Zoomorphology (2008) 127:249–258
DOI 10.1007/s00435-008-0068-2

ORIGINAL PAPER

Surface ultrastructure of the elasmobranchia parasitizing *Grillotiella exilis* and *Pseudonybelinia odontacantha* (Trypanorhyncha, Cestoda)

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Received: 11 June 2007 / Revised: 22 May 2008 / Accepted: 5 June 2008 / Published online: 28 June 2008

Abstract The surface ultrastructure of two monotypic trypanorhynch genera is described based on new material of *Grillotiella exilis* (Linton, 1909) and type material of *Pseudonybelinia odontacantha* Dollfus 1966. In *G. exilis*, spiniform microtriches cover the bothrial surfaces and the anterior part of the pars vaginalis posterior to the bothria. Bifurcate microtriches adorn the bothrial margins, filiform microtriches the scolex peduncle, and capilliform microtriches the posterior scolex end. This microthrix pattern resembles that found in, e.g., *Grillotia erinaceus* (van Beneden, 1858), with the difference that the anterior part of the pars vaginalis is covered with a collar of multidigitate palmate microtriches. The position of *Grillotiella* within the Grillotiinae, Lacistorhynchidae is supported based on these data. The bothria and scolex peduncle of *P. odontacantha* are covered with acerosate and unciniform microtriches on the distal bothrial surface and capilliform microtriches on the scolex peduncle. Short filiform microtriches cover the appendix. The microthrix pattern resembles that of the Tentaculariidae but with unciniform and acerosate microtriches densely covering the entire distal bothrial surface. Tegumental grooves are present on the posterior bothrial margin. They can be distinguished from bothrial pits in otobothrioid trypanorhynchs in having similar unciniform microtriches compared to the other parts of the bothrial surface and in lacking any spiniform microtriches. With the absence of bothrial pits as characteristic for the otobothrioids and its characteristic microthrix pattern, *P. odontacantha* together with *Paranybelinia otobothrioides* Dollfus 1966, both belonging to the Paranybeliniidae change their position in the most recent system from the Otobothrioidea into the Tentacularioidea.

Keywords Classification · Surface ultrastructure · Trypanorhyncha · *Grillotiella exilis* · *Pseudonybelinia odontacantha*

Introduction

Trypanorhynch cestodes typically parasitize the elasmobranchia as final hosts, where they are collected from the intestine or the stomach wall (Campbell and Beveridge 1994; Palm 2004). With widely distributed or migrating second intermediate and paratenic hosts, these cestodes are known for low-host specificity (Palm and Klimpel 2007; Palm and Caira 2008) and cosmopolitan distribution (Palm 2004; Palm et al. 2007). The cestode taxon Trypanorhyncha currently comprises 277 species, belonging to 15 taxa with the rank of families in traditional classification (Palm 2004; Beveridge and Campbell 2005, 2006; Beveridge and Justine 2006). The scolex morphology, especially the number of bothria, scolex proportions, the presence or absence of the characteristic prebulbar organs and bothrial pits as well as the arrangement of the hooks around the tentacles are used to distinguish the different taxa (Palm 2004). A problem in trypanorhynch systematics, however, lies in the lack of new material and incomplete descriptions, often lacking information on surface ultrastructure and strobilar characters of the adult worms, thus making it difficult to make an informed decision about the systematic placement of the species.

