: l = -10.5-11.8, b = 8.5-10.2) towards the antibothridial tentacle surface (basal: l = 5.3-7.2, b = 4.7-5.6; metabasal: l = 7.9-9.2, b = 7.2-8.5), and slightly increases in size towards the metabasal part of the tentacles. The scolex morphology and tentacular armature of the holotype of *N. oodes* correspond with those given for *H. estigmena*. Thus we conclude the synonymy of the above examined material with *H. estigmena*. This synonymy demonstrates that *Heteronybelinia estigmena* at Gorée can infest several teleost species. A wide host range of *Nybelinia* and *Heteronybelinia* species at the same locality has also been demonstrated for *Nybelinia africana* and *Heteronybelinia yamagutii* by Palm *et al.* (1997).

Within the collection of Dollfus at the MNHN, the slides carrying *Heteronybelinia estigmena*, *H. alloiotica*, *H. cadenati*, *H. senegalensis*, and *Heteronybelinia punctatissima* were labelled only as *Nybelinia* sp. Identification to species was difficult on the basis of morphometrical measurements due to the similarity between them. Assignment, however, was possible on the basis of original hosts and drawings (Dollfus 1960). A further specimen of *Nybelinia punctatissima* (MNHN 693 HF) from *Scomber scombrus* Linnaeus, 1758, labelled as the holotype but not described in Dollfus (1960), was re-identified as belonging to *N. lingualis*. Thus, *N. punctatissima*

is a junior synonym of *N. lingualis* (Cuvier, 1817) (see Remarks for *N. lingualis* above), and the specimens described as *N. punctatissima in* Dollfus (1960: 837-842, figs 54-59) are synonymous with *H. estigmena*.
Palm (1999) acted as first reviser chosing *N. estigmata* as the valid name for this taxon (article 24 of the *International Code of Zoological Nomenclature*).

Heteronybelinia eureia (Dollfus, 1960)

Nybelinia eureia Dollfus, 1960.

MATERIAL EXAMINED. – **Gorée.** Senegal, adequately described *in* Dollfus (1960), holotype and 2 paratypes from an unidentified congrid (*Paraconger* sp.), Dakar, Senegal, and *Mustelus canis* (Mitchill, 1815) (MNHN 709-711 HF).

REMARKS
Heteronybelinia eureia has a heteromorphous tentacular armature consisting of slender hooks. The species is similar to *Mixonybelinia edwinlintoni* in its hook form and size (see below). However, the basal hooks within *H. eureia* are heteromorphous.

Heteronybelinia minima Palm, 1999 (Fig. 7)

MATERIAL EXAMINED. — **Algiers.** Algeria, leg. M. Hanior, 2 postlarvae from the gills of *Chelidonichthys obscura* (Bloch & Schneider, 1801) (MNHN 782-783 HF).

DESCRIPTION
sl = 826, 994; sw = 462, 994; pbo = 336, 462; pv = 252, 448; pb = 224, 267; app = 378, 273; vel = 179, 113; bl = 206 (197-214), 186 (159-217); bw = 64 (62-66), 68 (62-72); br = 3.2:1, 2.7:1; sp = 1.5:1.1:1, 1.7:1.7:1. The tentacles are long, when inverted nearly reaching the apical end of the bulbs, tsw = 27-28, 25-28; tw basal 29, 28, a basal tentacular swelling is absent. Prebulbar organs are absent, a muscular ring around the basal part of the tentacle sheaths is visible within one specimen. The retractor muscles originate at the base of the bulbs.
The tentacular armature is homeoacanthous, heteromorphous and a characteristic basal armature is absent (Fig. 7C). The hooks diminish in size towards the basal part of the tentacle, the hook forms differ from compact and rose-thorn-shaped (bothridial) to slender falcate hooks with a stout base (antibothridial). The hook size in the metabasal armature of both specimens respectively ranges between l = 16.0-16.5, 17.5-18.0; b = 6.5-8.0, 9.5-10.0 (bothridial) and l = 16.5-17.0, 18.5-19.0; b = 6.0-7.0, 7.5-8.2 (antibothridial), and the hook size within the basal part of the tentacle was between l = 9.5-11.5, 9.5-11.5; b = 9.5-10, 9.5-10.0 (bothridial) and l = 7-8.5, 7-8.5.0; b = 4.0-6.0, 4.0-6.0 (antibothridial); hsr = 6.

REMARKS
The present specimens, found encapsulated in the gills of *Chelidonichthys obscura*, were identified as *Heteronybelinia minima*, though having smaller tentacular hooks than was observed in the type specimens by Palm (1999). Similarly, the hook form appeared to be more slender on the bothridial tentacle surface. However, the scolex morphology as well as scolex measurements appeared to be similar (Palm 1999: fig. 34). The tentacles were not visible from the same angle as in the type specimens, thus the shape of the tentacular hooks is not directly comparable with the types (BMNH). In both lots of material, the tentacular hooks increase distinctly in size towards the metabasal region on the bothridial and antibothridial tentacle surfaces, and in the types, the hooks decrease in size from the seventh row towards the apex. Thus, until better material becomes available, the present specimens are identified as *H. minima*, representing a new host and locality record from the Mediterranean.
Specimen MNHN 783 HF illustrates an interesting accidental case of "hyperparasitism". A second specimen of *H. minima* was found completely enclosed within a sl = 980 long *H. minima* (Fig. 7B). There appeared to be some space between the hyperparasite and the host tissue. Both specimens were situated within a single host capsule. A similar accidental case of hyperparasitism has been recorded for the tentaculariid *Tentacularia coryphaenae*

