

New records of trypanorhynch cestodes from the Gulf of Mexico, including *Kotorella pronosoma* (Stossich, 1901) and *Heteronybelinia palliata* (Linton, 1924) comb. n.

Harry W. Palm¹ and Robin M. Overstreet²

¹Marine Pathology Group, Abteilung Fischereibiologie, Institut für Meereskunde an der Universität Kiel, Düsternbrooker Weg 20, D-24105 Kiel, Germany;

²Gulf Coast Research Laboratory, The University of Southern Mississippi, P.O. Box 7000, Ocean Springs, Mississippi 39566-7000, USA

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Abstract. Four trypanorhynchs, *Kotorella pronosoma* (Stossich, 1901), *Nybelinia* cf. *bisulcata* (Linton, 1889), *Nybelinia scoliodoni* (Vijayalakshmi, Vijayalakshmi et Gangadharam, 1996), and *Dasyrhynchus pacificus* Robinson, 1965 are reported for the first time from the Gulf, which is now known to harbour at least 34 different species. In addition to the range extension for the trypanorhynchs listed above, 21 new host records are reported involving 13 cestode species. Characters of the genus *Kotorella* Euzet et Radujkovic, 1989 are emended, *Nybelinia narinari* MacCallum, 1917 is considered a junior synonym of *Kotorella pronosoma* (Stossich, 1901), and *Heteronybelinia palliata* (Linton, 1924) comb. n. is redescribed. The usefulness of the bulb ratio as a means to distinguish different tentaculicid species is discussed, and the importance of shallow water localities for the life cycle of trypanorhynch cestodes is emphasised.

The Gulf of Mexico is well known as a locality for many different trypanorhynch cestodes, both as metacestodes in invertebrates and teleosts and as adults in elasmobranchs. All superfamilies and most of the families recognised by Campbell and Beveridge (1994) and Palm (1995, 1997a) are represented. Accepted species reported from the Gulf to date are *Eutetrarhynchus lineatus* (Linton, 1909), *Oncomegas wagneri* (Linton, 1890), *Parachristianella dimegacantha* Kruse, 1959, *P. heteromegacantha* Feigenbaum, 1975, *P. monomegacantha* Kruse, 1959, *Prochristianella hispida* (Linton, 1890), *P. tenuispine* (Linton, 1890), *Trimacracanthus binuncus* (Linton, 1909), *Diplobothrium springeri* Chandler, 1942, *Otobothrium cysticum* (Mayer, 1842), *O. insigne* Linton, 1905, *O. penetrans* Linton, 1907, *Pseudotobothrium dipsacum* (Linton, 1897), *Poecilancistrum caryophyllum* (Diesing, 1850), *Hepatoxylon megacephalum* (Rudolphi, 1819), *Heteronybelinia estigmena* (Dollfus, 1960), *H. palliata* (Linton, 1924), *Nybelinia lingualis* (Cuvier, 1817), *Sphyricephalus* sp., *Tentacularia coryphaenae* Bosc, 1797, *Callitetrarhynchus gracilis* (Rudolphi, 1819), *Dasyrhynchus giganteus* (Diesing, 1850), *Grillotia perelica* Shuler, 1938, *G. similis* (Linton, 1900), *G. heptanchi*-group of Chandler (1954), *Pseudogrillotia pleistacantha* Dollfus, 1969, *P. zerbiae* Palm, 1995, *Gymnorhynchus gigas* (Cuvier, 1817), *Pterobothrium heteracanthum* (Diesing, 1850) and *P. lintoni* (MacCallum, 1916) (see Chandler 1954, Kruse 1959, Thatcher 1961, Aldrich 1965, Schlicht and

McFarland 1967, Nikolaeva and Paruhin 1968, Dollfus 1969, Henson 1975, Overstreet 1977, 1978b, Hildreth and Lumsden 1985, Palm 1995, Palm and Overstreet 2000). Metacestodes of a few other trypanorhynch species require confirmation or identification (e.g. Feigenbaum 1975, Cake 1977). Thus, the Gulf of Mexico constitutes one of the best-studied regions for these marine parasites.

Within the present study, a variety of trypanorhynch species from the Gulf of Mexico was identified. Most of the specimens are plerocercoids from teleosts, but we are including some records of adults from the blacktip shark, *Carcharhinus limbatus* (Valenciennes). New records allow observations on zoogeographical distribution as well as intraspecific variability. Palm and Overstreet (2000) proposed the shallow waters in the Gulf of Mexico to be important in the life cycle of *Otobothrium cysticum*. The importance of shallow waters for the life cycle of other trypanorhynch species reported from the region will also be discussed. Finally, the identity of *Nybelinia narinari* is clarified, and *Heteronybelinia palliata* comb. n. is redescribed.

MATERIALS AND METHODS

From June to July 1993, a sample of teleost and elasmobranch species from the Gulf of Mexico was examined for trypanorhynch cestodes by both authors, and, since 1969, other collections have been made by the junior author. Many of the fish were obtained with the help of small recreational and Gulf

Coast Research Laboratory vessels. Standard measurements and drawings were made using a Leitz Wetzlar Orthoplan microscope. Drawings were made using a Leitz Wetzlar Dialux 22 microscope with a drawing tube. To clarify the identity of some tentaculariids, we borrowed type material of *Nybelinia narinari* and *N. palliata* as well as material deposited as *N. bisulcata* from the U.S. National Parasite Collection, Beltsville (USNPC).

Measurements were taken on the following features: scolex length (SL), scolex width at level of pars bothridialis (SW), pars bothridialis (pbo), pars vaginalis (pv), pars bulbosa (pb), pars postbulbosa (ppb), velum (vel), appendix (app), bulb length (BL), bulb width (BW), bulb length to width ratio (BR), proportions of pbo : pv : pb (SP), tentacle width (TW) and tentacle sheath width (TSW). If possible, the tentacle length (TL) was estimated. Additionally, the tentacular armature was described as follows: armature homeomorphous or heteromorphous, hooks per half spiral row (hsr), total hook length (L), hook height (H) and the total length of the base (B).

