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Sensory receptors and surface ultrastructure of trypanorhynch cestodes

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Abstract The scolices of six different trypanorhynch species – *Heteronybelinia alloiotica* (Dollfus, 1960), *Pseudolacistorhynchus noodti* Palm, 1995, *Otobothrium cysticum* (Mayer, 1842), *O. penetrans* Linton, 1907, *Poecilancistrum caryophyllum* (Diesing, 1850), and *Prochristianella hispida* (Linton, 1890) – were examined for surface morphology and the occurrence of sensory receptors. Filamentous microtriches with different internal ultrastructural features were found. Acerosate, hook-like, and spiniform microtriches were detected on the surface of the tentaculariid *H. alloiotica*. Their internal structure clearly differed from that of pectinate microtriches observed in the other five trypanorhynch species lacking a basal and a junctional region. All pectinate microtriches had the same general architecture, independent of the number of digitiform processes. All trypanorhynchs studied harbored ciliated sensory receptors within the tegument. Even though sensory receptors were scarce in *H. alloiotica*, they were more abundant in the lacistorhynchid *P. noodti* and the otobothriids *P. caryophyllum* and *O. penetrans*, which exhibited two, six, and three kinds of receptors, respectively. Bothridial pits in *O. penetrans* and *O. cysticum* were invaginations of the bothridial surface, being characterized by the lack of sensory receptors and the presence of characteristic microtriches. These differed from other microtriches in that they were larger and had a base consisting of a widely enlarged matrix. The occurrence of different kinds of microtriches and sensory receptors within trypanorhynch cestodes is summarized, and the meaning of these surface structures and of bothridial pits as characters within future trypanorhynch classification is emphasized.

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Introduction

Sensory receptors within the Platyhelminthes have been described by various authors (see Rohde 1994). Within the cestodes, such structures are known from Amphilinidea, Gyrocotylidea (Allison 1980; Rohde 1994), and eucestodes belonging to the Tetraphyllidea, Pseudophyllidea, Proteocephalidea, Cyclophyllidea (Gabrion and Euzet-Sicard 1979; Fairweather and Threadgold 1983; Zdarska and Nebesarova 1997; Brunanska et al. 1998), and Trypanorhyncha (Davydov and Biserova 1985; Palm et al. 1998; Casado et al. 1999a).

Sensory receptors in the tegument of platyhelminths generally consist of a bulb-like elongation of a nerve cell containing mitochondria, different vesicles, and one or two electron-dense collars (Webb and Davey 1974; Lumsden and Specian 1980; Brunanska et al. 1998). The bulb is embedded within the distal cytoplasm and is connected to neighboring cells by septate desmosomes. It can possess cilia of different length that may emerge above the surface microtriches. More than a single form of sensory receptor can be found on the same specimen. Sensory receptors in trypanorhynchs have been described from *Grillotia erinaceus* (van Beneden, 1858), *Bomybycirhynchus sphyraenaicum* (Pintner, 1930), and *Gymnorhynchus gigas* (Cuvier, 1817) (see Davydov and Biserova 1985; Palm et al. 1998; Casado et al. 1999a). In the latter, four different types of receptors were found. Palm et al. (1998) attributed a mechanoreceptory function to a sensory receptor within tufts of microtriches on the bothridial surface, possibly enabling the worm to orientate within the host. However, current information on the occurrence and function of sensory receptors within trypanorhynch cestodes is scarce, in contrast to the more readily available information on microthrix morphology, which has been summarized by Richmond and Caira (1991), Palm (1995), Palm et al. (1998), and Jones and Beveridge (1998).

Other surface structures with an attributed sensory function are "sensory fossettes" or "ciliated pits," which Linton (1890) used to create the genus *Otobothrium*. Palm and Overstreet (2000a) renamed these structures bothridial pits, as they could not detect any cilia but documented microtriches within the pits of *O. cysticum*. Palm (1997a) presented an alternative classification of the Trypanorhyncha. The author considered the tentacular armature as being of minor importance for classification of higher taxa, and erected a superfamily on the basis of the bothridial pits. However, he was not sure about the function of these organs. Recently, Beveridge et al. (1999) failed to support a monophyletic origin of these structures using cladistic methods. Consequently, those authors encouraged comparative ultrastructure studies of the pits to clarify their morphological features and possible function.

The combination of molecular techniques with detailed ultrastructure investigations are of importance for further progress in the phylogenetic analysis of trypanorhynch cestodes. The purpose of the present report is to present an overview on sensory receptors from six trypanorhynch cestodes representing all the superfamilies defined by Campbell and Beveridge (1994) and Palm (1997a). The microthrix ultrastructure is described and the bothridial pits of *O. cysticum* and *O. penetrans* are examined and compared. Finally, the use of microtriches, sensory receptors, and bothridial pits as systematic characters within trypanorhynch cestode classification is discussed.

Materials and methods

Between 1993 and 1998, plerocerci and postlarvae of *Heteronybelinia alloiotica* (Dollfus, 1960), *Pseudolacistorhynchus noodti* Palm, 1995, *Otobothrium cysticum* (Mayer, 1842), *O. penetrans* Linton, 1907, *Poecilancistrum caryophyllum* (Diesing, 1850), and *Prochristianella hispida* (Linton, 1890), were collected from *Carcharhinus limbatus* (Valenciennes, 1841), *Pseudupeneus maculatus* (Bloch, 1793), *Peprilus burti* Fowler, 1944, *Tylosurus crocodilus* (Peron and Lesueur, 1821), *Cynoscion nebulosus* (Cuvier, 1830), and *Farfantepenaeus aztecus* (Ives, 1891), respectively. *H. alloiotica*, *O. cysticum*, *P. caryophyllum*, and *P. hispida* were collected near Ocean Springs, Mississippi (USA, Gulf of Mexico; 1 July 1993, 23 October 1996, 23 October 1996, and 13 May 1998, respectively); *P. noodti*, at Itamaraca Island, Brazil (Southeast Atlantic, 19 August 1993); and *O. penetrans*, at Pelabuhanratu, Java, Indonesia (Indian Ocean, 14 September 1998).

The trypanorhynchs obtained from Itamaraca (Brazil) and Pelabuhanratu (Indonesia) were fixed in 2.5% glutaraldehyde; transferred to cacodylate and phosphate buffer, respectively; and postfixed in osmium tetroxide for electron microscopy. The material from the Gulf of Mexico was fixed in Karnovsky's fluid, transferred to sodium cacodylate buffer, and postfixed in osmium tetroxide. For study of the tentacular armature and surface ultrastructure by scanning electron microscopy (SEM), the specimens were dehydrated in a graded ethanol series. They were then critical-point-dried and mounted with double-sided adhesive tape onto SEM stubs. The stubs were coated with gold in an argon atmosphere and examined under a Zeiss DSM 940 SEM operating at 14–25 kV. For transmission electron microscopy (TEM), after they had been postfixed in osmium tetroxide, specimens were dehydrated in graded ethanol series and propylenoxide and embedded in Spurr's resin. Ultrathin sections were cut with glass knives on a Reichert OmU3 ultramicrotome, stained with uranyl acetate and lead citrate, and examined with a Siemens Elmiskop 101 TEM.

The classification follows that described by Palm (1997a) and the orientation of the bothridial surfaces follows that reported byRichmond and Caira (1991). Most microthrix terms follow those defined by Stearn (1983). Where possible, the sensory receptors were classified into different types according to the classification system of Brunanska et al. (1998).

Results

Superfamily Tentacularioidea Poche, 1926

Family Tentaculariidae Poche, 1926

Heteronybelinia alloiotica (Dollfus, 1960)

Surface ultrastructure The scolex and bothridial surface of *H. alloiotica* is covered with filamentous microtriches. Along the bothridial margin a single band of hook-like (Figs. 1, 2) microtriches surrounded by spiniform microtriches is visible, interspersed with filamentous microtriches (Fig. 2). Acerosate (leaf-like) microtriches occur on the distal and proximal bothridial surfaces. A more detailed SEM documentation of the scolex surface of *H. alloiotica* has been provided by Palm (1995).