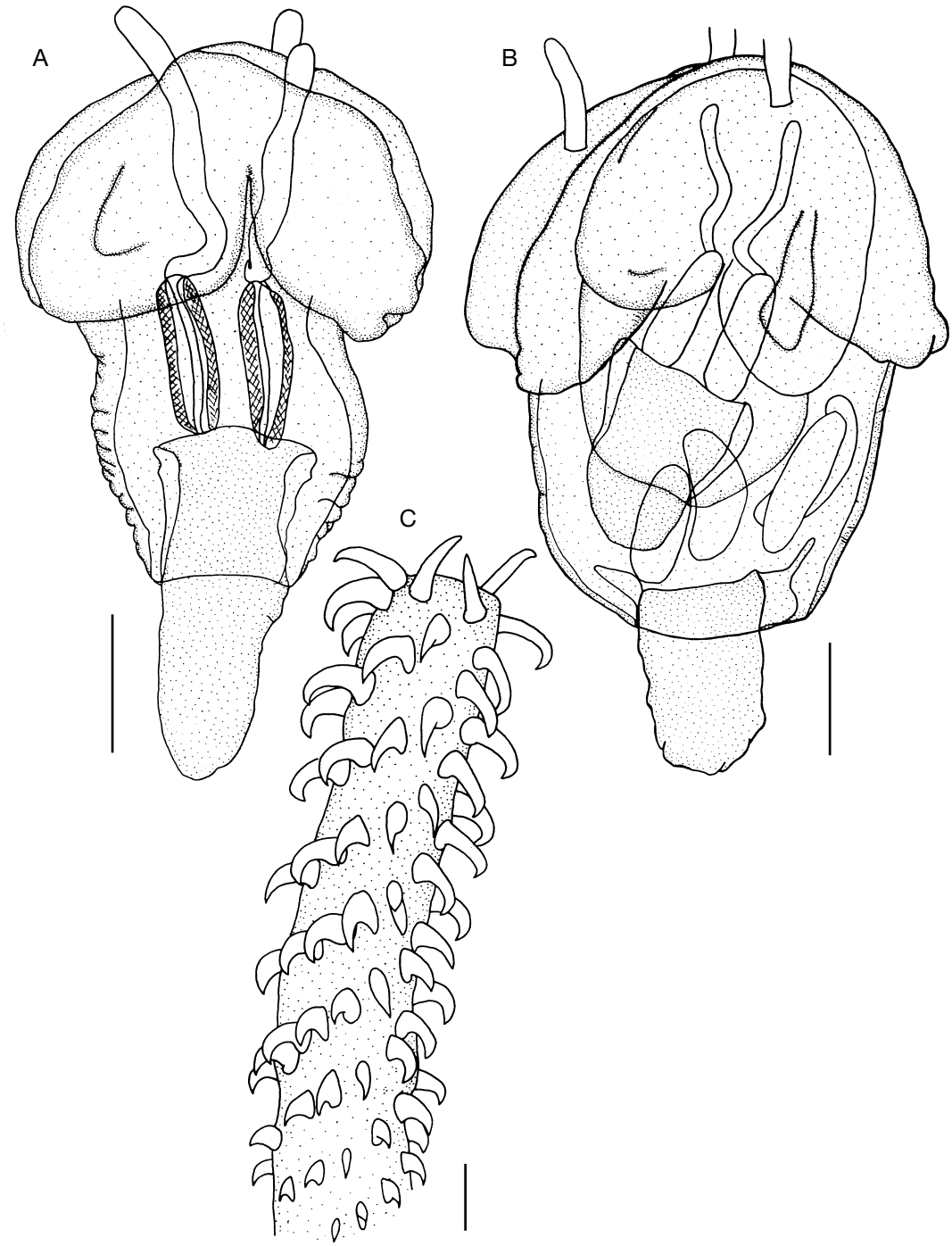

FIG. 7. — *Heteronybelinia minima* from *Chelidonichthyes obscura*; **A**, scolex; **B**, isolated from a single capsule obtained from the gills of *Chelidonichthyes obscura*, note a second specimen of *H. minima* embedded within the host parenchym; **C**, basal and metabasal armature, antibothridial face. Scale bars: A, B, 150 µm; C, 15 µm.

which was found within a specimen of *Phyllobothrium* (Tetraphyllidea) (Gaevskaja 1978).

Heteronybelinia nipponica (Yamaguti, 1952)

Nybelinia nipponica Yamaguti, 1952.

Nybelinia rougetcampanae Dollfus, 1960. New synonym.

MATERIAL EXAMINED. — Described by Dollfus (1960), holotype of *H. rougetcampanae* (Dollfus, 1960) from *Sphoeroides pachygaster* (Müller & Troschel, 1848) (junior synonym *Liosaccus cutaneus* [Günther, 1870]) (MNHN 716 HF).

REMARKS

The holotype of *H. rougetcampanae* (Dollfus, 1960) closely resembles *H. nipponica* (Yamaguti, 1952). Both species can be characterised by the presence of bill hooks in the basal armature and the general arrangement of claw-like metabasal hooks. The only real difference between the two species is the metabasal hook size (27 mm in *H. rougetcampanae* and 35-38 mm in *H. nipponica*). However, in its original description, *H. nipponica* also had a larger scolex size (1350-2900 *vs* 1220), which might explain the larger hook size. Dollfus (1960) commented that *N. rougetcampanae* was the only *Nybelinia* species with bill hooks in the basal armature. However, he overlooked the description of *N. nipponica* by Yamaguti (1952). Thus, we conclude that *H. rougetcampanae* is a junior synonym of *H. nipponica*, and that the latter species has a variable scolex and hook size, as has been described for a species with similar scolex and hook morphology and a wide geographic distribution, *Heteronybelinia yamagutii* (Dollfus, 1960).

Interestingly, *H. rougetcampanae* obtained from the hammerhead shark *Sphyrna lewini* from the Brazilian coast had a small scolex size (510-690) but metabasal hooks (26-29) similar in size to those described by Dollfus (Sao Clemente & Gomes 1992). The size of the scolex of the larvae can be distinctly greater than observed for adult specimens (Sao Clemente & Gomes 1992). This might be explained by a different scolex size which the postlarvae can reach in the second intermediate hosts (see Discussion).

Heteronybelinia robusta (Linton, 1890) (Fig. 8)

Tetrarhynchus robustum Linton, 1890.

MATERIAL EXAMINED. — III.1923, leg. T. Monod, 1 adult and 1 postlarva from the intestine of *Mustelus asterias* Cloquet, 1821 (MNHN 808-809 HF).

DESCRIPTION

Measurements for the adult and postlarva (Fig. 8A): sl = 1166, 1469; sw = 585, 871; pbo = 540, 533; pv = 278, 223; pb = 310, 360; app = not present, 962; vel = 530, 806; bl = 297 (292-302), 331 (318-345); bw = 80 (74-85), 85 (80-90); br = 3.7;1, 3.9:1; sp = 1.7:0.9:1, 1.5:0.7:1. The tentacle sheaths are coiled. tsw = 33-36, 29-33; tw basal 28-29, 26-27, tw metabasal 28, 26, a basal tentacular swelling is absent. Prebulbar organs are absent, muscular rings around the basal part of the tentacle sheaths not visible. The retractor muscles originate at the base 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. 8B). The hook size in the metabasal armature ranged between l = 9-13, 10-14; b = 7-9, 7-9, (bothridial) and l = 12-14, 12-15; b = 6-8, 6-8 (antibothridial), and hooks of the basal part of the tentacle were minute, between l = 5-6, 4-6; b = 5-6, 5-6 (bothridial) and l = 4-5, 4-5; b = 5-6, 5-6 (antibothridial), increasing gradually towards the tip; hsr = 6-7.