All measurements are given in micrometres unless otherwise indicated. Illustrations are provided where useful; otherwise, the reader is referred to illustrations of other authors. The classification follows that of Palm (1995, 1997a), and orientation of tentacle surfaces follows that of Campbell and Beveridge (1994).

RESULTS

Superfamily TENTACULARIOIDEA Poche, 1926

Family Tentaculariidae Poche, 1926

Kotorella pronosoma (Stossich, 1901) Figs. 1, 2

New synonymy: *Nybelinia narinari* (MacCallum, 1917)

Supplemental data (based on one adult specimen labelled as “type” of *Nybelinia narinari* MacCallum, 1917, USNPC 35813, G.A. MacCallum coll., 25.5.1916, from the spiral valve of *Aetobatis narinari* Euphrasen, Java, Jakarta (=Batavia), Java Sea, Indonesia): Scolex craspedote, 985 SL, 400 SW; bothridia 4, widely spaced, lateral margins free, longer than half scolex length, width 120-135, posterior portion of bothridia 280 wide, not attached to scolex peduncle, marginal band of hook-shaped microtriches in “V-shaped” pattern with apex of V pointing anteriorly; pbo 430; pv 540; pb 135; vel 250-280; BL 132 (130-135); BW 68 (67-70); BR 1.9:1; SP 3.2:4.1:1. Tentacles emerging pairwise, 290 long, slender, diminishing in size toward tip; TW 25 (basal) and 17 (apical); basal tentacular swelling lacking. Tentacle sheaths straight; TSW 13-17. Prebulbular organs lacking, muscular rings around basal part of tentacle sheath not visible. Retractor muscles originating in basal part of bulbs. Armature homeoacanthous, heteromorphous; tentacular hooks on antibothridial tentacle surface increasing in size toward distal portion of tentacle, slender, spiniform, without enlarged basal plates, more widely spaced than on bothridial surface; tentacular hooks on bothridial surface similar in size along tentacle, tightly packed, having broad diamond-shaped basal plate, with

9-10 L and 7-8 B, with distance between hooks larger toward apical part of tentacle; basal hooks 4-6 L, 2-4 B, 8 hsr; metabasal hooks 9-10 L, 2-3 B, 6-7 hsr. Strobila acraspedote, 300 wide, consisting of 46 proglottids, with last 6 proglottids longer (320) than wide (300, last proglottid). Testes spherical, 23-30 in diameter; other internal structures not seen.

Supplemental data (based on two postlarvae from *Cynoscion nebulosus* (Cuvier), Figs. 1, 2): Scolex as indicated above, 675 (670-680) SL (with appendix), 285 (270-300) SW, with posterior part 255 (240-270) wide and not attached to scolex peduncle (Fig. 2). Bothridia more than half length of scolex, 125 (120-130) wide; bothridial margins covered with band of microtriches in V-shaped pattern as reported for adult, 400 (370-430) pbo, 430 (420-440) pv, 108 (106-110) pb, 63 (60-66) vel, 173 (160-186) app, 96 (91-101) and 99 (88-101) BL, 56 (53-59) and 57 (56-59) BW; BR 1.7:1; SP 3.8:4:1 (3.7:4:1-3.9:4:1). Tentacles short, 225 (200-250), 25 TW (basal), 17 TW (apical); basal tentacular swelling lacking; tentacular sheaths straight, 15-17 TSW. Armature with 8-10 L, 5.0-7.5 B (basal and metabasal; bothridial surface), with 3-5 L, 1.5-2.0 B (basal; antibothridial surface), with 9-11 L, 2.0-2.5 B (metabasal; antibothridial surface); hsr 8-9 (basal), 6-7 (metabasal).