The acerosate microtriches are electron-dense and have a small base and an elongated, stout cap (Fig. 4). The cap appears slightly bifurcate in transverse section, as has also been demonstrated with SEM by Palm (1995, Fig. 24). These microtriches comprise an electron-dense medulla consisting of microfilaments and are surrounded by a distinct cortex and glycocalyx. A distinct basal region displaying a junctional region with junctional tubules is absent. The small base is anchored in small depressions into the distal cytoplasm. The hook-like and spiniform microtriches (stout microtriches

▶

Figs. 1–6 *Heteronybelinia alloiotica* from *Carcharhinus limbatus* and *Poecilancistrum caryophyllum* from *Cynoscion nebulosus*, SEM and TEM

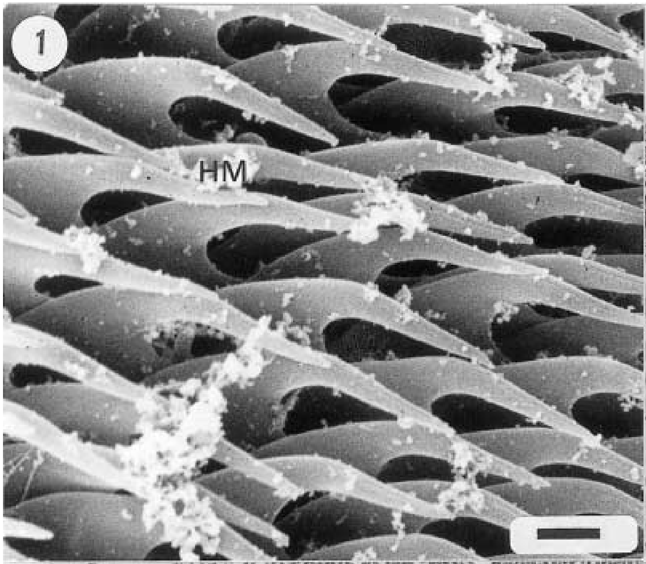
Figs. 1, 2 *H. alloiotica*, hook-like microtriches (*HM*) along the bothridial margins. Note the interspersed filamentous microtriches in Fig. 2. *Bars* 1 µm (Fig. 1), 3 µm (Fig. 2)

Fig. 3 Scolex surface between the bothridia. Note the filamentous microtriches and scolex glands. *Bar* 1 µm

Fig. 4 Acerosate microtriches and ciliated sensory receptor (*arrow*) at the tegumental surface. Note the cilium (*C*). *Bar* 300 nm

Fig. 5 *P. caryophyllum* from *C. nebulosus*, apical scolex part between the bothridia (*B*). The surface is covered with tufts of filamentous microtriches (*arrows*). *Bar* 50 µm

Fig. 6 Tuft of filamentous microtriches surrounding a cilium (*arrow*). *Bar* 1 µm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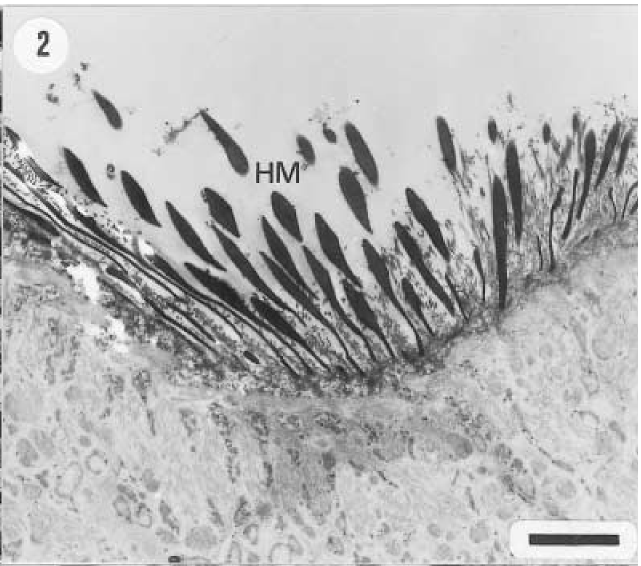
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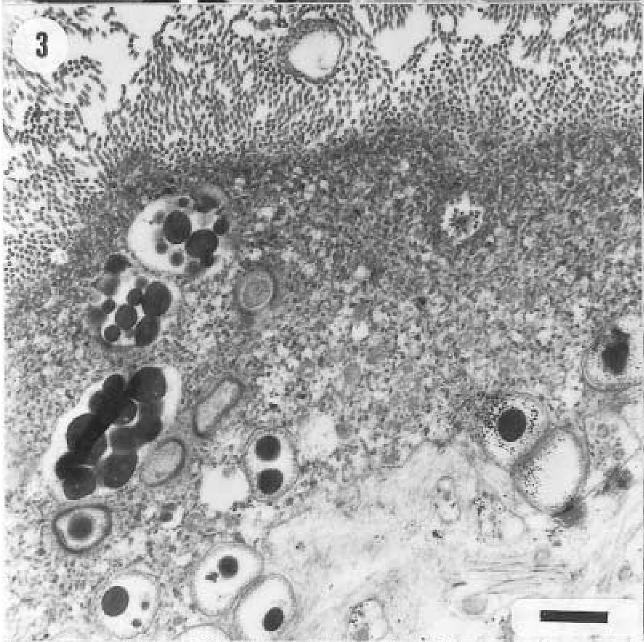
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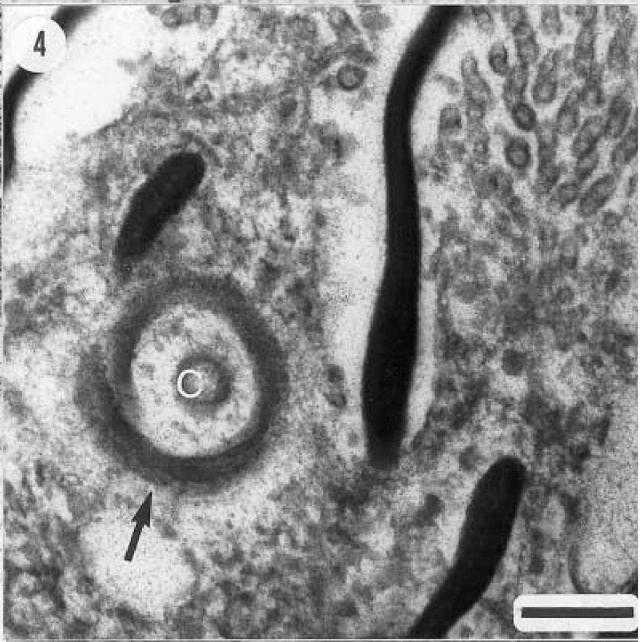
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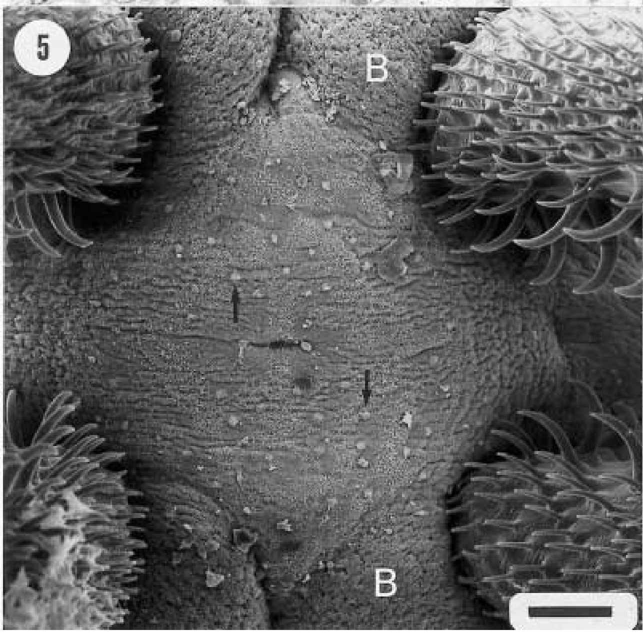
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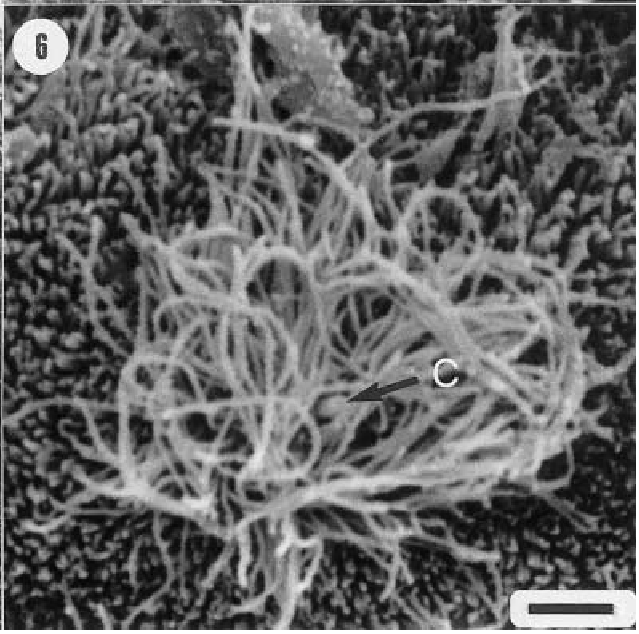
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described by Jones and Beveridge 1998) have a similar internal structure (Fig. 2). They can be distinguished from the acerosate microtriches by their larger size and their rounded, nonbifurcate cap (transverse section).