The incomplete strobila of the adult worm consists of about 65 acraspedote proglottids behind the velum (Fig. 8C). The first 15 proglottids behind the velum are short (40-70 long × 420-440 wide), the following enlarge in size (100-600 × 530-970). In mature proglottids, genital atrium ventro-submarginal, in anterior third of segment; genital pores alternate irregularly. Cirrus sac short, 300 × 65, directed anterio-medially and extending halfway to the centre of the proglottis, sac thin-walled; cirrus unarmed and coiled within sac, internal and external seminal vesicle absent; testes of

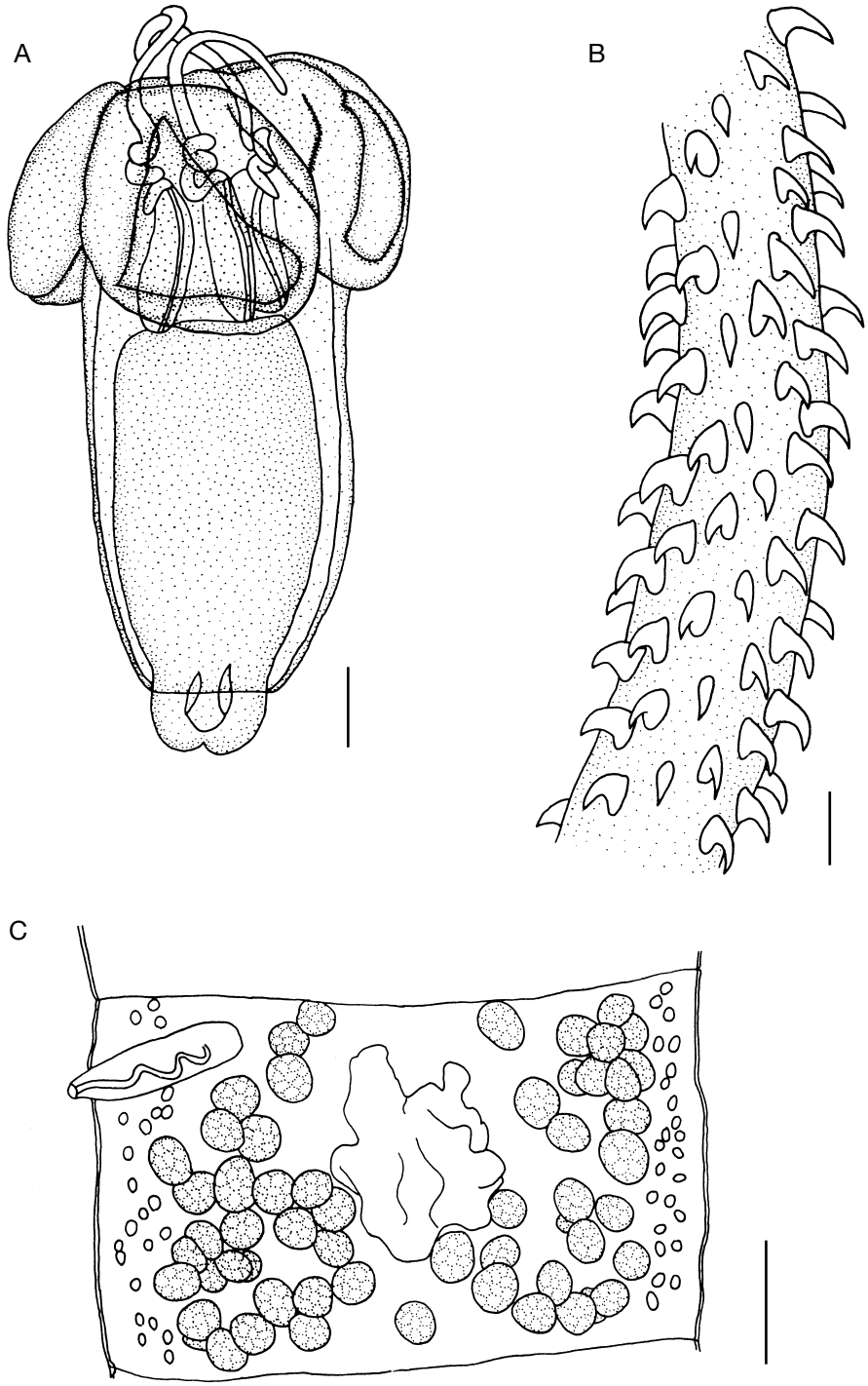

FIG. 8. — *Heteronybelinia robusta* from *Mustelus asterias*; **A**, scolex; **B**, metabasal armature, internal surface, antibothridial face on right hand side; **C**, acraspedote strobila. Scale bars: A, 150 µm; B, 15 µm; C, 200 µm.

different shape, often ovoid, 60-100 in diameter, arranged in more than a single layer; testis number 60-75 per proglottid, encircle female genital complex and occupy entire medulla except for region of female genital complex and anterior of it. Ovary central, follicular. Vitelline follicles 15-25 in diameter. Other internal structures not visible in the present specimen.

REMARKS

The present specimens correspond directly with the description of *H. robusta* by Palm (1999), with respect to scolex size as well as size and arrangement of the tentacular hooks. However, the bulb ratio is 3.7-3.9:1 in the present specimens compared with 3.0:1 in the specimen from *Carcharhinus limbatus* described by Palm (1999). It was obvious that within the same final host species, the postlarva had a larger scolex size than that of the adult worm. However, scolex length measured to the beginning of the velum was the same size in both specimens. *H. robusta* has been recorded from *Carcharhinus limbatus* (Müller & Henle, 1839), *Dasyatis centroura* (Mitchill, 1815), and *Mustelus asterias* Cloquet, 1821 as final hosts, the latter finding represents a new host record.

Heteronybelinia yamagutii (Dollfus, 1960)

Nybelinia yamagutii Dollfus, 1960.

MATERIAL EXAMINED. — Described by Dollfus (1960), Palm *et al.* (1997) and Palm (1999), holotype from *Sphoeroides pachygaster* (Müller & Troschel, 1848) (junior synonym *Liosaccus cutaneus* [Günther, 1870]) (MNHN 719-720 HF).

Mixonybelinia edwinlintoni (Dollfus, 1960) n. comb. (Fig. 9)

Nybelinia edwinlintoni Dollfus, 1960.

MATERIAL EXAMINED. — **Gorée.** Senegal, described by Dollfus (1960), holotype of *Nybelinia edwinlintoni* from *Sphyrna lewini* (Griffith & Smith, 1834) (junior synonym *Sphyrna diplana* Springer, 1941) (MNHN 721 HF).
Joal. Dakar, Senegal, 04.VI.1946, 2 adults from the intestine of *Sphyrna tudes* (Valenciennes, 1822) (MNHN 784-787 HF).
Itamaraca. Brazil, 19.VIII.1993, leg. H. W. Palm, 2 postlarvae from the body cavity of *Pseudupeneus maculatus* (Bloch, 1793) (MNHN 788-789 HF).