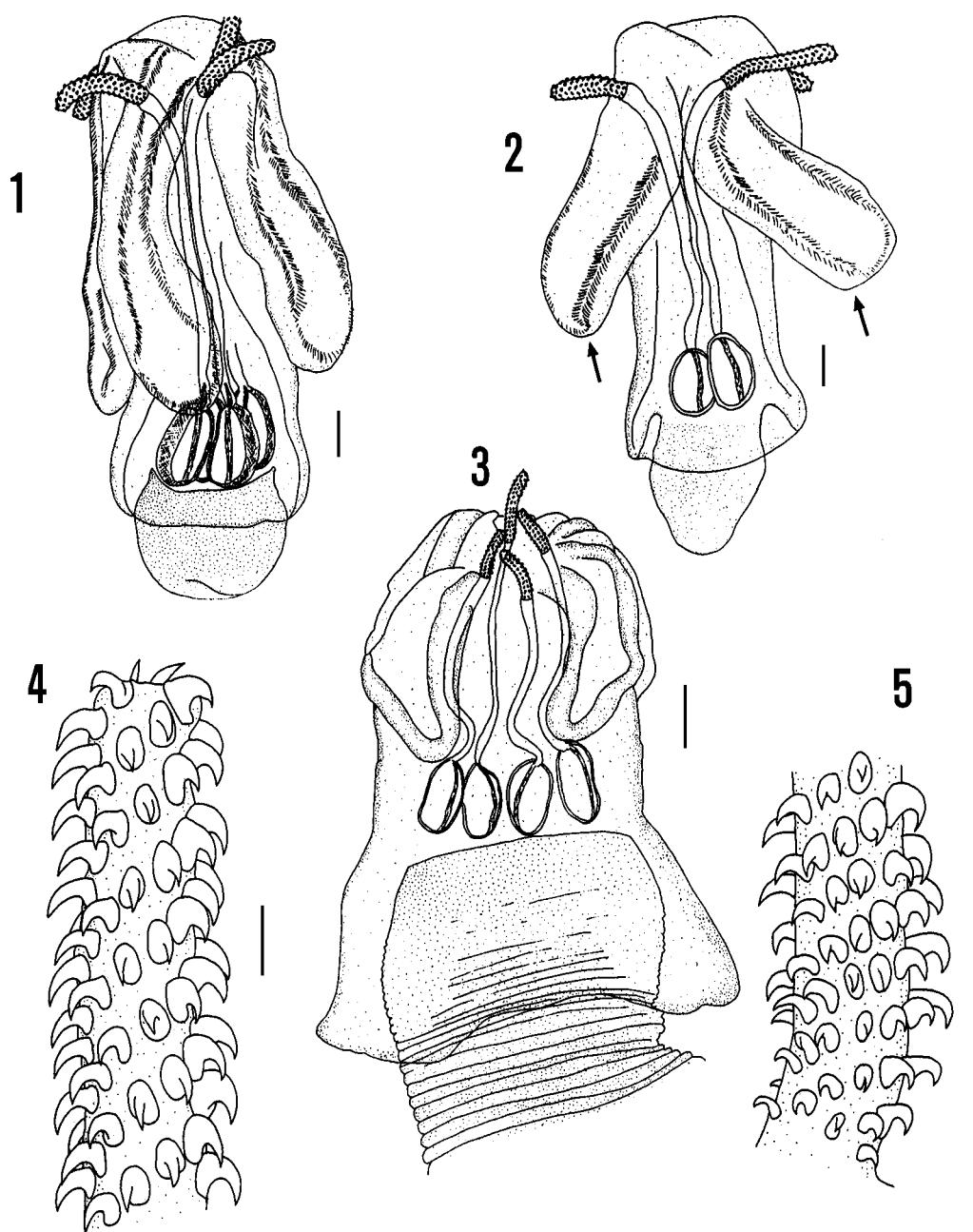
Host: *Cynoscion nebulosus* (Cuvier), spotted seatrout (Sciaenidae).

Site: Stomach wall.

Locality: Coastal waters off Ocean Springs, Mississippi, Gulf of Mexico.

Remarks: We consider *Nybelinia narinari* MacCallum, 1917 to be a junior subjective synonym of *Kotorella pronosoma* (Stossich, 1901). Euzet and Radujkovic (1989) redescribed *Rhynchobothrium pronosomum* Stossich, 1901 as *K. pronosoma* from the spiral valve of *Dasyatis pastinaca* (Linnaeus) from the Mediterranean Sea (Adriatic Sea). Our measurements, including those of material labelled as “type” of *N. narinari*, correspond with those provided by Euzet and Radujkovic (1989), especially the values for SL, pb, BL, BW, and TL. Also, hook sizes of the tentacular armature described by Euzet and Radujkovic (1989), Campbell and Beveridge (1994) and Palm and Walter (1999) are similar (L = 8-11 µm in the present study compared to 10-15 as summarised in Palm and Walter 1999). The scolex of *K. pronosoma* (as *N. narinari*) was well illustrated by MacCallum (1917, fig. 22), however, lacking a detailed description of the armature. The present description adds that the bothridia are widely spaced with free lateral margins, a character distinguishing the genus *Kotorella* from *Nybelinia*. The type specimen of *N. narinari* MacCallum, 1917 (= *K. pronosoma*) is mounted together with the type specimen of *Taenia narinari* MacCallum, 1917 on the same slide.

Our material of postlarvae obtained from a 17-cm long spotted seatrout *Cynoscion nebulosus* from the Gulf of Mexico also corresponds with the type material of



Figs. 1-2. Two different postlarvae of *Kotorella pronosoma* from *Cynoscion nebulosus*. Note the free posterior margins of the bothridia (arrow), clearly visible in the specimen in Fig. 2. **Figs. 3-5.** *Heteronybelinia palliata*. **Fig. 3.** Scolex isolated from *Sphyrna zygaena*. **Fig. 4.** Metabasal armature. **Fig. 5.** Basal armature. Scale bars: Figs. 1, 2 = 50 μ m; Fig. 3 = 200 μ m; Figs. 4, 5 = 20 μ m.

Nybelinia herdmani (Shipley et Hornell, 1906), a species recently redescribed and considered to be a junior synonym of *K. pronosoma* by Palm and Walter (1999) on the basis of comparable bulb ratio, scolex proportions and form and arrangement of the tentacular armature. Even though the size of the scolex and the 8-11 μ m tentacular hooks are smaller than the 13-15 μ m ones reported by Palm and Walter (1999), they are of similar form and

arrangement as those from the type specimen of *N. herdmani* as illustrated in Palm and Walter (1999, figs 8a-b). Thus, the present findings underline the synonymy of *N. herdmani* with *K. pronosoma*.

As described for adults of *K. pronosoma*, the present postlarvae possess long and slender bothridia with free lateral margins and characteristic marginal, hook-like microtriches in a V-shaped pattern, as can be seen under

the light microscope (Figs. 1, 2). The occurrence and arrangement of such microtriches closely resemble those described from the bothridial margins of *Tentacularia coryphaenae* and three species of *Nybelinia* reported by Palm (1995). This finding might support a close phylogenetic relationship between *Kotorella* and *Nybelinia* as proposed by Campbell and Beveridge (1994) and Palm (1995, 1997a). However, the free posterior margins of the bothridia of *K. pronosoma* are unique within Tentaculariidae, supporting recognition of the genus *Kotorella*. This feature of the posterior margins should be added to the generic diagnoses by Euzet and Radujkovic (1989) and by Campbell and Beveridge (1994) as the emendation “Posterior portions of bothridia free and not fused with pedunculus scolices.”