The filamentous microtriches on the scolex of *H. alloiotica* comprise a base with an electron-lucent core, an electron-dense tunic, and a cap consisting of an electron-dense medulla. In some microtriches, electron-lucent parts in the center of the cap are evident. The base is connected to the cap through a junctional region consisting of junctional tubules. Gland cells are visible within the distal cytoplasm between the bothridia (Fig. 3), including electron-dense granules. They are surrounded by a double membrane, which is strengthened by microfilaments.

Sensory receptors Ciliated sensory receptors were found under the surface of the distal cytoplasm of the bothridia (Fig. 4). The transverse section illustrates a sensory receptor near acerosate microtriches at the tegumental surface of the bothridia (receptor type IV in Brunanska et al. 1998). The receptor is surrounded by a double membrane and includes a single circular electron-dense collar and the basal body of a cilium (C), which consists of nine microtubule triplets.

Family Lacistorhynchidae Guiart, 1927

Pseudolacistorhynchus noodti Palm, 1995

Surface ultrastructure The scolex surface of *P. noodti* has four different kinds of microtriches. The distal bothridial surfaces are covered with tri- to quadridentate microtriches interspersed with papillate microtriches and long, slender microtriches with a bifurcate tip along the bothridial margins. The proximal surfaces are covered with bidentate microtriches interspersed with the same types of microtriches that intersperse in the distal surfaces. Hair-like microtriches cover the end of the pars postbulbosa. A detailed SEM documentation of the scolex surface of *P. noodti* has been provided by Palm (1995).

The ultrastructure of the pectinate microtriches consists of an electron-dense cap (medulla) with microfilaments, a junctional region, and a base with a matrix. An extension of the distal cytoplasm is inserted into the cuff of the matrix forming the base. The medulla is surrounded by a cortex and glycocalyx. The complex junction region is shaped like an inverted U, with a thin electron-dense lamina being present between two electron-lucent layers. The scolex surface is covered with small papillate microtriches as described above for the bothridial surface. Their internal structure consists of an electron-dense sheath and an electron-lucent center. Neither an electron-dense cap nor a junctional region was evident.

Sensory receptors Two kinds of ciliated sensory receptors were found on the surface of the bothridia. Both were located on elevations of the distal cytoplasm, which were covered with papillate microtriches. Additionally to receptor type IV, a second sensory receptor was found that differed in the absence of a characteristic basal body of the cilium. Other internal structures were not seen.

Superfamily Otobothrioidea Dollfus, 1942

Family Otobothriidae Dollfus, 1942

Poecilancistrum caryophyllum (Diesing, 1850)

Surface ultrastructure The scolex surface of *P. caryophyllum* is covered with five different kinds of microtriches; bidentate and tridentate microtriches cover the distal bothridial surface and margin, respectively, and small cap-dominated filamentous microtriches (see Palm et al. 1998) cover the scolex and the bothridia (between the pectinate microtriches). On the apical scolex between the bothridia are located regularly arranged tufts of long filamentous microtriches surrounding single cilia (Figs. 5, 6). Similar tufts of filamentous microtriches protruding above the pectinate ones are evident on the distal surface of the bothridia (Fig. 7). Long, slender microtriches are visible within the bothridial pits, and hair-like microtriches cover the end of the appendix. A detailed SEM documentation of the scolex surface of *P. caryophyllum* has been provided by Palm (1995).

The ultrastructure of the pectinate microtriches consists of an electron-dense cap, a complex inverted-U-shaped junctional region with a thin electron-dense lamina between two electron-lucent layers, and a base with an electron-dense matrix. An extension of the distal cytoplasm is inserted into the cuff of the matrix forming the base. The cap consists of an electron-dense medulla with microfilaments and is surrounded by a cortex and glycocalyx. The small cap-dominated filamentous

▶

Figs. 7–12 *P. caryophyllum* from *C. nebulosus*, SEM and TEM

Fig. 7 Three-fingered pectinate microtriches and a tuft of filamentous microtriches on the bothridial surface. *Bar* 1 μm

Fig. 8 Sensory receptor on the bothridial surface, consisting of a bulb with a cilium (*C*), one electron-dense collar, and electron lucent vesicles (*V*). Note the filamentous microtriches underneath the pectinate ones. *Bar* 300 nm

Fig. 9 Sensory receptor on the bothridial surface, consisting of a bulb with a cilium (*C*), two electron-dense collars (*Co*), and mitochondria (*Mi*). *Bar* 300 nm

Fig. 10 Nonciliated sensory receptor on the bothridial surface with a root (*R*), two collars, and an elongated bulb (*Nb*), including mitochondria and vesicles. *Bar* 300 nm

Fig. 11 Nonciliated sensory receptor with root (*R*) within the distal cytoplasm, distal to muscle fibers (*M*). *Bar* 300 nm

Fig. 12 Invaginated bothridial surface with pectinate and filamentous microtriches and sensory receptors (*S*). *Bar* 3 μm

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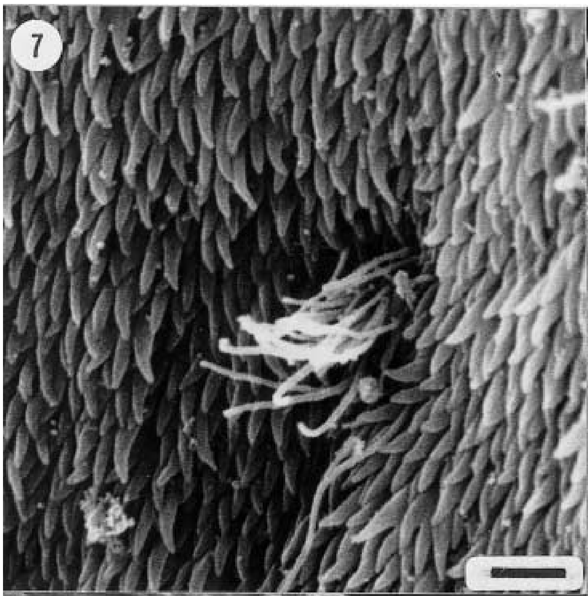