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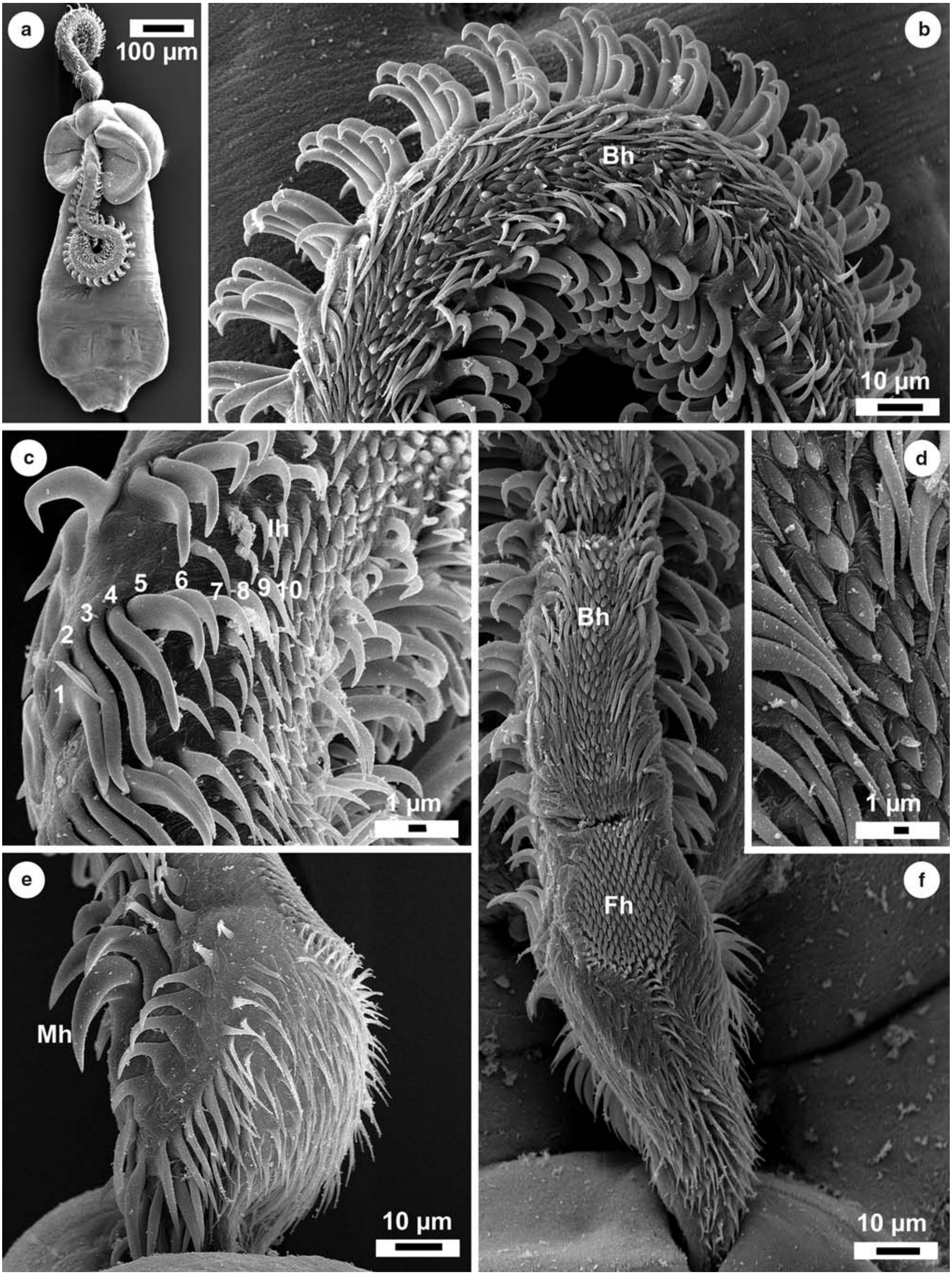
Analysis of the surface ultrastructure, especially the microtriches of the bothria and scolex peduncle as observed with scanning electron microscopy (SEM), provides additional information that can be utilized in trypanorhynch systematics. Following a detailed study of the microthrix pattern of *Floriceps minacanthus* Campbell and Beveridge, 1987 by Richmond and Caira (1991), a more extensive comparison of the surface ultrastructure in trypanorhynchs suggested considerable morphological diversity (Palm 1995) and also suggested that this character set could be used to distinguish among the taxa. Palm (2004) incorporated information on the microthrix structure into his new classification, considering these characters to be of significance not only at the species level but also for the larger groups. In the most recent classification, the placement of the two monotypic taxa *Grillotiella* and *Pseudonybelinia* was based upon the provided key; however, lacking information on the surface ultrastructure. While *Grillotiella* combines characters of morphologically distinct but related genera, *Pseudonybelinia* possesses a combination of characters of different higher taxa ("superfamilies" in traditional classification).

Grillotiella exilis (Linton, 1909) is a monotypic genus and holds a unique position among the other genera within the Grillotiinae. It possesses a heteroacanthous multiatypical armature with a large number of hooks in each principal row (as in *Pseudogrillotia* species) and an acraspedote and very small scolex (as in *Grillotia* species). The plerocerci of this species live inside the branchial arches of a scombrid teleost. The systematic position of *Pseudonybelinia odontacantha* Dollfus, 1966 has been widely debated with the genus shifting between Tentacularioidea and Otobothrioidea. Schmidt (1986), Campbell and Beveridge (1994), and Beveridge et al. (1999), the latter based on a cladistic analysis, affiliated the genus with the Tentaculariidae, Tentacularioidea, mainly because of a plerocercoid lacking a blastocyst and the homeoacanthous armature. Palm (1995, 1997, 2004), based on the presence of bothrial pits, as described in the original description assigned the genus to the Otobothrioidea. Campbell and Beveridge (1994) stated that the types of *Pseudonybelinia* were faded and shriveled and many details could not be confirmed. The present study was carried out in order to analyze the surface ultrastructure of these two monotypic genera based on new material of *G. exilis* from *Scomberomorus commerson* (Lacepède, 1800) and on the type material of *P. odontacantha*. The observed microthrix patterns are compared to the patterns of taxa examined previously in order to clarify the systematic position of both genera within the most recent trypanorhynch classification. Implications for the use of the detected surface structures as apomorphic characters for higher taxonomic groupings of trypanorhynch cestodes are discussed.

Fig. 1 Scolex and tentacular armature of *Grillotiella exilis* from *Scomberomorus commerson,* Indonesia. **a** Scolex, 800 μm total length from anterior to posterior scolex end, taken from Palm and Klimpel (2007). **b** External tentacle surface, metabasal armature, note the band of uncinate hooks (*Bh*). **c** Antibothrial surface, metabasal armature, note 7–8 intercalary hooks (*Ih*) adjoining with a band of hooks on the external surface. **d** External tentacle surface, metabasal armature, note the shape of the uncinate hooks. **e** Antibothrial surface, basal armature, note the enlarged uncinate hooks (*Mh*) on the internal surface and an area devoid of hooks. **f** External surface, basal armature, with field of small uncinate hooks (*Fh*) ▶