Postlarvae of *K. pronosoma* are recorded for the first time, from the teleost *C. nebulosus*. This finding represents a new host record and extends the known range of distribution for the species from the Mediterranean Sea and the Indian Ocean to the Western Atlantic region. *Kotorella pronosoma* can be considered a cosmopolitan species, with a distribution pattern similar to that of several other tentaculariid cestodes.

Nybelinia scoliodoni (Vijayalakshmi, Vijayalakshmi et Gangadharam, 1996)

Supplemental data (based on measurements of three postlarvae): Scolex 1230 (1087-1367) SL, 845 (834-867) SW, 671 (647-713) pbo, 329 (300-387) pv, 310 (294-320) pb, 47 (30-70) ppb, 510 (467-567) vel, 540 (400-634) app, 308 (300-320) BL, 110 (105-120) BW; BR 2.8:1 (2.6-2.9:1); SP 2.2:1.1:1. Tentacles 450-459 long (when about half still invaginated), basal tentacle swelling lacking; TW 28-37; tentacle sheaths sinuous, with 1-2 spirals (25-33 TSW); prebulbular organs and muscular rings around basal part of tentacle sheaths absent. Retractor muscles originating in basal part of bulbs. Metabasal armature homeoacanthous, homeomorphous, with characteristic basal armature, with hsr 4-5; basal armature consisting of about 11 rows, with compact rosethorn-shaped hooks, with hsr 6-7; hooks increasing in size; hooks in rows 1-5: 4.8-7.0 L, 4.8-6.3 B; hooks in rows 6-11: 9-11 L, 7-10 B; hooks in rows 12-14 changing to long and spiniform (22-25 L), with small basal plate (6.5-8.5 B).

Host: *Coryphaena hippurus* Linnaeus, common dolphin fish (Coryphaenidae).

Site: Postlarvae migrating out of the stomach wall.

Locality: Coastal waters off Ocean Springs, Mississippi, Gulf of Mexico.

Remarks: More than one hundred postlarvae were found in the stomach of a 131-cm long female of *Coryphaena hippurus* from waters off Ocean Springs. The postlarvae actively penetrated the stomach wall about one hour after the fish was dissected, which was several hours after the fish had been caught and kept on ice.

Even though scolex measurements of the present specimens are twice as large as those given for *N. scoliodoni* in the original description and by Palm (1999), the tentacular armature is identical to that described by Vijayalakshmi et al. (1996) and Palm (1999, fig. 17). The change in form from rosethorn-shaped basal to spiniform metabasal hooks is unique within the genus. Having a larger scolex, the present specimens also have basal hooks that are slightly larger (hooks in rows 1-5: 4.8-7.0 versus 3.5-5.6 L, 4.8-6.3 versus 3.5-4.9 B; in rows 6-11: 9-11 versus 7-9.8 L, 7-10 versus 5.6-8.4 B; hooks in rows 12-14: 22-25 versus 22-26 L, 6.5-8.5 versus 7.7-10.5 B) than those described by Palm (1999). However, Vijayalakshmi et al. (1996) reported a hook size of 8-11 for the rosethorn-shaped hooks, similar to the measurements of hooks in rows 6-11, and they also demonstrated more minute hooks in the basal part of the tentacle similar to those in rows 1-5 of the present specimens. The known range of distribution for the species is extended to the Gulf of Mexico, and *Coryphaena hippurus* represents a new host record.

Heteronybelinia* cf. *estigmena (Dollfus, 1960)

Supplemental data (based on one postlarva): Scolex with 2050 SL, 1235 SW, 1370 pbo, 967 pv, 435 pb, 0 ppb, 367 vel, 634 app; BL 384 (360-400); BW 119 (115-120); BR 3.2:1; SP 3.1:2.2:1. Tentacles 660 long, without basal tentacle swelling; TW 40-48; tentacle sheaths straight (37-43 TSW), with muscular rings around basal part of tentacle sheaths; prebulbular organs absent. Retractor muscles originating in basal part of bulb. Metabasal armature homeoacanthous, heteromorphous, without characteristic basal armature; metabasal armature consisting of rosethorn-shaped hooks on both bothridial and antibothridial portions; bothridial portion with 13-14 L, 12.5-13.3 B, 11.8-12 H; antibothridial portion 10-11.5 L, 10.5-11.8 B, 9.5-9.7 H; hooks decreasing slightly in size toward basal part of tentacle; hooks on bothridial portion 10-11.5 L, 10.5-11.8 B, 10.3-10.3 H; hooks on antibothridial portion 9.7-10.5 L, 9.7-10.5 B, 8.8-9.2 H; hsr 6-7.

Host: *Thunnus albacares* (Bonnaterre), yellowfin tuna (Scombridae).

Site: Stomach wall.

Locality: Coastal waters off Ocean Springs, Mississippi, Gulf of Mexico.

Remarks: The present specimen from a 137-cm long female yellowfin tuna clearly belongs to subgroup IIAa in Palm et al. (1997). However, the morphometrical data do not correspond directly with any particular species. The species shows similarities with *Heteronybelinia estigmena* of Dollfus (1960) (see Palm 1999). With a total length of about 2 mm and hooks up to 14 µm, the species appears slightly larger than *H. estigmena* (1 mm SL, bothridial hooks 10-11 µm, antibothridial 8-9 µm), but Dollfus (1960) described two additional varieties, one of them 1.9 mm long. Previous studies (Palm et al. 1997, Palm 1999,

Palm and Walter 1999) demonstrated that intraspecific variability can be high in tentaculidids, and Palm and Walter (2000) synonymised several *Heteronybelinia* species with *H. estigmene* (Dollfus, 1960). Palm (1995) already described this species (as *H. alloiotica*) from the coastal waters off Ocean Springs. Thus, on basis of a single postlarva, we prefer tentatively to consider the species *Heteronybelinia* cf. *estigmene*.