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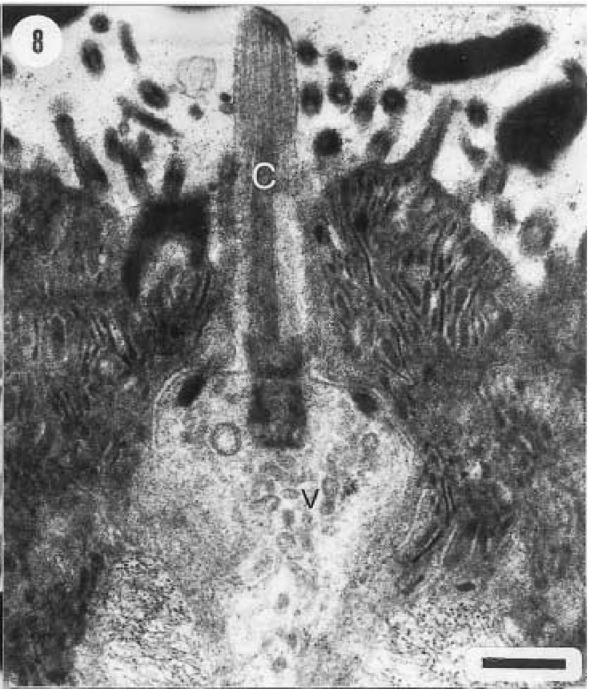

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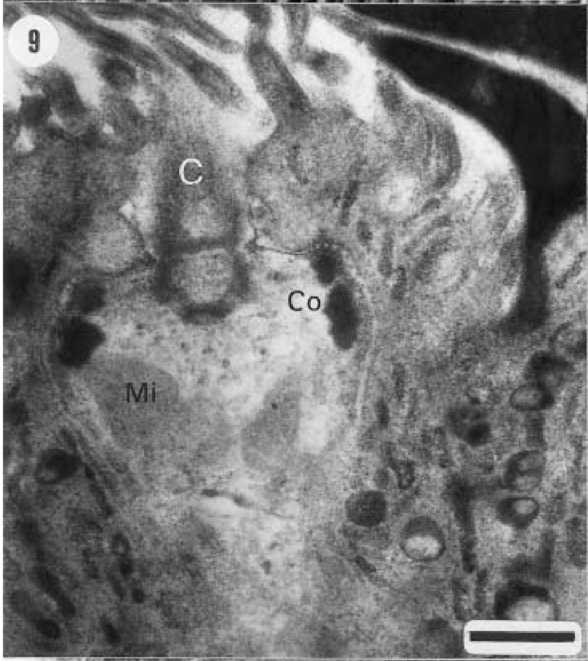

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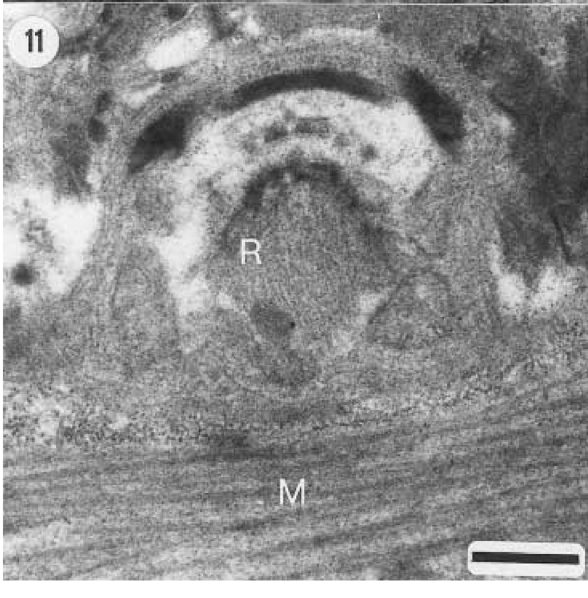

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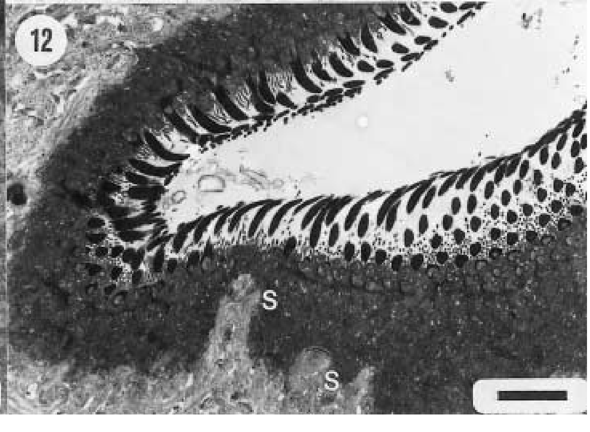

microtriches have an electron-lucent center, and a characteristic junctional region is present.

Sensory receptors Six different kinds of sensory receptors representing types III–V were found in *P. caryophyllum*. A ciliated sensory receptor from the bothridial tegument is shown in Fig. 8. The receptor is surrounded by filamentous and pectinate microtriches and has a cilium that is partly embedded into the distal cytoplasm and partly emerges above the bothridial surface. The cilium consists of microtubules and has a basal body. The bulb of the receptor includes one collar and electron-lucent vesicles and is surrounded by a double membrane with septate desmosomes (type IV). Figure 9 illustrates a sensory receptor displaying a cilium with a basal body and two collars. Mitochondria are visible within the bulb (type V). In some folds of the bothridial tegument, some ciliated sensory receptors occur within a few microns of each other. In Fig. 10 a nonciliated, rooted sensory receptor with a prolonged nerve bulb lying underneath the tegumental surface is connected with deep parts of the distal cytoplasm (type III). The bulb includes mitochondria and electron-lucent as well as electron-dense vesicles. Such receptors with a root and two collars can be found either distal to the tegumental musculature deep inside the distal cytoplasm (Fig. 11) or near the surface of the tegument (Fig. 12). Two additional ciliated sensory receptors were observed; one is without a basal body and has a single collar and the other has a basal body, a root, and two collars.

Otobothrium penetrans Linton, 1907

Surface ultrastructure The scolex surface of *O. penetrans* is covered with four different kinds of microtriches. Tridentate and tri- to quadridentate microtriches occur on the distal bothridial surface and bothridial border, respectively, and all are interspersed with small filamentous ones. The scolex is covered with villus-like projections (see Shields 1985) also bearing small filamentous microtriches. Long and slender microtriches with a bifurcate tip characterize the bothridial pits, and tufts of long filamentous microtriches surround some sensory receptors on the bothridial surface. Detailed SEM documentations of *O. penetrans* have been provided by Shields (1985; as *O. kurisi*), Palm et al. (1993), and Palm (2000).

The pectinate microtriches consist of an electron-dense cap, a complex junctional region with a thin electron-dense lamina between two electron-lucent layers, and a base with an electron-dense matrix. An extension of the distal cytoplasm is inserted into the cuff of the matrix forming the base. The cap consists of a medulla with microfilaments and is surrounded by a cortex and glycocalyx. The filamentous microtriches on the proximal bothridial surface consist of an electron-dense cap (two-thirds of the total microthrix length) and a base with a lucent core surrounded by an electron-dense tunic. A characteristic junction region was not seen. The long filamentous microtriches surrounding the sensory receptors on the bothridial surface are also cap-dominated.

Sensory receptors Three different kinds of sensory receptors are found in *O. penetrans*. Most common are ciliated sensory receptors at the tegumental surface; these have a cilium with a basal body and one or two collars. The bulb includes mitochondria and neurovesicles, and it is bound by a double membrane with septate desmosomes (type IV). In some folds of the bothridial tegument these ciliated sensory receptors appear densely packed, lying only a few microns apart (Fig. 13). Each 30–40 μm, such sensory receptors are covered by cap-dominated filamentous microtriches protruding above the bothridial surface, visible as tufts of microtriches on SEM and TEM (see Palm 2000). These filamentous microtriches extend above the pectinate ones. Sensory receptors without a cilium but with a root and a single collar occur within the distal cytoplasm. The bulb of these structures includes mitochondria and electron-lucent as well as electron-dense vesicles (similar to type III, but not with two collars).