Materials and methods

Specimens of *Grillotiella exilis* (Linton, 1909) (Lacistorhynchoidea, Lacistorhynchidae, and Grillotiinae) were collected from the gill arches of *Scomberomorus commerson* (Lacepède, 1800) obtained from a local fisherman on Barang Caddi Island (05°08′38S and 119°24′40E; part of the Pabbiring or Sangkarang Islands), off Makassar, South Sulawesi, Indonesia, in January 2004. The specimens were removed from the blastocysts in saline, fixed in 10% formalin and stored in 70% ethanol for subsequent investigation. Additional specimens from infected *S. commerson* that were not examined using electron microscopy in this study were collected from Bone Bay and Tolo Bay, Sulawesi. Voucher specimens as whole mounts have been deposited in the Natural History Museum, Berlin, Germany (ZMB 7431). Because no mounted type material of *Pseudonybelinia odontacantha* Dollfus, 1966 (Otobothrioidea, Paranybeliniidae) was found in the collection of the Museum National d′Histoire Naturelle, Paris, France, two specimens were taken from the original vial, C 75 (that had been deposited by R.P. Dollfus in the museum collection and included approximately 20–30 trypanorhynch specimens of two species, *Pseudonybelinia odontacantha* Dollfus, 1966, and *Paranybelinia otobothrioides* Dollfus, 1966, from the Cap Verde Islands, here considered as the type series), washed in 70% ethanol and prepared for scanning electron microscopic examination. Specimens with everted tentacles were left in the vial (to represent the type series), and further four specimens were dehydrated in an ethanol series for subsequent mounting in Canada balsam. They are now deposited in the Museum National d′Histoire Naturelle (MNHN No. 440–443 HG, drawer Cj 217 to Cj 219bis). Specimens of *Paranybelinia otobothrioides* obtained from the same vial, C 75, were processed as above, and are now deposited as whole mounts in the Museum National d′Histoire Naturelle, (MNHN No. 444–445 HG, drawer Cj 217 to Cj 219bis). This material of *P. otobothrioides*, however, is darkened and external and internal structures are not visible. All specimens prepared for SEM were transferred to acetone and dehydrated in a graded acetone series. They were then, critical point, dried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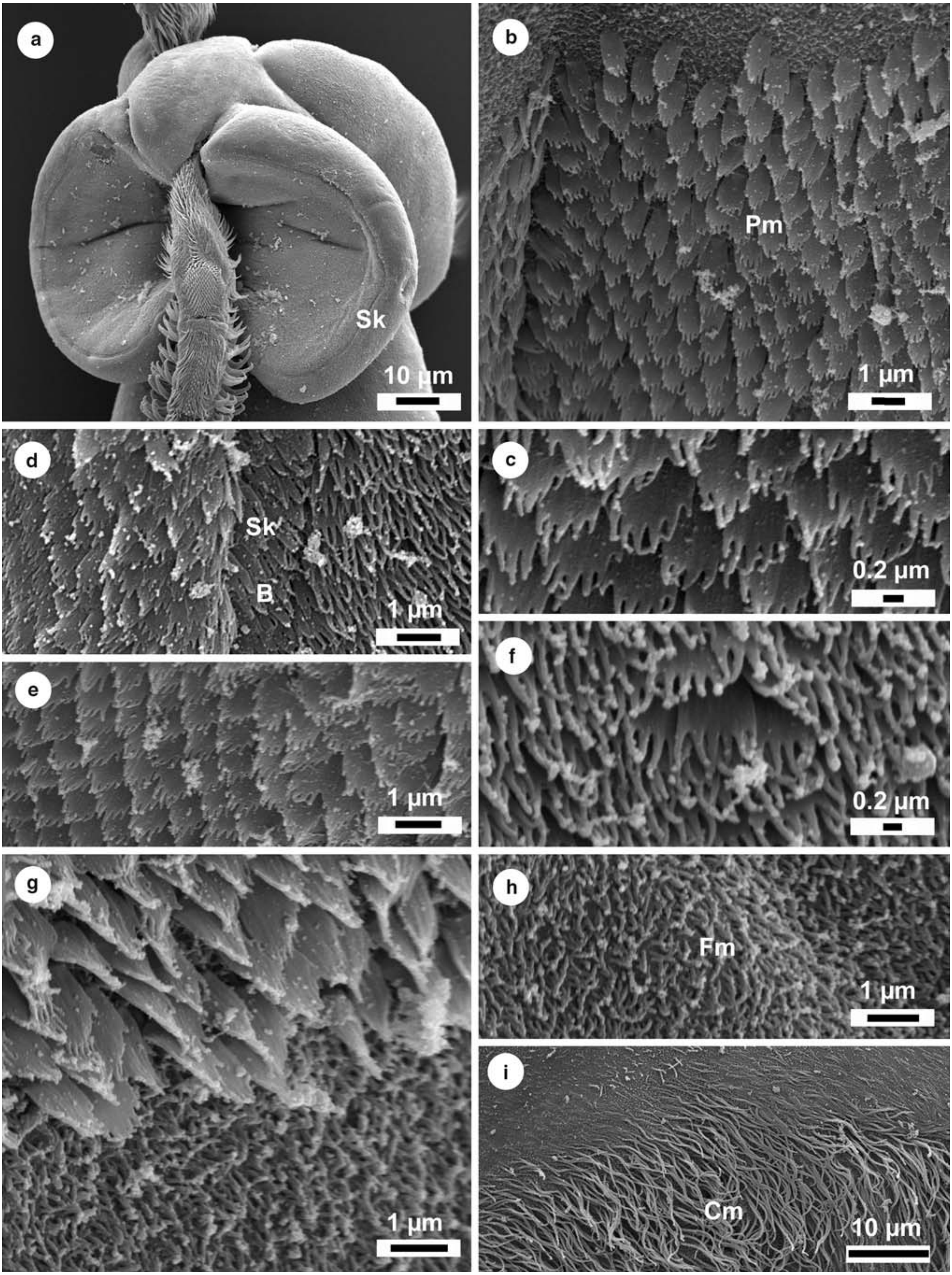
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◀ **Fig. 2** Surface ultrastructure of *Grillotiella exilis* from *Scomberomorus commerson,* Indonesia. **a** Pars bothrialis. **b–c** Apical part of bothrium, distal bothrial surface, hexa- to octadigitate palmate microtriches (*Pm*). **d** Bothrial border, bifurcate microtriches (*B*) ("Sinneskante", *SK*), flanked by penta-and hexadigitate palmate microtriches on distal and proximal bothrial surfaces. **e** Distal bothrial surface, hexa- to octadigitate palmate microtriches. **f** Proximal bothrial surface, hexadigitate palmate microtriches. **g** Pars vaginalis posterior to pars bothrialis, the posterior margin of a field of octadigitate palmate microtriches anterior to filiform microtriches. **h** Filiform microtriches on pars vaginalis (*Fm*). **i** Capilliform microtriches (*Cm*) at terminal end of pars post bulbosa

and mounted with a double-sided adhesive carbon tape onto SEM stubs. The stubs were coated with gold–palladium in an argon atmosphere and examined under a LEO 1430 VP SEM at 10–15 kV. The classification and terminology of the microtriches follows Palm (2004). Measurements are given in micrometers unless otherwise indicated.