DESCRIPTION

Measurements of two specimens from *Sphyrna lewini* and two specimens from *S. tudes*: sl = 1890, 1980, 2610, 2340; sw = 1080, 1190, 1710, 1080; pbo = 714, 1090, 1485, 1200; pv = 700, 900, 1215, 900; pb = 602, 588, 745, 750; ppb = 25, 45, 320, nm; vel = 560, 600, 210, 490; app = not present, 364, 490; bl = 581 (540-616), 523 (518-532), 623 (616-630), 581 (560-610); bw = 168 (154-182), 243 (238-252), 196 (182-196), 203 (196-210); br = 3.5:1, 2.2:1, 3.2:1, 2.9:1; sp = 1.2:1.2:1; 1.9:1.5:1, 2.0:1.6:1, 1.6:1.2:1. The tentacle sheaths are straight; tsw = 70-80, 85-95, 56-77, 86-95. Prebulbar organs absent, muscular rings around the basal part of the tentacle sheaths visible in some specimens. The retractor muscles originate in the basal part of the bulbs (Fig. 9A). A basal tentacular swelling is absent; tw basal = 88-90, 89-90, 72-76, 79-80, tw metabasal = nm, 90-91, 80-90, 86-89.
The metabasal armature of the latter three specimens is homeoacanthous, heteromorphous (Fig. 9B), a characteristic homeomorphous basal armature consisting of about 13-15 rows of slender hooks is present (Fig. 9C). Metabasal armature of strongly re-curved hooks along bothridial surface: l = 23.9-27.8, 24.0-29.1, 25.1-27.8; b = 15.0-18.1, 15.2-18.9, 15.0-17.8; slender falcate hooks along antibothridial surface: l = 27.0-30.0, 24.1-33.9, 28.0-30.8; b = 12.0-13.2, 12.9-17.1, 13.0-14.5. Basal hook size: l = 17.0-18.1, 16.9-23.1, 17.1-24.3; b = 13.1-13.5, 11.5-13.1, 12.5-14.0; hsr basal = 7-8; hsr metabasal = 8-9.
The strobila is craspedote (Fig. 9D), with about 216, 266 segments behind the velum. Proglottids wider than long, larger towards the end of strobila (420-670 × 41-130, 560-1050 × 56-112). Ovary median, follicular. Vitelline follicles numerous, in multiple layers, 13-27 in diameter, smallest follicles near periphery of proglottid. Other internal structures of the proglottids not visible.

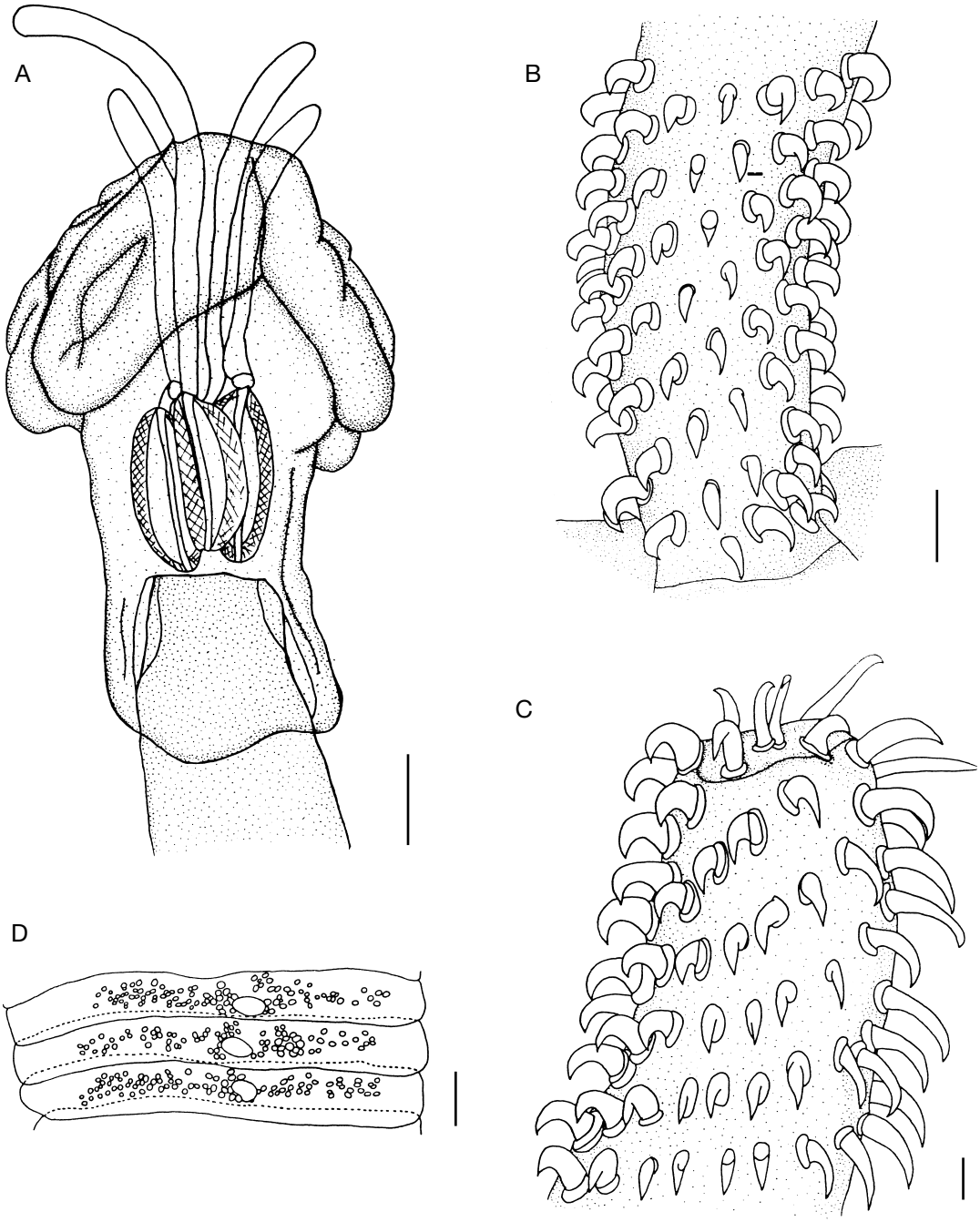

FIG. 9. — *Mixonybelinia edwinlintoni*; **A**, **D**, from *Sphyrna tudes*; **A**, scolex; **B**, **C**, from *Pseudupeneus maculatus*; **B**, basal armature; **C**, heteromorphous metabasal armature, internal surface, antibothridial face on right hand side; **D**, craspedote strobila. Scale bars: A, 300 µm; B, C, 30 µm; D, 200 µm.

REMARKS

The type specimen of *Mixonybelinia edwinlintoni* n. comb. has only partly everted tentacles with 12-13 rows of hooks. Re-examination of that material revealed a homeomorphous armature. Two further specimens in the Dollfus collection labelled as *Nybelinia* sp. (MNHN 784-787 HF) and also collected from the Dakar region revealed a homeomorphous basal armature of about 13 rows of hooks and a heteromorphous metabasal armature, consisting of slender strongly re-curved hooks on the bothridial tentacle surface. Measurements of the basal hooks and the scolex appeared to be similar to the type material of *N. edwinlintoni* and therefore was identified as accordingly. The same tentacular armature was also observed in specimens obtained from *Pseudupeneus maculatus* from the north-east Brazilian coast, which were also identified as belonging to *N. edwinlintoni* by Palm (1997b). The author overlooked the change of the hook form from homeomorphous towards heteromorphous in some specimens with completely everted tentacles. The scolex measurements correspond between these specimens. Thus, *N. edwinlintoni* can be considered as species with a homeomorphous basal armature of about 13 rows and a heteromorphous metabasal armature, occurring in the tropical East and West Atlantic. The present finding is the first record of the adult *M. edwinlintoni* and *Sphyrna tudes* represents a new host record.

Kotorella pronosoma (Stossich, 1901)

Rhynchobothrium pronosomum Stossich, 1901.

Nybelinia rhynchobatus Yang *et al.*, 1995. New synonym.

MATERIAL EXAMINED. — **Agigea.** Romania, leg. N. Bacesco, 2 adults from the intestine of *Dasyatis pastinaca* (Linnaeus, 1758) (MNHN 727 HF).