Bothridial pits The ultrastructure of the U-shaped bothridial pit of *O. penetrans* is illustrated in Fig. 14. The pit is an invagination of the bothridium that has surface ultrastructural features similar to those of the surrounding bothridial surface. The retractile musculature, responsible for evagination of the pits, is clearly visible in Fig. 14. The ultrastructure of the bothridial pits can be distinguished from the bothridial surface by its characteristic, long microtriches and the lack of sensory receptors. The microthrix ultrastructure is specific, involving an enlarged, less electron-dense matrix (Fig. 15); a bifurcate tip (Fig. 16); and an additional electron-dense structure within the base (Fig. 17). These structures correspond to the pectinate microthrix ultrastructure in that they consist of a cap comprising an electron-dense medulla with microfilaments (Fig. 16), a cortex and glycocalyx, a complex junctional region with a thin electron-dense lamina between two electron-lucent layers (Fig. 15), and a base with a matrix. An extension

▶

Fig. 13–17 *Otobothrium penetrans* from *Tylosurus crocodilus*, LM and TEM

Fig. 13 Invaginated bothridial surface with pectinate and filamentous microtriches and sensory receptors (*S*) with cilium (*C*). *Bar* 300 nm

Fig. 14 Invaginated bothridial pit with characteristic microtriches. Note the retractile musculature (*M*). *Bar* 3 μm

Fig. 15 Microthrix within the bothridial pit, surrounded by filamentous microtriches. Note the enlarged matrix and the junctional region with a narrow electron-dense lamina in the middle. *Bar* 300 nm

Fig. 16 Bifurcate apical tips and microfilaments of microtriches within bothridial pits. *Bar* 100 nm

Fig. 17 Thickened matrix of microtriches within bothridial pits with electron-dense structures (*E*). *Bar* 300 nm

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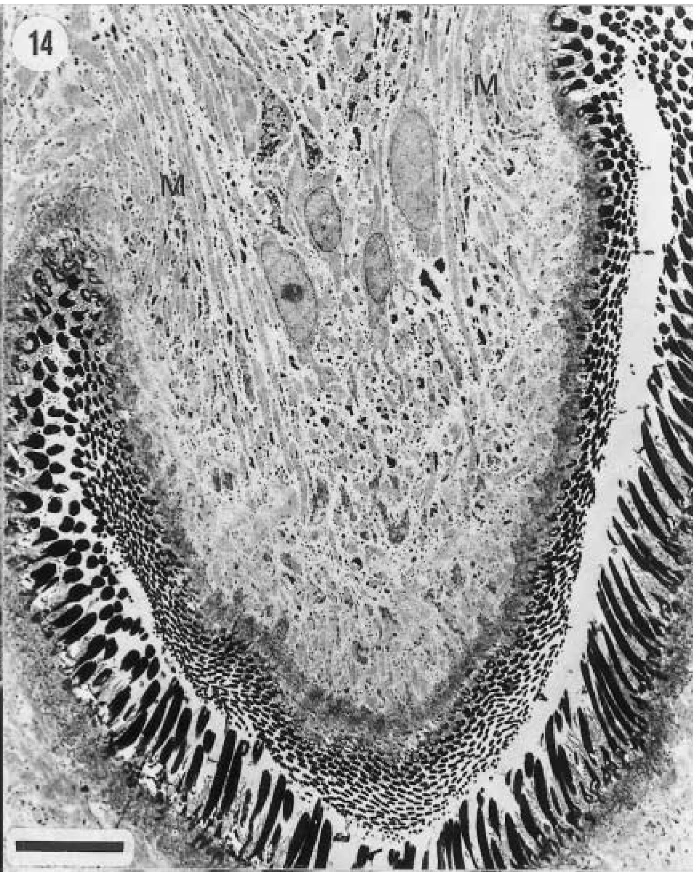

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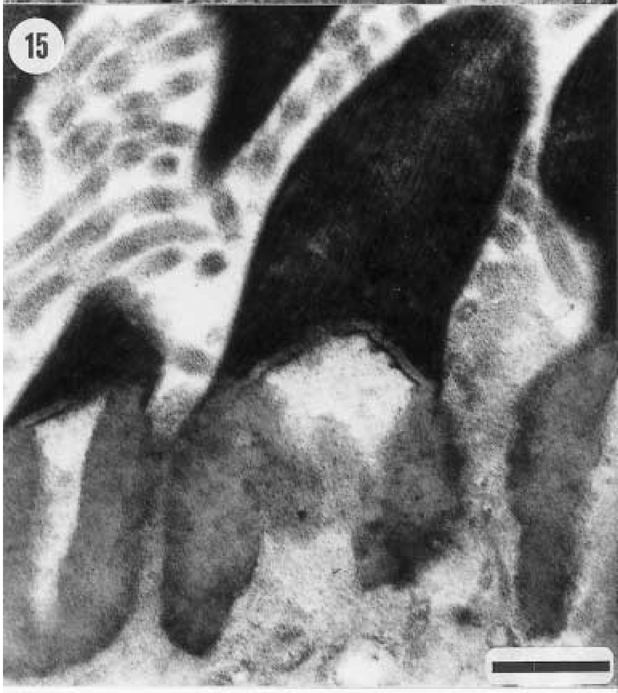

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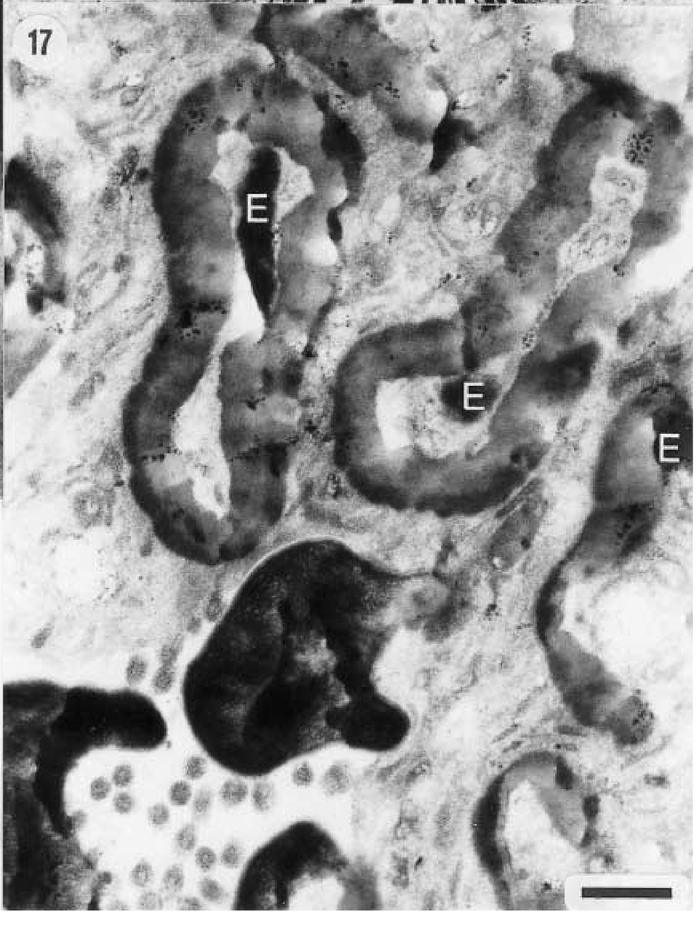


of the distal cytoplasm is inserted into the cuff of the base-forming matrix.