Results

Each species was found to have a characteristic surface ultrastructure that has not been recorded from any other trypanorhynch species previously.

The scolex features and hook counts for *Grillotiella exilis* (Linton, 1909) as articulated in Palm (2004) could be confirmed with SEM. The small acraspedote scolex is illustrated in Fig. 1a. The metabasal armature is heteroacanthous multiatypical with principal hooks arranged in ascending half spirals of ten hooks (Fig. 1b, c). The hooks 1(1′) on the internal surface are uncinate, with the hooks 2(2′) to 9(9′) slender, falciform, and gradually decreasing in length. Between the sixth and tenth principal hook, 6–8 intercalary hooks are arranged in two rows (Fig. 1c), adjacent to a band of small microhooks on the middle of the external surface (Fig. 1b–d, f). The band of hooks is about five hooks wide. A characteristic basal armature is present. The internal surface is adorned with six rows of hooks. The hooks in the first three rows are weakly re-curved and in the second three rows enlarged and uncinate (Fig. 1e). The number of hooks in each half turn is three to seven. On the external surface, the proximal part of tentacle has longitudinal rows of spiniform hooks (Fig. 1f). Above these, a field of small uncinate hooks proceeds into the band of microhooks on the external metabasal armature. On the bothrial and antibothrial tentacle surfaces, areas devoid of hooks are evident (Fig. 1e).

The surface ultrastructure consists of various different kinds of microtriches. The scolex is covered with four types of microtriches, two types of spiniform (palmate and bifurcate), and short filiform and capilliform microtriches. Hexa- to octadigitate microtriches, length $(L) = 1.0–1.5$, width $(W) = 0.7–1.0$, regularly arranged, cover the distal (Fig. 2a–c, e) and proximal (Fig. 2f) bothrial surfaces. Penta- and hexadigitate palmate microtriches of similar size cover the distal surface along the bothrial margins (Fig. 2d). The shape and arrangement of the spiniform microtriches is in accordance with the multidigitate microtriche often with six or more digitiform projections that cover the bothrial surface in other trypanorhynchs. Underneath the palmate microtriches are filiform microtriches (Fig. 2b). The bothrial border is distinct with slender bifurcate microtriches along the margins (forming a so-called "Sinneskante") (Fig. 2d). Filiform microtriches, $L = 0.1–0.3$, cover the apical scolex region, bothria and scolex peduncle (Fig. 2g, h). The anterior region of the pars vaginalis near the pars bothrialis is covered with a collar of hepta- to octadigitate palmate microtriches (Fig. 2g). A field of capilliform microtriches covers the posterior end of the pars proliferans scolecis (Fig. 2i).

The deposited type material of *Pseudonybelinia odontacantha* Dollfus, 1966 revealed details of the scolex and tentacular armature as well as of its surface ultrastructure. The medium-sized, craspedote scolex is illustrated in Fig. 3a, e. Two large bothria cover over half of the scolex length, and extend into the pars bulbosa scolecis. The lateral bothrial margins are not fused with the scolex peduncle. A tegumental groove (formerly bothrial pit) at the posterior bothrial margins of the bothria is illustrated in Fig. 3e. The metabasal armature is homeoacanthous homeomorphous with odontacanth hooks of similar size along the entire tentacle (Fig. 3b, c). A characteristic basal armature is absent.

The surface ultrastructure of the scolex reveals four types of microtriches, acerosate, unciniform, filiform, and capilliform. Capilliform microtriches, $L = 10–15$, $W = 0.5$, cover the apical scolex region (Figs. 3d, 4a). Acerosate and unciniform microtriches with extended bases, $L = 4–6$, $W = 0.5–1$, cover the distal bothrial surface (Fig. 4b–d). At the posterior margin of the bothria, tegumental grooves are evident that show similar microtriches to the surrounding bothrial surface. The microtriches in the tegumental groove appear unciniform. The scolex peduncle is covered with capilliform microtriches (Fig. 4e), and short filiform microtriches adorn the entire appendix (Fig. 4f, g). Capilliform microtriches are absent from the appendix (Fig. 4h).