DESCRIPTION

sl = 483, 616; sw = 240, 168; pbo = 392, 392; pv = 336, 440; pb = 79, 83; vel = 69, 98; bl = 84 (82-86), 76 (74-79); bw = 42 (41-43), 38 (36-39); br = 2.0:1, 2.0:1; sp = 5.0:4.0:1, 4.7:5.3:1. tw basal = 20, nm. A basal tentacular swelling is absent. The tentacle sheaths are straight; tsw = 15-17, 15-17. Prebulbar organs and muscular rings around the basal part of the tentacle sheaths are not visible. The retractor muscles originate in the basal part of the bulbs.

The armature is homeoacanthous, heteromorphous. The basal hooks on the bothridial surface measured l = 6.5-7.0; b = 5.0-5.5.

The strobila is acraspedote, with about 40 segments. The first 30 proglottids are wider than long (112-210 wide × 20-140 long), latter proglottids increase in size towards 224-336 wide × 238-378 long. Testes in single layer of differing shapes, 17-30 in diameter in the first and 50-70 in final proglottids, 57-62 testes per proglottid.

REMARKS

The specimens described here from the Black Sea have small scoleces, but correspond in scolex morphology and hook size with the worms as described by Euzet & Radujkovic (1989), which were collected from *Dasyatis pastinaca* from the Mediterranean. Thus, the present specimens are considered conspecific with *Kotorella pronosoma*. It is interesting to note that the testes number of 57-62 we observed differed from the value of 37 observed by Euzet & Radujkovic (1989: fig. 2). However, Palm & Walter (1999) recorded up to 48 testes per proglottis for *K. pronosoma*, and the testes diameter with 17-70 and 37-64 depending on the size of the proglottid lies within the same range. The present findings from the Black Sea represent a new locality record.

Kotorella pronosoma is a species with a wide geographical distribution, as is seen by its occurrence in the Mediterranean, the Gulf of Mexico, Sri Lanka and Indonesia (Euzet & Radujkovic 1989; Palm & Walter 1999; Palm & Overstreet 2000). Recently, Yang *et al.* (1995) described *N. rhynchobatus* Yang *et al.*, 1995. Judging by the illustrations given by the authors (fig. 1a-d), *N. rhynchobatus* has elongated, distinctly spaced bothridia, short bulbs and a pars bothridialis not overlapping the pars bulbosa. More importantly, fig. 1c-d shows acraspedote proglottids, longer than wide, with a pre-equatorial genital atrium. The cirrus sac is directed medially from the genital atrium, and the testes number is 36-48. This

corresponds exactly with the descriptions of *Kotorella pronosoma* and the medially orientated cirrus sac is not known in any species of *Nybelinia*, *Heteronybelinia* and *Mixonybelinia* species. Thus, we consider *Nybelinia rhynchobatus* to be conspecific with *K. pronosoma*.

Nybelinia sp.

MATERIAL EXAMINED. — Deposited as *Nybelinia* sp. but not identifiable due to partly or completely invaginated tentacles.
Sète. France, 10.IV.1951, leg. L. Euzet, postlarva from the intestine wall of *Scyliorhinus canicula* (Linnaeus, 1758) (MNHN 722 HF).
Banyuls. France, 13.VI.1950, leg. J. Theodorides, postlarva from the oesophagus wall of *Trigla* sp. (MNHN 723 HF).
Rabat. Morocco, 30.III.1949, 5 postlarvae from intestine wall of *Merluccius merluccius* (Linnaeus, 1758) (MNHN 724-726 HF).
Coast of France. 3 adults from *Raja* sp. (MNHN 790-795 HF).
Concarneau. France, 13.IV.1938, leg. R. Legendre, postlarva from the body cavity of *Mullus barbatus* Linnaeus, 1758 (MNHN 796 HF).
Ajaccio. Corsica, IV.1948, leg. G. Houdemer, postlarva from between the tunica of the stomach wall of *Scomber scombrus* Linnaeus, 1758 (MNHN 797 HF).
Arcachon. Gironde, France, 1949, leg. H. Nouvel, postlarva from *Chelidonichthys lucerna* (Linnaeus, 1758) (MNHN 798 HF); 1949, leg. H. Nouvel, postlarva from *Chelidonichthys obscurus* (Bloch & Schneider, 1801) (MNHN 799 HF).
Unknown locality. 1866, leg. P. J. Van Beneden, 2 postlarvae from unknown host (MNHN 800-801 HF); 1866, leg. P. J. Van Beneden, 2 adults from *Galeorhinus galeus* (Linnaeus, 1758) (junior synonym *Galeus canis* Bonaparte, 1834) (MNHN 802-805 HF).
Gorée. Senegal, 21.V.1951, leg. Y. Rouget-Campana, 1 adult from *Sphyrna lewini* (Griffith & Smith, 1834) (junior synonym *Sphyrna diplana* Springer, 1941) (MNHN 810 HF).

CURRENT SPECIES WITHIN THE TENTACULARIIDAE POCHE, 1926 *SENSU* PALM (1997A)

On the basis of the present study, the tentaculariid genera *Kotorella* Euzet & Radujkovic, 1989, *Nybelinia* Poche, 1926, *Heteronybelinia* Palm, 1999, *Mixonybelinia* Palm, 1999 and *Tentacularia* Bosc, 1797 are represented by 39 different species. Three further species were considered as species of uncertain status by Palm *et al.* (1997), two species are considered as *species inquirendae* in the present study, *Nybelinia* sp. *in* Palm (1999) needs to be re-examined, and two species, *N. bisulcata* and *N. tenuis*, require re-description from type material to confirm their validity.

Genus *Nybelinia* Poche, 1926

TYPE SPECIES. — *Tetrarhynchus lingualis* Cuvier, 1817.

SPECIES INCLUDED. — *N. africana* Dollfus, 1960 (synonym *N. perideraeus* [Shipley & Hornell, 1906]); *N. aequidentata* (Shipley and Hornell, 1906); *N. anguillae* Yamaguti, 1952; *N. anthicosum* Heinz & Dailey, 1974; *N. basimegacantha* Carvajal, Campbell & Cornford, 1976; *N. bengalensis* Reimer, 1980; *N. erythraea* Dollfus, 1960 (species synonymy discussed above); *N. gopalai* Chandra & Hanumantha Rao, 1985; *N. goreensis* Dollfus, 1960; *N. indica* Chandra, 1986 (species synonomy with *N. scoliodoni* discussed *in* Palm 1999); *N. jayapaulazariahi* Reimer, 1980; *N. lingualis* (Cuvier, 1817) (synonyms *N. infulata* [Molin, 1858] and *N. punctatissima* Dollfus, 1960, others see Dollfus [1942]); *N. manazo* Yamaguti, 1952; *N. pintneri* Yamaguti, 1934; *N. queenslandensis* Jones & Beveridge, 1998; *N. riseri* Dollfus, 1960; *N. sakanariae* Palm, 1999; *N. schmidti* Palm, 1999; *N. scoliodoni* (Vijayalakshmi, Vijayalakshmi & Gangadharam, 1996); *N. sphyrnae* Yamaguti, 1952; *N. strongyla* Dollfus, 1960; *N. surmenicola* Okada, 1929; *N. syngenes* (Pintner, 1929); *N. thyrsites* Korotaeva, 1971.