O. cysticum (Mayer, 1842)

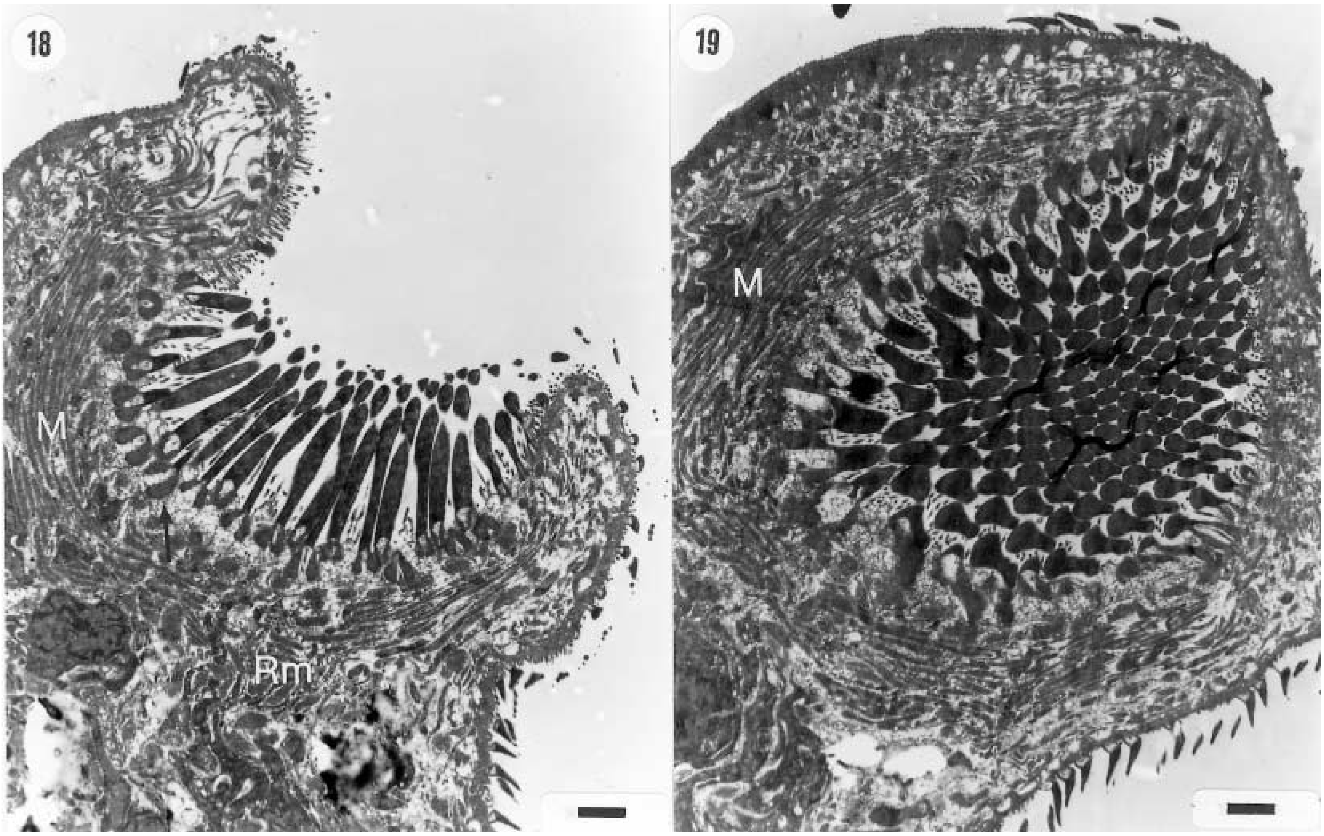
Surface ultrastructure The scolex of *O. cysticum* is covered with four kinds of microtriches. On the distal and proximal bothridial surface, tridentate to palmate and palmate to hexadentate microtriches are evident. They are interspersed with small papillate microtriches, and hair-like microtriches cover the appendix. A further type occurs within the bothridial pits. An SEM documentation of the surface has been provided by Palm (1995) and Palm and Overstreet (2000a).

The pectinate microtriches comprise of an electron-dense cap consisting of a medulla with microfilaments, which is surrounded by a cortex and glycocalyx. A complex junctional region with a thin electron-dense lamina between two electron-lucent layers as well as a base with an electron-dense matrix are present. The distal cytoplasm fills the cuff of the matrix forming the base. The small papillate microtriches on the distal bothridial surface have an electron-lucent center. A characteristic junctional region was not seen.

Sensory receptors Two different kinds of ciliated sensory receptors were found. The nerve bulbs consist of a double membrane with septate desmosomes and one or two collars and a cilium with a basal body (type IV). The cilium is surrounded by papillate microtriches. The second kind of receptor lacks a basal body.

Bothridial pits The ultrastructure of the circular bothridial pits of *O. cysticum* is illustrated in Figs. 18 and 19. The bothridial pit is an invagination of the bothridium with a surface ultrastructure similar to that of the surrounding bothridial surface. The retractile musculature, responsible for evagination of the pits, surrounds the pit (Fig. 18). Several retractor muscles can be seen in Figs. 18 and 19. The ultrastructure of the bothridial pits can be distinguished from the bothridial surface by the characteristic, elongated microtriches and lack of sensory receptors in the bothridial surface. The microthrix ultrastructure is specific in that it has no apical process, is oval to round in cross section (apical part), and has a widely enlarged, less electron-dense matrix that firmly anchors the microtriches within the distal cytoplasm. The microtriches stand in a circle, with the longest microtriches occurring in the center of the pit. Also, the general architecture corresponds to that of pectinate microtriches in that it comprises a cap consisting of a medulla with microfilaments, a junctional region, and a base with a matrix. An extension of the distal cytoplasm protrudes into the cuff of the matrix forming the base. The elongated microtriches are interspersed with small and filamentous microtriches.

Figs. 18, 19 *O. cysticum* from *Peprilus burti*. The bothridial pit is partly invaginated. Note the elongated microtriches with an enlarged matrix (*arrow*) and the circular (*M*) retractor musculature (*Rm*). *Bar* 1 μm



Superfamily Eutetrarhynchoidea Guiart, 1927

Family Eutetrarhynchidae Guiart, 1927

Prochristianella hispida (Linton, 1890)

Surface ultrastructure The surface of *P. hispida* is covered with three kinds of microtriches. Uni- and bidentate pectinate microtriches occur on the distal bothridial surface, and they have an electron-dense medulla consisting of microfilaments, a junctional region, and an electron-dense matrix. The base of these microtriches is filled with distal cytoplasm that is free of electron-dense vesicles. Filamentous and, sometimes, papillate microtriches can be recognized along the bothridial margin and the distal bothridial surface and on the rest of the scolex. The filamentous microtriches have an electron-lucent center and a junctional region, and the papilla-like ones are shorter and have no junctional region.

Sensory receptors Two kinds of ciliated sensory receptors were detected in the present specimens. The cilium, consisting of microtubules and a basal body, protrudes above the bothridial surface (type IV or V). In some receptors an additional root underneath the basal body is evident. The bulb has a double membrane and includes two collars and mitochondria.

Discussion

Surface ultrastructure

Filamentous microtriches

Filamentous microtriches have been recorded from all cestode groups examined (e.g., Caryophyllidea: Hayunga 1991; Trypanorhyncha: Hildreth and Lumsden 1987; Palm et al. 1998; Proteocephalidea: Thompson et al. 1980; Cyclophyllidea: Hess and Guggenheim 1977; Ubelaker 1980); they are most abundant and were previously considered as the prototype microthrix by Holy and Oaks (1986). Also in the present study these microtriches were found on all six species examined and in all different scolex portions.

Filamentous microtriches often consist of an electron-dense cap, a junction region with a junctional tubule, and a base consisting of a core and a core tunic. Palm et al. (1998) found different cap lengths within the trypanorhynch *Bombycirhynchus sphyraenaicum* (Pintner, 1930). During the present study, such filamentous microtriches were recorded for *Heteronybelinia alloiotica* and, within tufts of filamentous microtriches, in *Otobothrium penetrans*. Filamentous microtriches with an electron-dense cap, a core, and a core tunic but without a junctional region were found on the surface of *O. penetrans* and *Tentacularia coryphaenae* Bosc, 1797 (see Palm 2000), and electron-lucent ones with an electron-dense sheath and a junctional region were observed on the bothridial surface of *Poecilancistrum caryophyllum* and *Prochristianella hispida*. Several authors have suggested a nutritional function for filamentous microtriches (Lumsden 1975; MacKinnon and Burt 1983), and Rothman (1963) and Hayunga (1991) have proposed an anchoring function for the caps and a nutritional function for the bases. The present study demonstrates that further morphological variability exists, indicating the high degree of specialization and the possibility of multiple functions for filamentous microtriches.