Discussion

Microtriche morphology and trypanorhynch classification

Previous analyses demonstrated that the surface ultrastructure is a useful tool to determine the relationships within trypanorhynch cestodes (Richmond and Caira 1991; Palm 1995, 1997, 2004). Although the surface ultrastructure of only a few representatives have been analyzed, it is becoming

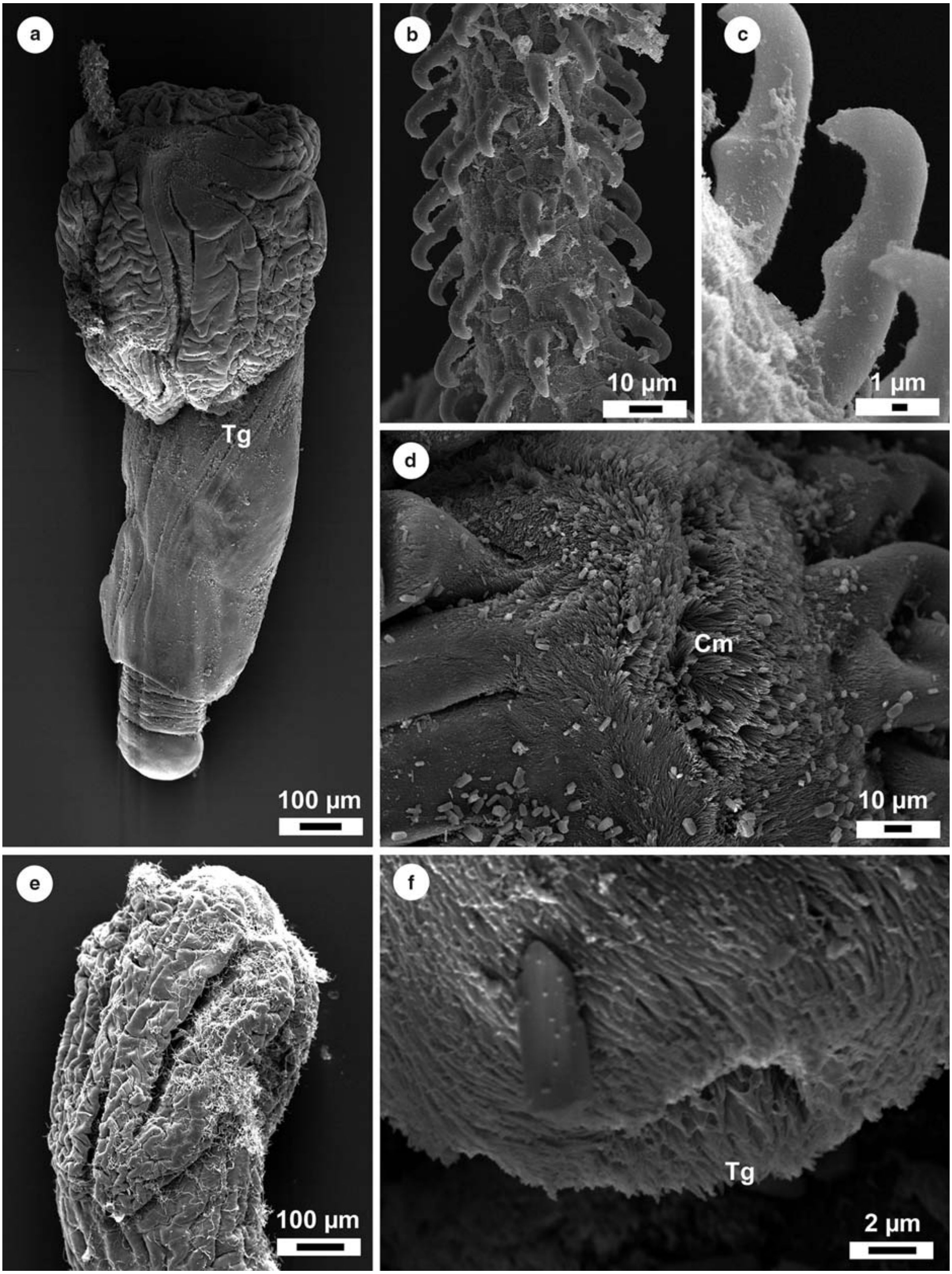


Fig. 3 Scolex and tentacular armature of *Pseudonybelinia odontacantha* from marine plankton. **a** Scolex. Note anteriorly fused bothria with the tegumental groove (*Tg*). **b–c** Metabasal armature with the characteristic odontacanth hooks. **d** Anterior part of the scolex with capilliform microtriches (*Cm*). **e** Pars bothrialis with the tegumental groove (*Tg*) at the posterior end. Note the incompletely fused bothria at the posterior end. **f** Tegumental grove at the posterior part of the bothria