DEFINITION

Trypanorhynchs with the characters of the Tentaculariidae Poche, 1926. Scolex compact, four triangular bothridia, with hook-like microtriches along bothridial borders and filamentous microtriches on remainder of bothridia and scolex. Posterior margins of bothridia fused with peduncle. Four tentacles of variable length and width, armed with hooks; metabasal tentacular armature homeoacanthous with homeomorphous hooks. Basal hooks homeomorphous or heteromorphous, characteristic basal armature absent or present. Retractor muscle originates at base of bulbs. Proglottids acraspedote or craspedote, cirrus unarmed, genital pores alternate irregularly (24 species).

Genus *Heteronybelinia* Palm, 1999

TYPE SPECIES. — *Nybelinia estigmena* Dollfus, 1960.

SPECIES INCLUDED. — *H. elongata* (Shah & Bilqees, 1979); *H. estigmena* (Dollfus, 1960) (synonyms *H. alloiotica* [Dollfus, 1960], *H. cadenati* [Dollfus, 1960]; *H. senegalensis* [Dollfus, 1960], *H. punctatissima* [*in* Dollfus 1960], *N. oodes* Dollfus, 1960); *H. eureia* (Dollfus, 1960); *H. heteromorphi* Palm, 1999; *H. minima* Palm, 1999; *H. nipponica* (Yamaguti, 1952) (synonym *Heteronybelinia rougetcampanae* [Dollfus, 1960]); *H. palliata* (Linton, 1924); *H. perideraeus* (Shipley & Hornell, 1906); *H. robusta* (Linton, 1890); *H. yamagutii* (Dollfus, 1960).

DEFINITION

Trypanorhynchs with the characters of the Tentaculariidae Poche, 1926. Scolex compact, four triangular bothridia, with hook-like microtriches along the bothridial borders and filamentous microtriches on the rest of the bothridia and the scolex. Posterior margins of bothridia fused with peduncle. Four tentacles 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. Retractor muscle originates at base of bulbs. Proglottids acraspedote or craspedote, cirrus unarmed, genital pores alternate irregularly (10 species).

Genus *Mixonybelinia* Palm, 1999

TYPE SPECIES. — *Nybelinia beveridgei* Palm, Walter, Schwerdtfeger & Reimer, 1997.

SPECIES INCLUDED. — *M. beveridgei* (Palm, Walter, Schwerdtfeger & Reimer, 1997); *M. edwinlintoni* (Dollfus, 1960); *M. southwelli* (Palm & Walter, 1999).

DEFINITION

Trypanorhynchs with the characters of the Tentaculariidae Poche, 1926. Scolex compact, four triangular bothridia, with hook-like microtriches along the bothridial borders and filamentous microtriches on the rest of the bothridia and the scolex. Posterior margins of bothridia fused with peduncle. Four tentacles of variable 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. Retractor muscle originates at base of bulbs. Proglottids acraspedote or craspedote, cirrus unarmed, genital pores alternate irregularly (three species).

Genus *Kotorella* Euzet & Radujkovic, 1989

TYPE SPECIES. — *Rhynchobothrium pronosomum* Stossich, 1901.

SPECIES INCLUDED. — *Kotorella pronosoma* (Stossich, 1901) (synonyms *Nybelinia herdmani* [Shipley & Hornell, 1906], *N. narinari* [MacCallum, 1917], *N. rhynchobatus* Yang *et al.*, 1995, others see Palm & Walter [1999]).

DEFINITION

Trypanorhynchs with the characters of the Tentaculariidae Poche, 1926. Scolex compact, four elongated spaced bothridia, with hook-like microtriches along the bothridial borders and filamentous microtriches on the rest of the bothridia and scolex. Posterior margins of bothridia free and not fused with the peduncle. Four tentacles emerging from scolex; metabasal tentacular armature homeoacanthous with heteromorphous hooks on different tentacle surfaces. Basal hooks heteromorphous, characteristic basal armature absent. Retractor muscle originates at base of bulbs. Strobila acraspedote, cirrus unarmed, Genital pores lateral, alternate irregularly, in the middle of proglottids or slightly pre-equatorial.

Genus *Tentacularia* Bosc, 1797

TYPE SPECIES. — *Tentacularia coryphaenae* Bosc, 1797.

SPECIES INCLUDED. — *Tentacularia coryphaenae* Bosc, 1797 (synonym *Nybelinia lamontae* Nigrelli, 1938 [Palm *et al.* 1997], others see Dollfus [1942]).

DEFINITION

Trypanorhynchs with the characters of the Tentaculariidae Poche, 1926. Scolex elongated, four elongate sessile narrow bothridia lie along

the scolex, with hook-like microtriches along the bothridial borders and filamentous microtriches on the rest of the bothridia and scolex. Four tentacles emerging from scolex; metabasal tentacular armature homeoacanthous homeomorphous. Characteristic basal armature present. Retractor muscle originates at base of bulbs. Strobila acraspedote, cirrus unarmed, genital pores lateral, alternate irregularly, in anterior third of proglottids.

SPECIES NOT CONSIDERED

Nybelinia anantaramanorum Reimer, 1980. See Remarks under *N. goreensis*;
N. bisulcata (Linton, 1889). Linton deposited voucher specimens of different *Nybelinia*, *Heteronybelinia* and *Mixonybelinia* species under the name *N. bisulcata* in the National Helminthological Collection, Beltsville, USA. The identity of the species needs to be clarified;
N. congri Guiart, 1935 (Palm *et al.* 1997);
N. macrocephala Asmi, 1983 *in* Bilqees & Khurshid (1987) (Palm *et al.* 1997);
N. tenuis (Linton, 1890). The identity of the species needs to be clarified;
N. trisulcata in Reimer (1980) (Palm *et al.* 1997);
Heteronybelinia karachii (Khurshid & Bilqees, 1988). The incomplete original description of *H. karachii* does not indicate the number of bothridia, and Khurshid & Bilqees (1988: fig. 1a) demonstrate a trypanorhynch specimen with two bothridia. Without re-examination of the type material, *H. karachii* can not be assigned to any tentaculariid genus. Thus, the species should be treated as *species inquirenda*.

DISCUSSION

The present study summarises the state of knowledge within the genera *Nybelinia*, *Heteronybelinia*, *Mixonybelinia* and *Kotorella*. A further species (*M. edwinlintoni* n. comb.) is transferred to the genus *Mixonybelinia* Palm, 1999, and *Nybelinia oodes*, *Heteronybelinia alloiotica*, *H. cadenati*, and *H. senegalensis* are considered synonyms of *H. estigmena* (all described *in* Dollfus 1960). *H. punctatissima* is considered a synonym of *N. lingualis* (Cuvier, 1817), while the specimens described and illustrated as *H. punctatissima in* Dollfus (1960) are specimens of *H. estigmena* (Dollfus, 1960). *H. rougetcampanae* (Dollfus, 1960) is considered a synonym of *H. nipponica* (Yamaguti, 1952), and *N. rhynchobatus* Yang *et al.*, 1995 a synonym of *Kotorella pronosoma* (Stossich, 1901). To date, a total of 38 species can be recognised within the genera *Nybelinia*, *Heteronybelinia*, *Mixonybelinia*, and *Kotorella*. The two species *N. tenuis* and *N. bisulcata* need further examination.