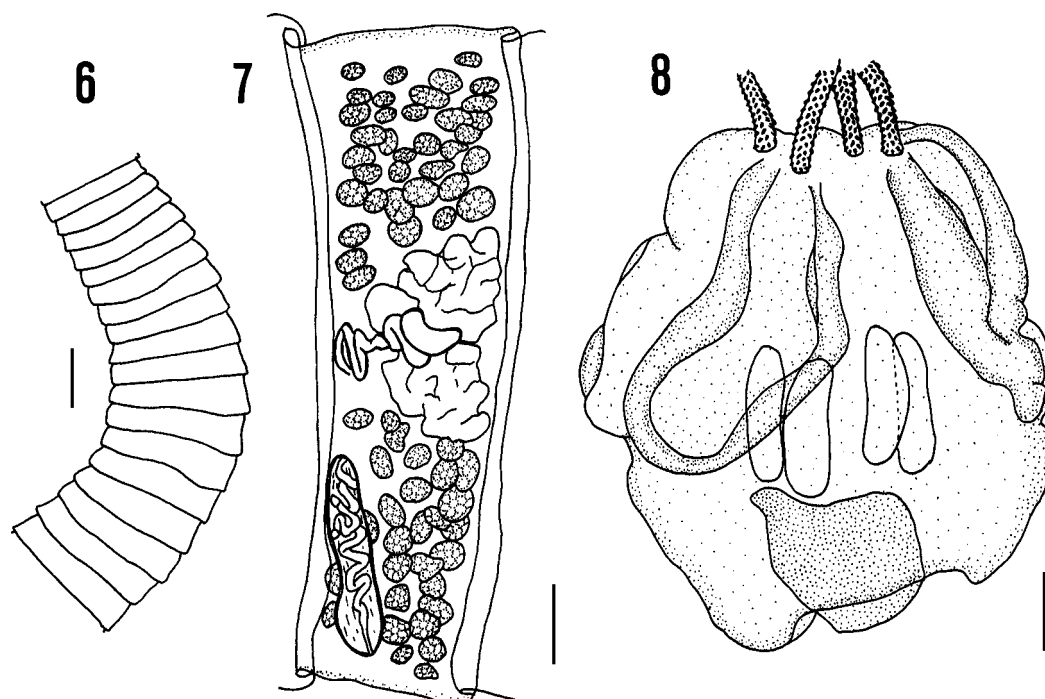
Heteronybelinia palliata (Linton, 1924) comb. n.

Figs. 3-8

Redescription (based on three adult syntypes of *Tetrarhynchus palliatus* Linton, 1924 from *Sphyrna zygaena* (Linnaeus) [USNPC 7726], one with invaginated tentacles): Scolex craspedote, 1621 (1472-1856) SL with velum (Fig. 3), 828 (715-1040) SW, 763 (715-806) pbo, 650 (519-780) pv, 377 (351-392) pb, 615 (533-676) vel, 335 (277-368) BL, 144 (140-147) BW; BR 2.3 (1.9:1-2.6:1); SP 2.0:1.7:1 (2.3:2.2:1, 1.8:1.3:1, 2.0:1.7:1). Tentacles with basal swelling lacking (n = 2), 300-420 TL, 30-32 TW (basal), 33-33 TW (metabasal), 33-33 TSW, with prebulbular organs and muscular rings around tentacle sheaths lacking, with retractor muscle inserting in basal part of bulb. Tentacular armature homeoacanthous, heteromorphous (Fig. 4), with hooks of similar size and of different shape on internal and external tentacle surfaces

(n = 2); hooks on internal surface compact and rosethorn-shaped, 17-18 L, 14.0-15.5 B, diminishing in size (Fig. 5) toward basal part of tentacle to 12.5-14.0 L, 9.0-10.5 B; hooks on external surface more slender and spiniform than those on internal surface, 16.5-18.0 L, 8.5-10.0 B, diminishing in size towards basal part of the tentacle to 12.5-14.0 L, 6-8 B; hsr 6-7 (basal), 6-7 (metabasal).

Strobila (n = 3) craspedote, consisting of 71, 80 and 108 proglottids, with about 20 of those proglottids overlapped by velum of scolex. Proglottids wider than long (Figs. 6, 7), with size increasing continuously; with proglottis 40 = 140 × 950, 80 × 900, 70 × 1260, with proglottis 70 = 350 × 1900, 250 × 1270, 330 × 1970, and with proglottis 100 = 670 × 2270, 400 × 1840. Testes in proglottis 70 numbering 60-70, in several layers, 40-80 in diameter, relatively large and ovoid around female genital complex, smaller and oval-shaped along margin of proglottid, with some present anterior to cirrus sac; cirrus sac elongate, 530-600 long, 65-80 wide, thin-walled, directed anteriomedially from genital atrium; cirrus unarmed, 750-800 long, with internal and external seminal vesicles not evident; genital atrium ventro-submarginal in anterior third of proglottid, alternating irregularly. Ovary bilobed. Further details of the reproductive organs are given by Linton (1924, p. 96).



Figs. 6-8. *Heteronybelinia palliata*. Fig. 6. Strobila between the 45th and 62nd proglottids behind the velum. Fig. 7. Mature proglottid. Fig. 8. Postlarva isolated from *Paralichthys dentatus*. Scale bars: Fig. 6 = 1 mm; Figs. 7, 8 = 200 µm.