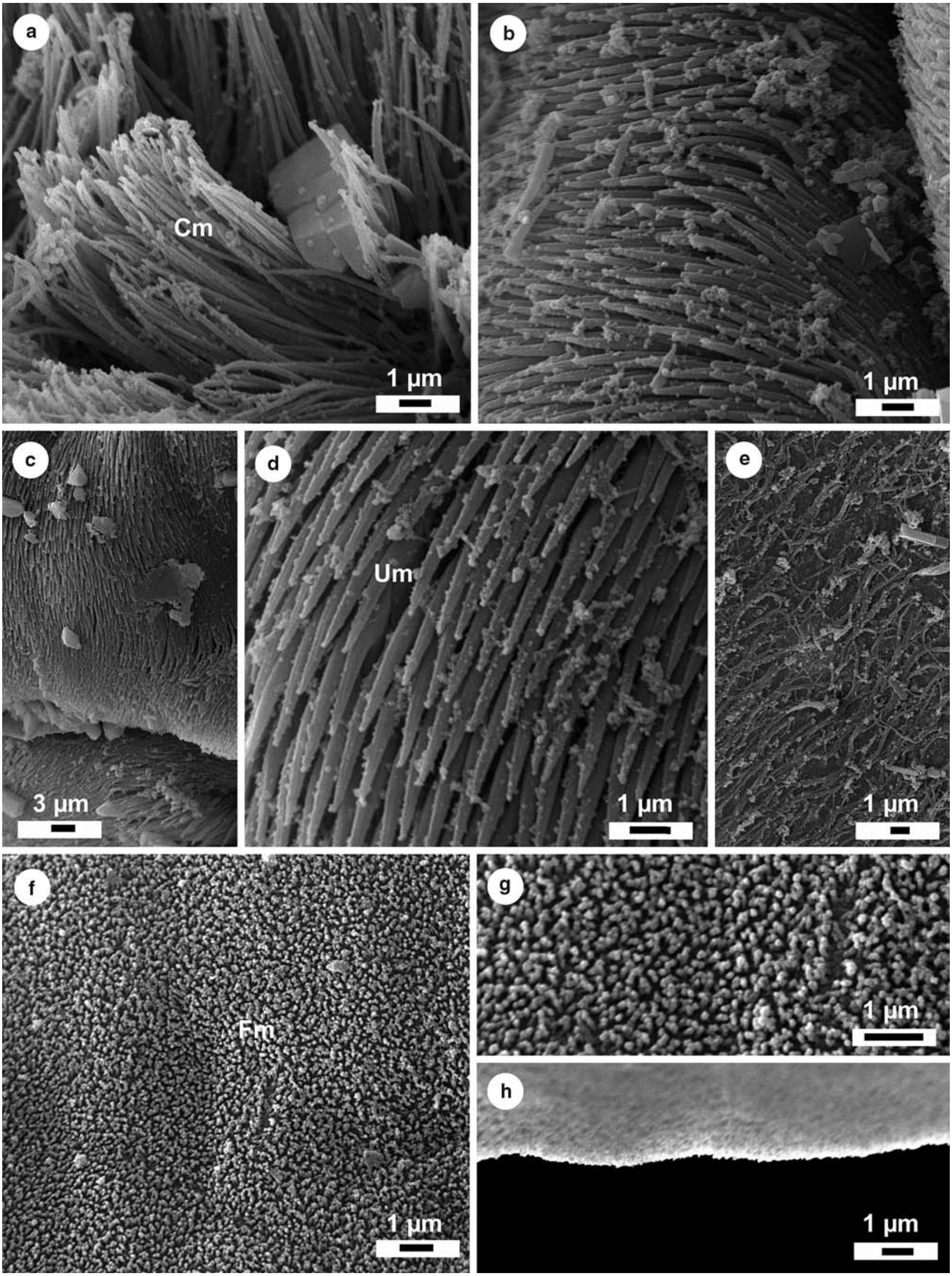
clear that the different groups seem to have relatively uniform microtriche patterns and that these patterns can be used to differentiate the taxa. The Tentaculariidae, Tentacularioidea have filiform microtriches on the scolex peduncle and unciniform and acerosate microtriches of characteristic internal ultrastructure along the bothrial borders (Palm 2000; Palm et al. 2000). Capilliform microtriches are absent on the posterior part of the appendix. Species of the Lacistorhynchidae and Otobothriidae are covered with spiniform microtriches that have digitiform projections thus appearing palmate or pectinate. These spiniform microtriches, also of distinct internal ultrastructure (Palm et al. 1998, 2000), can be present on the bothria alone (e.g. *Grillotia* species and *Otobothrium* species) or can cover the entire scolex peduncle (e.g. *Pseudogrillotia*, *Dasyrhynchus*, and *Callitetrarhynchus* species, e.g., Palm 2004; Abdou and Palm 2008). Capilliform microtriches are present at the posterior end of the scolex in all these genera. The presence of palmate microtriches on the bothria and scolex peduncle, bifid microtriches along the bothrial borders forming a bothrial groove (“Sinneskante”), the absence of bothrial pits and the presence of capilliform microtriches on the posterior pars postbulbosa in *Grillotiella exilis* unequivocally affiliate this species with the Lacistorhynchidae. The presence of unciniform microtriches on the bothrial surface and margins in *Pseudonybelinia odontacantha* with the absence of spiniform microtriches from these regions and the absence of bothrial pits and capilliform microtriches on the appendix allows assignment of this species to the Tentacularioidea and not to the Otobothrioidea.

The Lacistorhynchidae were divided into two higher taxa by Palm (2004) on basis of the tentacular armature (multiatypical vs. atypical) and microthrix morphology. The members of the Grillotiinae studied thus far bear palmate microtriches with six or more digitiform projections, while the Lacistorhynchinae has microtriches with fewer than 3–6 digits. The scolex of *G. exilis* exhibits palmate microtriches with 5–8 projections, thus allowing assignment of *Grillotiella* to the Grillotiinae. Within this group, microthrix patterns thus far described are either entirely covered with palmate microtriches on the bothrial surfaces and on most of the scolex peduncle (e.g., *Protogrillota, Pseudogrillotia*, and *Dasyrhynchus* species) or have such microtriches on the bothrial surface only (*Grillotia* species). *Grillotiella exilis* shows a unique pattern. The palmate spiniform microtriches cover the distal and proximal bothrial surface as well as the most anterior part of the pars vaginalis just posterior to the bothria. This microthrix pattern resembles that found in *Grillotia erinaceus* (van Beneden, 1858). In contrast to *Protogrillota, Pseudogrillotia*, and *Dasyrhynchus* species the transition between the collar of spiniform microtriches and the filiform microtriches on the remainder of the pars vaginalis is clearly demarcated. The cladistic analysis of the trypanorhynch genera by Palm (2004) placed *Grillotiella* within a monophyletic group within the Grillotiinae, Lacistorhynchidae. The surface ultrastructure suggests a monophyletic grouping of the genus *Grillotiella* together with *Pseudogrillotia*, *Dasyrhynchus,* and *Grillotia*. This result is supported by the fact that other characters such as the scolex shape and tentacular armature are a combination of those found in these genera (see above). Thus, the observed microthrix pattern supports its status as a monotypic genus within the Grillotiinae.