Palm *et al.* (1997), Palm (1999) and Palm & Walter (1999) discussed the zoogeographical distribution of different species of these tentaculariid genera. The authors recorded a wide geographical distribution for *N. africana*, *H. robusta*, *H. yamagutii* and *M. beveridgei* (Palm *et al.* 1997) as well as for *N. perideraeus*, *K. pronosoma* (Palm & Walter 1999), *N. lingualis*, *N. scoliodoni*, *H. estigmena*, and *H. heteromorphi* (Palm 1999). The present results add *N. riseri*, *H. nipponica*, *H. minima*, and *M. edwinlintoni* to the list of widely distributed species. Thus, 14 species have a wide distribution, indicating an transoceanic or sometimes interoceanic occurrence. However, other species seem to be regionally distributed, such as *N. surmenicola* (mainly recorded from the North Pacific Ocean and only once from the Southern Pacific, Oliva *et al.* 1996), *N. thyrsites*, and *N. queenslandensis* (New Zealand, East Australian coast). Whether this difference is real or only a matter of limited information can not be decided at present.

Tentaculariid trypanorhynchs exhibit a low level of host-specificity and a wide host range within a single locality (Dollfus 1942, 1960; Palm *et al.* 1997, present study). The low host specificity not only applies to the teleost intermediate but also the final elasmobranch hosts. For example, *N. africana*, *N. scoliodoni*, and *H. robusta* infest four, three, and three elasmobranch species, respectively, including sharks with a wide zoogeographical distribution. Marcogliese (1995) stated that marine helminths exhibit very limited host-

specificity in zooplankton intermediate hosts, and similarly in fish as intermediate (Holmes 1990) and birds as final hosts (Bush 1990). This has been interpreted as spreading the risk of failure to complete their life cycles in the marine environment. The same pattern seems to be also true for tentacullariid trypanorhynchs.

The present study demonstrates that four further species, *N. erythraea*, *N. lingualis*, *N. surmenicola* and *H. minima*, have muscular rings around the tentacle sheaths directly above the bulbs, which have not been described previously for these species. Palm *et al.* (1997) proposed a possible systematic value of such muscular rings, which have been earlier described from *Heteronybelinia* species, e.g., *H. elongata* and *H. estigmena*. It seems that muscular rings around the tentacle sheaths are a common feature within these trypanorhynchs, however, they are not always visible, most probably due to different fixation and staining methods. This questions the use of this structure as a systematic character within tentacullariid cestodes. *N. africana* and *N. goreensis* had smaller hooks in the apical than in the metabasal armature. This has been described also for *Nybelinia aequidentata* by Pintner (1927), and thus seems to occur in several different *Nybelinia* species. This also demonstrates the apical armature as an important taxonomic character, which should be considered in future species descriptions.

It is evident that several of the above recorded tentacullariids have a high intraspecific morphological variability (see also Palm *et al.* 1997; Palm 1999). Interestingly, within the same host species, postlarvae can have a larger scolex size than the adult worms, as with *Heteronybelinia nipponica* (= *H. rougetcampanae*). The postlarvae ranged between 1 220-2 900 (Yamaguti 1952; Dollfus 1960), and the adults between 510-690 (Sao Clemente & Gomes 1992). Similarly, the scolex sizes of postlarvae and adults of *Nybelinia africana* varied between 1 118-1 568 (Dollfus 1960; Palm *et al.* 1997) and 440-536 (Palm 1999), and of *H. yamagutii* between 1 183-3 904 (Dollfus 1960; Palm *et al.* 1997) and 2 646 (Palm 1999), respectively. Sao Clemente & Gomes (1992) referred a smaller scolex size of adult worms to the shrinkage condition. Palm *et al.* (1993) found a similar scolex variability within the non-tentacullariid *Otobothrium penetrans* Linton, 1907, and referred it to the plerocercoid age and/or type of fixation and storage. Campbell *et al.* (1999) referred the occurrence of two different morphotypes of adult *Paroncomegas araya* to different age, development or population density. Additionally we propose that the scolex size within the final host is influenced by the growth rate of the metacestodes within the first and second intermediate hosts. It could be demonstrated that within another fish parasitic helminth, the nematode *Hysterothylacium aduncum* (Rudolphi, 1802), the life-cycle depends on the size the larvae reach within the first and second intermediate hosts (Køie 1993). This might be also true for tentacullariid trypanorhynchs.

Summarising the above, tentacullariid trypanorhynchs are characterised by a characteristic scolex morphology, the lack of a blastocyst, and a wide distribution pattern. The low host-specificity might be another character of these trypanorhynchs, facilitating the wide distribution. As the first intermediate hosts of these cestodes are still unknown, it remains unclear whether these trypanorhynchs also have a specific life cycle with characteristic first intermediate hosts, which might be different to intermediate hosts of other trypanorhynchs. Further data on the zoogeographical distribution of the different species, especially their occurrence also in the central parts of the oceans, as well as information on the first intermediate hosts are needed to really establish the possibly oceanic life cycle pattern of these unspecific trypanorhynchs.

Acknowledgements

We wish to thank Prof. J.-L. Justine, MNHN for the possibility to study tentacullariid trypanorhynchs of the MNHN collection, Prof. L. W. Reimer for access to his collection, and S. Klimpel who assisted during our stay in Paris. Financial support was provided by the Institut für Meereskunde Kiel, the EU-Parasyst programme, and the German Research Council DFG PA 664/3-1 and 3-2.

REFERENCES

Bates R. M. 1990. — A checklist of the Trypanorhyncha (Platyhelminthes: Cestoda) of the world (1935-1985). *National Museum of Wales*, *Zoological Series* No. 1, 218 p.

Beveridge I & Campbell R. A. 1996. — New records and descriptions of trypanorhynch cestodes from Australian fishes. *Records of the South Australian Museum* 29: 1-22.

Bilqees F. M. & Khurshid N. 1987. — Trypanorhyncha from fishes of Karachi coast. *Proceedings of Parasitology (Pakistan)* 3: 54-130.

Bush A. O. 1990. — Helminth communities in avian hosts: determinants of patterns: 197-232, *in* Esch G. W., Bush A. O. & Aho J. M. (eds), *Parasite Communities: Patterns and Processes*. Chapman & Hall, London.

Campbell R. A. & Beveridge I. 1994. — Order Trypanorhyncha Diesing, 1863: 51-82, *in* Khalil L. F., Jones A. & Bray R. A. (eds), *Keys to the Cestode Parasites of Vertebrates*. CAB International, Wallingford.

Campbell R., Marques F., Ivanov V. 1999. — *Paroncomegas Araya* (Woodland, 1934) n. gen. et comb. (Cestoda: Trypanorhyncha: Eutetrarhynchidae) from the freshwater stingray *Potamotrygon motoro* in South America. *Journal of Parasitology* 85: 313-320.

Carvajal J., Campbell R. A. & Cornford E. M. 1976. — Some trypanorhynch cestodes from Hawaiian fishes, with description of four new species. *Journal of Parasitology* 62: 70-77.