Papillate microtriches

Papillate microtriches, which have been recorded from *Pterobothrium kingstoni* Campbell and Beveridge, 1996, *Pseudolacistorhynchus noodti*, and *Poeciloacanthum oweni* Palm, 1995 by Palm (1995) and from *Gymnorhynchus gigas* (Cuvier, 1817) (“knob-like structures”) by Casado et al. (1999b), are described from the bothridia of *P. noodti*, *O. cysticum*, and *P. hispida* in the present report. These “truncated microtriches” or “microvilli” of Rogan and Richards (1987) and Lumsden et al. (1982) are distinctly shorter than the pectinate microtriches, have no junctional region, and lack an electron-dense medulla. An electron-lucent center is surrounded by an electron-dense sheath. The ultrastructure of these microtriches appears to be similar to that of some of the above-described filamentous ones. Thus, they might perform a similar nutritional function.

Pectinate microtriches

The internal ultrastructure of pectinate microtriches has been studied in species of the genera *Lacistorhynchus*, *Grillotia*, *Bombycirhynchus*, and *Otobothrium*, respectively, by Lumsden and Hildreth (1983), Biserova (1987), Palm et al. (1998), and Hildreth and Lumsden (1987). In the present study these microtriches were also found on the bothridial surfaces of the lacistorhynchid, the otobothriids, and the eutetrarhynchid; however, they were not recorded from the tentaculariid *Heteronybelinia* species examined. This type of microthrix exhibits a general ultrastructure, independent of the number of digitiform processes, as previously proposed by Palm et al. (1998). These microtriches typically consist of an electron-dense medulla of microfilaments surrounded by a cortex and glycocalyx, a junctional region of different electron-dense and electron-lucent layers, and a base with a matrix. The number of processes can differ within a single species, as has been illustrated by Palm (1995). The function of these microtriches has not yet been confirmed, but Palm et al. (1998) have proposed that they serve for anchoring and traction as the worm penetrates the host tissue. We also propose that they might enlarge the interspace between filamentous microtriches (serving for nutrition; see above) and the host microvilli and that they might serve as a protective covering for the bothridia and scolex surface.

Hook-like and acerosate microtriches

Hook-like and acerosate microtriches have been recorded only within the tentaculariids, such as members of *Tentacularia*, *Nybelinia*, *Heteronybelinia*, and *Kotorella* (Palm 1995, 2000; Jones and Beveridge 1998; Palm and Overstreet 2000b). Their ultrastructure consists of an electron-dense medulla with a cortex but without a junctional and basal region. The base of the hook-like microtriches within *T. coryphaenae* is sometimes split and anchored within the distal cytoplasm (Palm 2000). In *H. alloiotica* and *N. queenslandensis* Jones and Beveridge 1998 the bases of the hook-like microtriches are also anchored, occurring within small depressions. This indicates a possible function for anchoring and movement as previously proposed by Palm (1997b). However, Jones and Beveridge (1998) did not detect that the bothridia of *N. queenslandensis* grasp into the mucosa of the pyloric stomach to provide a tight junction between the hook-like microtriches and the host tissue. Therefore, these microtriches may not serve to anchor the bothridia.

Sensory receptors

In the present study, sensory receptors were detected in species belonging to all superfamilies as defined by Campbell and Beveridge (1994) and Palm (1997a). In general, two different sensory receptors were found: ciliated and nonciliated ones, the latter often having no connection to the tegumental surface. These receptors were similar in that they had septate desmosomes, one or two electron-dense collars, and different kinds of vesicles within the nerve bulbs. Within the ciliated sensory receptors, further character combinations could be observed; the cilium either had or lacked a basal body (Brunanska et al. 1998 detected only sensory receptors with a cilium and a basal body) and either had or lacked an additional root. Nonciliated receptors always appeared to have a root. The receptor types III–V of Brunanska et al. (1998) were found in *P. caryophyllum*, and type IV was also common in the other trypanorhynchs studied. However, with six different kinds of sensory receptors occurring in *P. caryophyllum*, they seem to be even more variable, as is also indicated by the results reported by Brunanska et al. (1998, 2000) for the proteocephalid cestode *Proteocephalus longicollis* (Zeder, 1800).

Sensory receptors have been described from many different free-living and parasitic platyhelminths (Rohde 1994) as well as from trypanorhynch cestodes (Davydov and Biserova 1985; Palm et al. 1998; Casado et al. 1999a, b). In the present study, similar receptors were recorded from *P. noodti*, *O. penetrans*, *O. cysticum*, *P. hispida*, and *H. alloiotica*, with *P. caryophyllum* having a total of six different kinds of ciliated and nonciliated receptors. Receptors were most common on the bothridial surfaces, and, sometimes, groups of them appeared close together (see Figs. 12, 13). Interestingly, no sensory receptor was found on the scolex surface of *T. coryphaenae* (see Palm 2000), and *H. alloiotica* (present study) had only a single kind of ciliated sensory receptor, and it was rarely found at the bothridial tegument. Jones and Beveridge (1998) studied in detail the scolex ultrastructure of *N. queenslandensis* but did not record any sensory receptor. Tentaculariid trypanorhynchs may have few sensory receptors within the bothridial tegument, but these structures are abundant and display high degrees of morphological variability within lacistorhynchid, otobothriid, and eutetrarhynchid trypanorhynchs.

The functional specialization of the cestode tegument for sensory reception is not well understood, and the sensory nature of the above-mentioned receptors has not been demonstrated in experimental and behavioral studies (Palm et al. 1998). However, several different functions have been attributed to ciliated receptors, such as chemoreception, by Allison (1980); osmoregulation, by Hess and Guggenheim (1977); and mechanoreception, by Morseth (1967), Webb and Davey (1974), and Andersen (1975). Lumsden and Murphy (1980) have proposed that the tapeworm integument may be an example of an "epidermal" tissue exerting a modulating effect on muscle tissue. The presence of basal bodies or roots of the cilium within the nerve bulb as well as septate desmosomes and one or two collars demonstrates that the cilium is firmly connected within the nerve bulb, which itself is firmly connected to the distal cytoplasm. In contrast, the apical part of the cilium can move freely above the bothridial surface. Additional cap-dominated filamentous microtriches might serve as transducers (Palm et al. 1998). This supports the concept of a mechanoreceptory function for ciliated sensory receptors, which might help the worm to orientate within its host. That function would also explain the abundance of the ciliated receptors within the trypanorhynch bothridial tegument. The function of receptors without a cilium might be multiple, as would also be indicated by their different locations. They have been treated as mechano- or proprioreceptors by Andersen (1975), Fairweather and Threadgold (1983), and Webb and Davey (1975), but Brunanska et al. (1998) have speculated on pressure reception.

On the basis of their having sensory receptors, tentaculariid trypanorhynchs differ from lacistorhynchid, otobothriid, and eutetrarhynchid species. This difference corresponds to strikingly different scolex features, including their tentacular armature. Palm (1995, 1997a) has stated that the tentacular homeoacanthous armature of tentaculariids reflects their different attachment site within the final host, which is most often the stomach wall rather than the intestinal wall of the spiral valve, which is the typical attachment site of many heteroacanth and poeciloacanth trypanorhynchs. Thus, a reduced number of surface sensory receptors within tentaculariid trypanorhynchs might also reflect a different need for such structures within the stomach environment.