Supplemental data (based on two postlarvae from *Paralichthys dentatus* (Linnaeus), USNPC 80723): Scolex craspedote (Fig. 8), 1489 (1378-1600) SL with velum, 1170 SW, 930 (923-936) pbo, 748 (624-871) pv, 406 (387-424) pb, 443 (325-520) vel, 350 (300-400) app, 373 (360-386) BL, 110 (106-114) BW; BR 3.4:1; SP 2.4:2.3:1 / 2.2:1.5:1. Tentacle with basal swelling lacking, 450-500 TL, 33-39 TW (basal), 20-33 TW (metabasal), 16 TSW, prebulbular organs and muscular rings around tentacle sheaths lacking; retractor muscles inserting into basal part of bulbs; hooks on internal tentacle surface compact and rosethorn-shaped, 17.5-19.0 L, 13.5-15.0 B, diminishing in size toward basal part of tentacle to 13.0-14.5 L, 9.0-10.5 B; hooks on external surface more slender and spiniform than internal ones, 18.0-19.5 L, 8.5-10.0 B, diminishing in size toward basal part of tentacle to 13-14 L, 6.5-8.0 B; basal armature similar to metabasal armature in hook form and pattern, with hsr 6-7 (basal), 6-7 (metabasal).

Material examined: syntypes – USNPC 7726, E. Linton coll., 19.07.1915, 5 adults from the stomach wall of *S. zygaena*, Woods Hole, Massachusetts (MA), USA; other material, labelled as *Nybelinia bisulcata* – USNPC 35764, MacCallum coll., 02.07.1915, 4 adults from the stomach wall of *S. zygaena*, Woods Hole, MA; USNPC 80723, 1980, 3 postlarvae from *P. dentatus*, Chesapeake Bay, Virginia, USA.

Remarks: Chandler (1942) reported *Nybelinia palliata* from the smooth hammerhead, *Sphyrna zygaena*, in the Gulf of Mexico; however, we could not locate his material at the USNPC or elsewhere. Nevertheless, we obtained syntype material, which was from the same host species at Woods Hole but not adequately described, and we redescribed it. Linton (1924) described *N. palliata* as having hooks *nearly uniform* in size and shape, however, he did not comment on the hook shape on different tentacle surfaces. Linton (1924, fig. 82) illustrated the tentacular armature, however, it is not possible to distinguish between hook forms on opposite tentacle surfaces on basis of his illustration. Re-examination of the syntypes (see above) revealed two distinct hook forms on opposite tentacle surfaces, belonging to the homeoacanth type II as given by Campbell and Beveridge (1994). Thus, we accept *Nybelinia palliata* as a valid species, however, our present description of heteromorphous tentacular hooks assigns it to the genus *Heteronybelinia* as described by Palm (1999). Palm et al. (1997) assigned *N. palliata* to *Nybelinia* subgroup IAa and Palm (1999) to the genus *Nybelinia*, erroneously interpreting the hooks on basis of Linton's description as having a homeomorphous armature. We now consider the species to belong to the genus *Heteronybelinia* Palm, 1999 as *Heteronybelinia palliata* (Linton, 1924) comb. n.

The characteristic tentacular armature with hooks of similar size but of different shape on opposite tentacle surfaces now conflicts with the identification of some material deposited as *N. bisulcata* (Linton, 1889) in the

U.S. National Parasite Collection, Beltsville (specimens USNPC 35764 and 80723). Based on features of those specimens, they are conspecific with *H. palliata*. The tentacular armature was identical, and scolex measurements overlapped. However, even though the scolex proportions correspond, the bulb ratio differed between adult (1.9-2.6:1) and postlarval (3.4:1) specimens.

Heteronybelinia palliata is now recognised from *S. zygaena* along the eastern North American coast (MacCallum 1921, Linton 1924) and the Gulf of Mexico (Chandler 1942). The summer flounder, *Paralichthys dentatus*, represents a new intermediate host record for *H. palliata* in Chesapeake Bay, where Jansen and Bureson (1990) reported a prevalence of the species as *N. bisulcata* to be 11% (341 fish examined).

Other plerocercoids from the northern Gulf of Mexico in or adjacent to Mississippi

- *Callitetrarhynchus gracilis* (Rudolphi, 1819) from the mesentery of **Arius felis* (Linnaeus), **Elops saurus* (Linnaeus), **Lutjanus campechanus* (Poey), **Scomberomorus cavalla* (Cuvier) and *S. maculatus* (Mitchill);