The surface ultrastructure of *P. odontacantha* resembles that of specimens of the Tentaculariidae having a combination of acerosate/unciniform microtriches on the distal bothrial surface and filiform microtriches that cover the entire scolex peduncle. Within the Tentaculariidae, several species such as *Nybelinia indica* Chandra, 1986, *Heteronybelinia estigmena* Dollfus, 1960, and *Mixonybelinia lepturi* Palm, 2004, are reported to possess a band of unciniform and acerosate microtriches along the bothrial margins and elongated filiform microtriches on the entire scolex (Palm 1995, 2004). Capilliform microtriches on the proximal part of the appendix are absent in these groups. The microthrix pattern of *Pseudonybelinia odontacantha* is most consistent with the tentaculariid type with the exception that the unciniform microtriches cover the entire bothrial surface. Because *P. odontacantha* has two dorsal and ventral bothria instead of four triangular bothria that are entirely separated from each other, the Paranybeliniidae can be distinguished from the Tentaculariidae and remains valid. This taxon is herewith transferred into the Tentacularioidea. The type species *Paranybelinia otobothrioides* could not be examined due to the poor condition of the material deposited in the MNHN and the lack of new material. The number of bothria was described as two, though this cannot be confirmed at present. It is also transferred together with the Paranybeliniidae into the Tentacularioidea until further material becomes available.

Surface ultrastructure as apomorphic characters in trypanorhynch taxonomy

Special notice can be made concerning the tegumental grooves at the posterior margin of the bothria. Dollfus (1966, 1967) named these structures at the posterior margin of the bothria in *P. odontacantha* as bothrial pits, a name that was originally introduced by Linton (1890) for characteristic pit-like structures at the posterior bothrial margin in the genus *Otobothrium*. Palm (1995, 1997) utilized this character to distinguish the otobothrioids from all other species within the trypanorhynchs. However, the observed structure is unlike those found in members of the Otobothrioidea that have been examined with TEM and SEM. Jones (2000), Palm and Overstreet (2000), and Palm et al.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◀ **Fig. 4** Scolex and tentacular armature of *Pseudonybelinia odontacantha* from marine plankton. **a** Capilliform microtriches (*Cm*) at the anterior end of scolex. **b**, **d** Unciniform microtriches (*Um*) on the distal bothrial surface. **c** Acerosate microtriches on the distal bothrial surface. **e** Capilliform microtriches on the pars postbulbosa (also on pars vaginalis and bulbosa). **f, g**. Appendix, short filiform microtriches (*Fm*). **h** Appendix end. Note the absence of any capilliform microtriches

(1998, 2000) analyzed the ultrastructure of the bothrial pits in otobothriid species [*O. mugilis* Hiscock, 1954, *O. cysticum* (Mayer, 1842) Palm and Overstreet, 2000, *O. penetrans* Linton, 1907] using transmission electron microscopy and identified spiniform microtriches of similar ultrastructure to the palmate microtriches on the distal bothrial surface. In all cases, the shape of the microtriches in SEM was distinctly different from those of the surrounding bothrial surfaces. A relationship between the bothrial pits and the so-called “Sinneskante” (bothrial groove with specifically shaped, slender bifid microtriches, also see Fig. 2a) in lacistorhynchoid trypanorhynchs was evident (Pintner, 1934; Jones, 2000; Palm et al. 2000). The pseudotobothriid *Parotobothrium balli* (Southwell, 1929) Palm 2004 combined both structures, having a characteristic bothrial margin ending just before a lateral bothrial pit. In the case of *P. odontacantha*, no spiniform microtriches can be seen, and the tegumental grooves of *P. odontacantha* located at the posterior margin of the bothria are covered with unciniform microtriches that cannot be distinguished by SEM from those covering the remainder of the bothrial surface. Consequently, the tegumental grooves at the posterior end of the bothria are not corresponding to the bothrial pits according to the descriptions by Linton (1890), Jones (2000), and Palm et al. (2000). To distinguish the bothrial structures in the Paranybeliniidae from those in the Pseudotobothriidae and Otobothriidae, the former are termed tegumental grooves that are covered with unciniform microtriches and the latter bothrial pits that are covered with spiniform microtriches. The tegumental grooves are considered autapomorphic for the Paranybeliniidae and the bothrial pits are considered synapomorphic for the Otobothrioidea, as earlier suggested by Palm (1995, 1997, 2004).

A close affinity of the Paranybeliniidae with the Tentaculariidae is also supported by our knowledge of the life cycles stages in both groups. Larvae of *Pseudonybelinia* and *Paranybelinia* were originally collected free from marine plankton in the presence of euphausiids around the Cape Verde Islands (Dollfus 1966, 1967) and Shimazu (1982) recorded *P. odontacantha* from *Euphausia recurva* Hansen, 1905 in the China Sea near Japan. Euphausiids are known as intermediate hosts of *Nybelinia surmenicola* Okada, 1929 (Palm, 2004). Consequently, the oceanic life cycle most probably involving Euphausiacea as second intermediate hosts is shared by both families. Re-assignment of the genus *Pseudonybelinia* together with the Paranybeliniidae into the Tentacularioidea allows reconsideration of the morphological characters that were used in the most recent trypanorhynch classification by Palm (2004). Both prebulbar organs and bothrial pits are synapomorphic characters for the Eutetrarhynchoidea and Otobothrioidea, respectively, as suggested by Palm (1995, 1997). Solid or a combination with hollow hooks has been recorded from the eutetrarhynchoids and tentacularioids (synapomorphic), with hollow hooks in the remaining trypanorhynchs. The scolex, larval morphology, and surface ultrastructure distinguish the Tentacularioidea and Lacistorhynchoidea, and the segment anatomy and larval morphology the Gymnorhynchoidea. The number of bothria separates the Paranybeliniidae from the Tentaculariidae, being a reliable character for different groups within the higher taxa. Further comparative analyses, especially exploring the surface ultrastructure of the different species, are needed in order to better define the higher taxonomic groups within this interesting order of marine cestodes.