Bothridial pits

The present study on the ultrastructure of the bothridial pits of *O. penetrans* and *O. cysticum* corroborates the findings by Palm and Overstreet (2000a) that there are no cilia but just microtriches within these bothridial structures. The pits are invaginations of the bothridium whose ultrastructure is similar to that of the surrounding bothridial surface. A difference lies in the occurrence of characteristic microtriches with an enlarged, less electron-lucent matrix; the lack of sensory receptors; and the occurrence of strong retractor musculature that enables the worm to evaginate the pit. Pintner (1934) has proposed a relationship between these retractile organs and the bothridial borders ("Sinneskante") of other trypanorhynchs such as *G. heptanchi* (Vaullegeard, 1899) (=*Heterotetrarhynchus institatum*) and the lacistorhynchid *Callitetrarhynchus speciosus* (Linton, 1897) (see Fig. 121 in Palm 1995). Our findings from two different species of *Otobothrium* support this assumption, especially since the enlarged bifurcate microtriches from the bothridial borders of *C. speciosus* and *P. noodti* appear to be similar to those observed in the bothridial pits of *O. penetrans* (see also Palm et al. 1993). A relatedness of the "Sinneskante" with the bothridial pits may also explain the occurrence of bothridial pits in different positions along the bothridial margins, such as at the posterior end of the bothridia in *O. penetrans* (see Palm et al. 1993) or laterally in *O. propecysticum* (see Dollfus 1969). However, the ultrastructure of the bifurcate microtriches along the bothridial borders ("Sinneskante") within the trypanorhynchs needs to be clarified.

Because we did not detect any sensory receptor within the bothridial pits, we do not think that the latter serve in sensory reception. They might serve for attachment and anchoring within the host tissue, thus corresponding to a special bothridial adaptation similar to that represented by the hooklet microtriches of tentaculariid trypanorhynchs. However, because of the observed variation in the size of the bothridial pits as well as the kind of microtriches present, these structures are nonetheless specialized organs that might perform different functions.

Classification and phylogeny

Richmond and Caira (1991) as well as Palm (1995) have concluded that microtriches are systematically informative for trypanorhynchs. Some types such as filamentous and papillate microtriches appear to occur in all known cestodes, and much remains to be determined about the intraspecific and interspecific morphological variability of microtriches in trypanorhynchs. Also, similar hair-like microtriches were found on the end of the pars postbulbosa/appendix of the lacistorhynchids *P. noodti* and *B. sphyraenaicum* as well as the otobothriids *P. caryophyllum, Pseudotobothrium dipsacum* Linton, 1897, and *O. cysticum* (Palm 1995; Palm and Overstreet 2000a). How those similar structures might reflect any possible phylogenetic relationship between these species has not yet been decided.

Pectinate microtriches have been described in species from different cestode orders; however, they appear to be absent within tentaculariid trypanorhynchs. In contrast, hook-like, spiniform, and acerosate microtriches have thus far been recorded only from the tentaculariid genera *Tentacularia* (Palm 2000), *Nybelinia* (Jones and Beveridge 1998), *Heteronybelinia*, *Mixonybelinia* (Palm 1995), and *Kotorella* (Palm and Overstreet 2000b; all Tentaculariidae). Both kinds of microtriches clearly differ in their general architecture; thus, their presence appears to have systematic value. An examination of the microthrix ultrastructure along the bothridial margins might help to clarify the real relationship of the different taxa to tentaculariid or nontentaculariid trypanorhynchs, such as that proposed for the Hepatoxylidae/Sphyriocephalidae as a sister clade of the Tentaculariidae by Campbell and Beveridge (1994), Palm (1997a), and Beveridge et al. (1999). Whereas pectinate microtriches have been reported from members of the Pseudophyllidea (Lumsden et al. 1982), Proteocephalidea (Thomsen et al. 1980), and Cyclophyllidea (Rogan and Richards 1987), indicating a plesiomorphic origin, the hook-like, acerosate, and spiniform microtriches of the tentaculariids appear to be apomorphic.

Pectinate microtriches are taxonomically useful. However, given the present state of knowledge, it is difficult to use them to distinguish among different families or genera within nontentaculariid trypanorhynchs. Although species within some genera such as *Callitetrarhynchus*, *Floriceps*, and *Grillotia* appear to have a similar microthrix pattern, those species in genera such as *Otobothrium* appear more variable. Pectinate microtriches have also been found on the pedunculus scolices of *O. cysticum* (Palm and Overstreet 2000a) as well as in species of *Callitetrarhynchus* and *Floriceps*. In contrast, congeners such as *O. penetrans* have pectinate microtriches on the bothridia only, with the rest of the scolex having villus-like projections with filamentous microtriches. Such a microthrix pattern has been described by Palm (1995) from other otobothriids and different species belonging to the genus *Grillotia*. Thus, the occurrence of pectinate microtriches can differ even between species within the same trypanorhynch genus, which currently makes it difficult to use them as a systematic character within nontentaculariid trypanorhynch cestodes.

Tentaculariid trypanorhynchs differ from lacistorhynchid, otobothriid, and eutetrarhynchid species on the basis of the occurrence of sensory receptors. Although ciliated receptors can be found on tentaculariids (Table 1), they are not abundant and not very variable. In contrast, nontentaculariids have several different types of sensory receptors, which are abundant within

Table 1 General types of sensory receptors found within trypanorhynch cestodes

Superfamily Species	Number of kinds of receptors	Ciliated receptor		Noncilated receptor	
		Receptors associated with tufts of filamentous microtriches	Receptors without tufts of filamentous microtriches	Receptors under the scolex surface	Receptors near muscle layers
Tentacularioidea					
Heteronybelinia alloiotica	1	–	+	–	–
Nybelinia queenslandensis[a,b]	(–)	(–)	(–)	(–)	(–)
Tentacularia coryphaenae[c]	–	–	–	–	–
Bombycirhynchus sphyraenaicum[d]	1	+	(–)	(–)	(–)
Grillotia erinaceus[e]	1	(–)	+	(–)	(–)
Gymnorhynchus gigas[f]	4	+	+	+	+
Pseudolacistorhynchus noodti	2	–	+	–	–
Otobothrioidea					
Otobothrium cysticum	2	–	+	–	–
O. penetrans	3	+	+	+	+
Poecilancistrum caryophyllum	6	+	+	+	+
Eutetrarhynchoidea					
Prochristianella hispida	2	–	+	–	–

[a] Jones and Beveridge (1998)
[b] No sensory receptor was recorded in this very detailed study on the surface ultrastructure
[c] Palm (2000)
[d] Palm et al. (1998)
[e] Davydov and Biserova (1985)
[f] Casado et al. (1999a, b)

the bothridial tegument. This difference corresponds to a different microthrix ultrastructure (see above) as well as to a strikingly different scolex morphology. However, the current state of knowledge, with only a few trypanorynch species having been studied, causes difficulties in their use as genus- or family-distinguishing characters.

The presence of bothridial pits (i.e., ciliated pits) has previously been used to characterize the superfamily Otobothrioidea by Palm (1995, 1997a). This study demonstrates that the bothridial pits are invaginations of the surface, apparently without sensory function. They might resemble bothridial borders in other trypanorhynchs, indicating that otobothriids might be related as well to lacistorhynchids (see Campbell and Beveridge 1994; Beveridge et al. 1999). However, the bothridial pits are covered with a characteristic kind of microtriches, which have not been recorded from other trypanorhynchs. In summary, the following new aspects might be included within future trypanorhynch classifications. On the basis of the microthrix features and the occurrence of sensory receptors, we think that Tentaculariidae is a clearly distinct trypanorhynch family, deserving classification as its own superfamily similar as previously proposed by Campbell and Beveridge (1994). The status of Sphyriocephalidae sensu Palm (1997a) as well as the Paranybeliniidae, which has previously been placed with Tentaculariidae, remains to be clarified, and this might be done by assessment of the microthrix ultrastructure, especially that of the bothridial margins. The lack of a sensory function by the bothridial pits does not exclude the use of these structures as phylogenetic characters at the superfamily level. Since they seem to be related to the bothridial margins and appear to have characteristic microtriches that have not been recorded from other trypanorhynchs, they might well be of monophyletic origin.

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