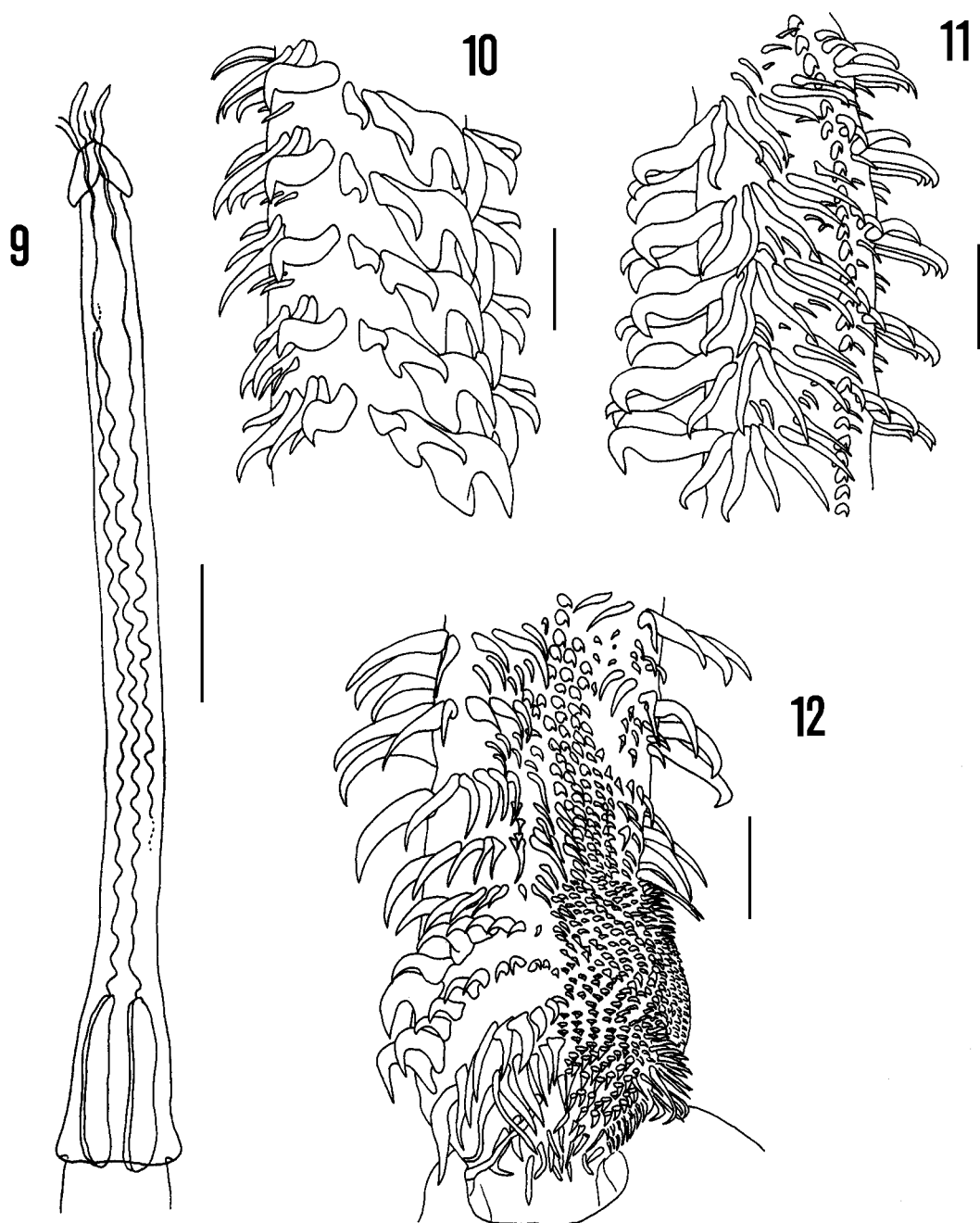
- *Dasyrhynchus pacificus* Robinson, 1965 from **Mugil curema* Valenciennes and **Mugil cephalus* Linnaeus. Details of the scolex of a specimen from *M. curema* are given in Figs. 9-12. The specimen shows an elongated pars vaginalis with short bulbs, which is not corresponding directly to the description of *Dasyrhynchus pacificus* by Beveridge and Campbell (1993, fig. 6). However, the tentacular armature appeared to be the same.

- *Otobothrium cysticum* (Mayer, 1842) from the mesentery of **Arius felis*, **Caranx crysos* (Mitchill), **Lutjanus campechanus* and **Paralichthys lethostigma* Jordan et Gilbert;

- *Tentacularia coryphaenae* Bosc, 1797 from the mesentery of **Rachycentron canadum* (Linnaeus);

- *Gymnorhynchus gigas* (Cuvier, 1817) Rudolphi, 1819 from musculature of **Brama brama* (Bonnaterre) (from an unspecified location of Florida, provided by NMFS Seafood Inspection Laboratory in Pascagoula, Mississippi).

Remarks: Species indicated above by an asterisk (*) represent new host records. *Dasyrhynchus pacificus* has been recorded from the Pacific and South-West Atlantic Ocean (Beveridge and Campbell 1993). This is its first record from the Gulf of Mexico, but the identification should be corroborated with adult material. The illustration labelled as *?Callitetrarhynchus* sp. from the kidney of *Mugil cephalus* by Overstreet (1978a, fig. 122) shows a specimen from the same plerocercoid material. The species identified as *Dasyrhynchus* sp. from the musculature, especially in the dorsum of the head, of *Caranx hippos* (Linnaeus) (crevalle jack) in fig. 120 of Overstreet (1978a) is *D. giganteus*, also reported from Brazil from the same host by Sao Clemente et al. (1993) and Palm (1997b).



Figs. 9-12. *Dasyrhynchus pacificus* from *Mugil curema*. **Fig. 9.** Scolex. **Fig. 10.** Metabasal armature, internal surface. **Fig. 11.** Metabasal armature, antibothridial surface. **Fig. 12.** Basal armature, external surface. Scale bars: Fig. 9 = 1 mm; Figs. 10-12 = 50 μ m.

Other adult trypanorhynchids

A series of 19 specimens of the blacktip shark, *Carcharhinus limbatus* (Valenciennes), from off Mississippi and off Sarasota, Florida, was examined for parasites. The shark hosted adult specimens of *Heteronybelinia estigmene* (Dollfus, 1960), *Nybelinia lingualis* (Cuvier, 1817), *Nybelinia* cf. *bisulcata* (Linton, 1889), *Callitetrarhynchus gracilis* (Rudolphi, 1819), *Oto-*

bothrium insigne Linton, 1905, and *Grillotia perelica* Shuler, 1938.

Remarks: All the species collected from *C. limbatus* were found off Florida, and all but *N. lingualis* and *O. insigne* also occurred off Mississippi. Of these, all but *H. estigmene* are new host records for that shark, and *N. cf. bisulcata* is a range extension into the Gulf of Mexico. That species, however, is in need of a critical revision as

what is called *N. bisulcata* seems to represent a complex of more than one species as indicated by our treatment of *H. palliata*.