Dollfus R. P. 1929. — Addenum à mon « Énumération des cestodes du plancton et des invertebrés marins ». *Annales de Parasitologie humaine et comparée* 7: 325-347.

Dollfus R. P. 1942. — Études critiques sur les Tétrarhynques du Muséum de Paris. *Archives du Muséum national d'Histoire naturelle* 19: 1-466.

Dollfus R. P. 1960. — Sur une collection de Tétrarhynques homéacanthes de la famille des Tentaculariidae récoltées principalement dans la région de Dakar. *Bulletin de l'Institut francais d'Afrique noire* 22 (A): 788-852.

Dollfus R. P. 1969. — De quelques Cestodes Tétrarhynques (Hétéracantes et Pécilacanthes) récoltés chez des poissons de la Méditerranée. *Vie et Milieu* Série 20 (A): 491-542.

Euzet L. & Radujkovic B. M. 1989. — *Kotorella pronosoma* (Stossich, 1901) n. gen., n. comb., type des Kotorellidae, nouvelle famille de Trypanorhyncha (Cestoda), parasite intestinal de *Dasyatis pastinaca* (L., 1758). *Annales de Parasitologie humaine et comparée* 64: 420-425.

Froese R. & Pauly D. 1998. — *Fish Base 98 CD ROM*. International Centre for Living Aquatic Resources Management, Manila.

Gaevskaja A. V. 1978. — Several cases of accidental hyperparasitism on the cestodes. *Zoologicheskii Zhurnal* 57: 1262-1263.

Holmes J. C. 1990. — Helminth communities in marine fishes: 101-130, *in* Esch G. W., Bush A. O. & Aho J. M. (eds), *Parasite Communities: Patterns and Processes*. Chapman & Hall, London.

Khurshid N. & Bilqees F. M. 1988. — *Nybelinia karachii* new species from the fish *Cybium guttatum* of Karachi coast. *Pakistan Journal of Zoology* 20: 239-242.

Kinne O. 1990 — *Diseases of Marine Animals*. Vol. III: *Introduction*, *Cephalopoda*, *Annelida*, *Crustacea*, *Chaetognatha*, *Echinodermata*, *Urochordata*. Biologische Anstalt Helgoland, Hamburg, 696 p.

Køie M. 1993. — Aspects of the life cycle and morphology of *Hysterothylacium aduncum* (Rudolphi, 1802) (Nematoda, Ascaridoidea, Anisakidae). *Canadian Journal of Zoology* 71: 1289-1296.

Marcogliese D. J. 1995. — The role of zooplankton in the transmission of helminth parasites to fish. *Review in Fish Biology and Fisheries* 5: 336-371.

Oliva M. E., Castro R. E. & Burgos R. 1996. — Parasites of the flatfish *Paralichthys adspersus* (Steindachner, 1867) (Pleuronectiformes) from northern Chile. *Memorias do Instituto Oswaldo Cruz*, *Rio de Janeiro* 91: 301-306.

Palm H. W. 1995. — Untersuchungen zur Systematik von Rüsselbandwürmern (Cestoda: Trypanorhyncha) aus atlantischen Fischen. *Berichte aus dem Institut für Meereskunde*, *Kiel* 275: 1-238.

Palm H. W. 1997a. — An alternative classification of trypanorhynch cestodes considering the tentacular armature as being of limited importance. *Systematic Parasitology* 37: 81-92.

Palm H. W. 1997b. — Trypanorhynch cestodes of commercial fishes from northeast Brazilian coastal waters. *Memorias do Instituto Oswaldo Cruz*, *Rio de Janeiro* 92: 69-79.

Palm H. W. 1999. — *Nybelinia* Poche, 1926, *Heteronybelinia* gen. nov. and *Mixonybelinia* gen. nov. (Cestoda: Trypanorhyncha) in the collections of The Natural History Museum, London. *Bulletin of the Natural History Museum of London (Zoology series)* 65: 133-153.

Palm H. W. 2000. — Trypanorhynch cestodes from Indonesian coastal waters (East Indian Ocean). *Folia Parasitologica* 47: 123-134.

Palm H. W. & Overstreet R. 2000. — New records of Trypanorhynch cestodes from the Gulf of Mexico, including *Kotorella pronosoma* (Stossich, 1901) and *Heteronybelinia palliata* (Linton, 1924) comb. n. *Folia Parasitologica* 47: 293-302.

Palm H. W. & Walter T. 1999. — *Nybelinia southwelli* sp. nov. (Cestoda: Trypanorhyncha) with the re-description of *N. perideraeus* (Shipley & Hornell, 1906) and synonymy of *N. herdmani* (Shipley & Hornell, 1906) with *Kotorella pronosoma* (Stossich,

1901). *Bulletin of the Natural History Museum of London (Zoology Series)* 65: 123-131.
Palm H. W., Möller H. & Petersen F. 1993. — *Otobothrium penetrans* (Cestoda: Trypanorhyncha) in the flesh of belonid fish from Philippine waters. *International Journal for Parasitology* 23: 749-755.
Palm H. W., Walter T., Schwerdtfeger G. & Reimer L. W. 1997. — *Nybelinia* Poche, 1926 (Cestoda: Trypanorhyncha) from the Mocambique coast, with description of *N. beveridgei* sp. nov. and systematic consideration on the genus. *South African Journal of Marine Science* 18: 273-285.
Pintner T. 1927. — Kritische Beiträge zum System der Tetrarhynchen. *Zoologische Jahrbücher* 53: 559-590.
Roper C. F. E., Sweeney M. J. & Nauen C. E. 1984. — FAO species catalogue. Vol. 3: Cephalopods of the world. An annotated and illustrated catalogue of species of interest to fisheries. *FAO Fisheries Synopsis* (125) 3: 277 p.
Sao Clemente S. C. & Gomes D. C. 1992. — Description of the adult form of *Nybelinia* (*Syngenes*) *rougetcampanae* Dollfus, 1960 and some new data on *N.* (*N.*) *bisulcata* (Linton, 1989) (Trypanorhyncha: Tentaculariidae). *Memorias do Instituto Oswaldo Cruz*, Supplemente 1: 251-255.
Shimazu T. 1975. — A description of the adult of *Nybelinia surmenicola* with discussions on its life-history (Cestoda: Trypanorhyncha: Tentaculariidae). *Bulletin of the Japanese Society of Scientific Fisheries* 41: 823-830.
Vijayalakshmi C., Vijayalakshmi J. & Gangadharam T. 1996. — Some trypanorhynch cestodes from the shark *Scoliodon palasorrah* (Cuvier) with the description of a new species, *Tentacularia scoliodoni*. *Rivista di Parassitologia* 13: 83-89.
Yamaguti S. 1952. — Studies on the helminth fauna of Japan. Part 49: Cestodes of fishes, II. *Acta Medicinae Okayama* 8: 1-76.
Yang W., Lin Y., Liu G. & Peng W. 1995. — Five species of Trypanorhyncha from marine fishes in Xiamen, Fujian, China. *Journal of the Xiamen University (Natural Science)* 34: 811-817.

Submitted on 27 October 1999;
accepted on 18 February 2000.