Acknowledgments I would like to thank Gunarto Latama, UNHAS University, Makassar, Indonesia, and Jimmy Cassone, Museum National d'Histoire Naturelle Paris, for allowing access to the material. Many thanks are to Rod Bray, Natural History Museum London, for reading an earlier version of this manuscript. This study was financially supported by the German Research Council (DFG PA 664/4-1) and the European Union under COLPARASYST 2003.

References

Abdou NE-S, Palm HW (2008) New record of two genera of trypanorhynch cestodes infecting Red Sea fishes in Egypt. J Egypt Soc Parasitol 38:281–292

Beveridge I, Campbell RA (2005) Three new genera of trypanorhynch cestodes from Australian elasmobranch fishes. Syst Parasitol 60:211–224. doi:10.1007/s11230-004-6350-x

Beveridge I, Campbell RA (2006) Three new genera and seven new species of trypanorhynch cestodes (family Eutetrarhynchidae) from manta rays, *Mobula* spp. (Mobulidae) from the Gulf of California, Mexico. Folia Parasitol (Praha) 53:255–275

Beveridge I, Justine J-L (2006) Gilquiniid cestodes (Trypanorhyncha) from elasmobranch fishes off New Caledonia with descriptions of two new genera and a new species. Syst Parasitol 65:235–249. doi:10.1007/s11230-006-9052-8

Beveridge I, Campbell RA, Palm HW (1999) Preliminary cladistic analysis of genera of the cestode order Trypanorhyncha Diesing, 1863. Syst Parasitol 42:29–49. doi:10.1023/A:1006011512221

Campbell RA, Beveridge I (1994) Order Trypanorhyncha Diesing, 1863. In: Khalil LF, Jones A, Bray RA (eds) Keys to the cestode parasites of vertebrates. CAB International, Wallingford, pp 51–148

Dollfus RP (1966) Organismes dont la présence dans le plancton marin était, jusqu' à présent, ignorée: larves et postlarves de Cestodes Tétrarhynques. Comptes Rendus des Séances de l'Académie des Sciences de Paris. Ser D 262:2612–2615

Dollfus RP (1967) Énumeration des Cestodes du plankton et des Invertebrés marins (7ème Contribution). Ann Parasitologie Paris 42:155–178

Jones MK (2000) Ultrastructure of the scolex, rhyncheal system and bothridial pits of *Otobothrium mugilis* (Cestoda: Trypanorhyncha). Folia Parasitol (Praha) 47:29–38

Linton E (1890) Notes on Entozoa of marine fishes of New England, with descriptions of several new species. Part II. Annu Rep US Commission Fish 1887:719–900 (Pl I–XV)

Palm HW (1995) Untersuchungen zur Systematik von Rüsselbandwürmern (Cestoda: Trypanorhyncha) aus atlantischen Fischen. Berichte aus dem Institut für Meereskunde an der Christian-Albrechts-Universität Kiel, No 275:1–238

Palm HW (1997) An alternative classification of trypanorhynch cestodes considering the tentacular armature as being of limited importance. Syst Parasitol 37:81–92. doi:10.1023/A:1005765126294

Palm HW (2000) Trypanorhynch cestodes from Indonesian coastal waters (East Indian Ocean). Folia Parasitol (Praha) 47:123–134

Palm HW (2004) The Trypanorhyncha Diesing, 1863. PKSPL-IPB Press, Bogor

Palm HW, Caira JN (2008) Host specificity of adult versus larval cestodes of the elasmobranch tapeworm order Trypanorhyncha. Int J Parasitol 38:381–388. doi:10.1016/j.ijpara.2007.08.011

Palm HW, Klimpel S (2007) Evolution of the parasitic life in the Ocean. Trends Parasitol 23:10–12. doi:10.1016/j.pt.2006.11.001

Palm HW, Overstreet R (2000) *Otobothrium cysticum* (Cestoda: Trypanorhyncha) from the muscle of butterfishes (Stromateidae). Parasitol Res 86:41–53. doi:10.1007/PL00008505

Palm HW, Poynton SL, Rutledge P (1998) Surface ultrastructure of the plerocercoid of *Bombycirhynchus spyraenaicum* (Pintner, 1930) (Cestoda: Trypanorhyncha). Parasitol Res 84:195–204. doi:10.1007/s004360050382

Palm HW, Mundt U, Overstreet R (2000) Sensory receptors and surface ultrastructure within trypanorhynch cestodes. Parasitol Res 86:821–833. doi:10.1007/PL00008508

Palm HW, Waeschenbach A, Littlewood DTJ (2007) Genetic diversity in the trypanorhynch cestode *Tentacularia coryphaenae* Bosc, 1797: evidence for a cosmopolitan distribution and low host specificity in the teleost intermediate host. Parasitol Res 101:153–159. doi:10.1007/s00436-006-0435-1

Pintner T (1934) Bruchstücke zur Kenntnis der Rüsselbandwürmer. Zool Jahrb Abt Anat Ontogenie Tiere 58:1–20

Richmond C, Caira JN (1991) Morphological investigations into *Floriceps minacanthus* (Trypanorhyncha: Lacistorhynchidae) with analysis of the systematic utility of scolex microtriches. Syst Parasitol 19:25–32

Schmidt GD (1986) Handbook of tapeworm identification. CRC Press Inc, Boca Raton

Shimazu T (1982) Some helminth parasites of marine planktonic invertebrates. J Naganoken Jr Coll 32:11–29