DISCUSSION

The number of trypanorhynchs in the Gulf of Mexico, indicated here as 34 of about 220 confirmed species or roughly 15%, is presumably low. Based on the junior author's field observations, few of the many intermediate hosts have been reported. Many of the plerocercoids in crustaceans, molluscs, and fishes have not yet been identified, and adults from many elasmobranchs have not yet been studied and taxonomically evaluated. For example, from 19 blacktip sharks recently examined over a relatively short period, we found six trypanorhynch species, and all but one had not been reported previously from that shark. Moreover, that host, *Carcharhinus limbatus*, is cosmopolitan and probably serves as a host for many other species. Not counting reported species of *Otobothrium* and *Nybelinia/Heteronybelinia* (see Palm 1999), we did not encounter in the blacktip shark, *Poecilancistrum caryophyllum*, reported as *P. robustum* by Thatcher (1961) from Louisiana, *Dasyrhynchus pacificus*, reported by Beveridge and Campbell (1993) from Rio de Janeiro, Brazil, nor did we encounter *Tentacularia coryphaenae*, *Floriceps saccatus*, or *Dasyrhynchus giganteus* reported by Heinz and Dailey (1974) and Carvajal et al. (1976) from the Pacific Ocean. The latter three species also either already have been reported from or are expected to occur in the Gulf of Mexico. However, the specimens from Hawaii reported as *D. giganteus* were immature and when re-examined by Beveridge and Campbell (1993), the authors suggested the specimens were *D. variouuncinatus* (Pintner, 1913) because a mature specimen of that species occurred in *Carcharhinus falciformis* (Bibron) (silky shark) off Hawaii. All records of *D. variouuncinatus* from the Atlantic Ocean (see Dollfus 1969) were considered by Beveridge and Campbell (1993) to represent *D. giganteus*.

As indicated above, the low estimate of 34 trypanorhynchs recorded from the Gulf of Mexico still makes the Gulf of Mexico one of the richest known regions for trypanorhynchs in the world (four species are newly recorded from the Gulf of Mexico within the present study). The Gulf of Mexico can be characterised as a relatively shallow-water marine system, and most of the specimens we examined were from near-shore species or from fish that had migrated to near shore. Shallow-water tropical habitats have been demonstrated to be a common locality for trypanorhynch cestodes that occur as plerocercoids in fishes from both, inshore and offshore waters, such as *Grillotia perelica* (see Schramm 1991), *Callitetrarhynchus gracilis* (see Palm 1997b) and *Otobothrium cysticum* (see Palm et al. 1994, Palm and Overstreet 2000). This indicates that the rich, relatively

warm and shallow nearshore localities provide a suitable habitat for many different trypanorhynchs. Beside a species-rich intermediate and final host fauna within the Gulf, the Gulf of Mexico water also interfaces with the Atlantic Ocean. Thus, oceanic fish species, such as the common dolphin fish, *Coryphaena hippurus*, and the cobia, *Rachycentron canadum*, allow cosmopolitan trypanorhynchs (e.g., *T. coryphaenae*) to spread into the Gulf of Mexico.

The presence of *Kotorella pronosoma* from the Gulf of Mexico demonstrates a cosmopolitan distribution for the species, as indicated by Palm and Walter (1999). *Cynoscion nebulosus* is the first known second intermediate host for the species. With emendation of the generic diagnosis, we corroborate the placement of *Kotorella* within Tentaculariidae. Beveridge et al. (1999) discussed the phylogenetic relationship between *Kotorella* and *Nybelinia*. The bothridia of the present metacestodes have similarities to both tentaculariid and non-tentaculariid trypanorhynchs. The large bothridia with free posterior margins, overlapping half the scolex, resemble those described for *Bombycyrhynchus sphyraenaeum* (see Pintner 1930, Palm et al. 1998). Similarly, free posterior margins are characteristic for members of lacistorhynchid genera, such as *Callitetrarhynchus* and *Pseudolacistorhynchus* (see Dollfus 1942, Palm 1995). These genera additionally have characteristic marginal bands of microtriches (Palm 1995). If these structures could be considered homologous characters, they would be useful for future trypanorhynch classifications. *Kotorella pronosoma* can also be considered as a species with individuals having a large range in size. Length of plerocercoid scolex ranges from 650 to 1000 µm, and, depending on the scolex size, hooks vary from 8 to 14 µm in length. This species further demonstrates the remarkable variability that can occur within a tentaculariid species, as earlier observed (Palm et al. 1993, 1997, Palm 1999, Palm and Walter 1999, 2000).

The difference in bulb ratio between adult (2.3 : 1) and postlarval (3.4 : 1) specimens of *Heteronybelinia palliata* demonstrates a problem in identifying some tentaculariids. Dollfus (1960) showed a range in bulb ratio of postlarvae of *Nybelinia africana* (2.7 : 1 to 3.1 : 1). Consequently, at least in a species of both *Heteronybelinia* and *Nybelinia*, the ratio can vary up to 50%. This difference questions the usage of the ratio as a primary diagnostic feature, such as used by Dollfus (1960) to separate *Nybelinia alioitica*, *N. cadenati* and *N. senegalensis* from *N. dakari*, *N. estigmena* and *N. punctatissima*. Palm (1999) already discussed the similarity of several species within a species complex of "*N. aequidentata*" and another species complex of "*H. estigmena*". This explains our difficulty to identify *Nybelinia* cf. *estigmena* in the present study. Moreover, Jones and Beveridge (1998) pointed out that requisite information to differentiate many of the 47 nominal species of *Nybelinia* is not available.

In conclusion, the Gulf of Mexico serves as a rich habitat for trypanorhynchs, and some of these have a high intraspecific morphological variability, often combined with both a wide host range and a wide zoogeographical distribution. Whether differences in scolex features depend on age, stage of development, host, geographic locality or a combination of factors cannot be determined at present; however, the reason for these differences needs to be considered for future trypanorhynchean taxonomic work. We recommend that identifications based on minor size differences in structures such as hook size should be treated with care until inter- and intraspecific morphological variability is clarified.

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