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Surface ultrastructure of plerocercoids of *Bombycirhynchus sphyraenaicum* (Pintner, 1930) (Cestoda: Trypanorhyncha)

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Abstract Light microscopy studies have previously shown that *Bombycirhynchus sphyraenaicum* is an exceptional trypanorhynch cestode, characterised by a poeciloacanthous armature and two enormous bothridia, which overlap parts of the pars bulbosa, a character combination unique within the trypanorhynchs. Plerocercoids of *B. sphyraenaicum* from the fish *Lates calcarifer* (Centropomidae) were investigated by scanning and transmission electron microscopy. Results revealed that the tegument of the anterior margin of the distal bothridial surface bears three kinds of microtriche; palmate microtriches, 8 μm high, with seven to eight digitiform processes; equalized filamentous microtriches, 5–6 μm long, with cap and base each forming 50% of the length, borne on undulations beneath the palmate microtriches, and cap-dominated filamentous microtriches, 5–6 μm long, with the cap forming 75% of the length, borne on the apex of putative sensory papillae. Integumental connections link the bases of the palmate microtriches, forming transverse girdles around the worm, which may serve to coordinate traction. At regular intervals between the palmate microtriches are papillae, covered with filamentous microtriches extending above the palmate microtriches. A cilium emerges from a bulb at the apex of each papilla; other structures in the bulb include an electron-dense cuff, and two electron dense collars. The posterior part of the bulb tapers and passes into the tegumental cytoplasm. These adorned papillae, observed for the first time in trypanorhynch cestodes, are identified as putative mechanoreceptors.

Introduction

The highly active outer surface of cestodes, the tegument, is multifunctional, serving for absorption, digestion, protection and excretion (Coil 1991; Featherston 1972; Hayunga 1991; Lumsden 1975a; Thompson et al. 1980), and possibly anchoring (Morseth 1966; Rothman 1963; Thompson et al. 1980) and traction for locomotion (Berger and Mettrick 1971; Rothman 1963). As the parasite-host interface, it additionally serves for chemical and tactile reception (Featherston 1972; Hess and Guggenheim 1977; Jones 1975; 1988; Webb and Davey 1974).

Having such diverse functions necessitates a high degree of morphological specialisation. The most dominant feature of the cestode tegument is the covering by microtriches, which are thought to be responsible for nutrition and protection, and possibly also the mechanical functions of anchoring and traction. Microtriches show a wide range of morphologies, varying between species and somatic regions. For example, the tegument of *Floriceps minacanthus* (Trypanorhyncha) has six different kinds of microtriches at different positions on the scolex (Richmond and Caira 1991), while *Taenia hydatigena* (Cyclophyllidea) has only three (Featherston 1972). In contrast, Richmond and Caira (1991) as well as Palm (1995) suggested no difference in the microthrix pattern of plerocercoids in comparison to adult trypanorhynchs. Other surface structures, such as the sensory apparatus and secretory structures, also appear to be polymorphic (Hess and Guggenheim 1977; Webb and Davey 1974). However, mechanoreceptors generally consist of a tactile cilium, emerging from

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a bulb embedded in the tegumental surface, while chemoreceptors may be surrounded by a protective structure or situated in chambers with cilia protected by mucus (Webb and Davey 1974).

Most of the ultrastructural investigations of cestode tegument focus on species of medical or veterinary importance, such as *Diphyllobothrium* spp. (Pseudophyllidea), *Hymenolepis* spp. and *Taenia* spp. (Cyclophyllidea). In contrast, groups such as the tetraphyllids and trypanorhynchs have been relatively little studied, especially by transmission electron microscopy, despite the fact that they have a worldwide distribution, and are the most abundant cestodes in the marine environment. During a comprehensive ultrastructural study of trypanorhynch surface morphology (Palm 1995), *Patellobothrium quinquecatenatum* Beveridge and Campbell, 1989 [herein considered a junior synonym of *Bombycirhynchus sphyraenaicum* (Pintner, 1930) consistent with Beveridge and Campbell (in press)] was found to have a highly specialised tegument. Previously, its pair of enormous patelliform bothridia, unique for a poeciloacanth trypanorhynch, had been described by Pintner (1930) and Beveridge and Campbell (1989). In the present publication, we present the unique features of the bothridial surface, which are suggested to be adapted for nutrition, traction and tactile sensory reception; they demonstrate remarkable functional morphology within the trypanorhynchs.

Material and methods

B. sphyraenaicum was obtained from the collection of the British Museum (Natural History), registration numbers 1980.7.11.31–35. Plerocercoids of this unusual and little-known trypanorhynch species were collected by I. Owen from around the intestine and gonads of the giant perch *Lates calcarifer* (Centropomidae), the second intermediate host, from Papua New Guinea.

Scolices of the formalin-stored specimens were freed from the blastocysts. For scanning electron microscopy, two scolices were transferred to ethanol and dehydrated in a graded ethanol series. They were then critical-point dried and mounted with a double-sided adhesive tape onto scanning electron microscopy stubs. The stubs were coated with gold-palladium in an argon atmosphere and examined under a Zeiss DSM 940 scanning electron microscope at 10–15 kV (Palm 1995). The high-magnification scanning electron micrographs presented in this paper were taken of a region at the anterior margin of the distal bothridial surface (as illustrated by Richmond and Caira 1991). For transmission electron microscopy, the bothridia of a single specimen were transferred from formalin, via a series of Sorensen's phosphate buffers (pH 7.3) and graded alcohols, back to Sorensen's buffer, and then osmicated in 1% osmium tetroxide in Sorensen's buffer. The bothridia were embedded in Spurr's embedding resin, and sectioned at 600 Å. The sections were stained with lead citrate and uranyl acetate and examined in a Zeiss 10 CA transmission electron microscope. Though formalin is not the ideal fixative for transmission electron microscopy, this was the only material available and the technique described above provided satisfactory results.

In describing the ultrastructure of the microtriches, we have followed the terminology of Holy and Oaks (1986). In using the term matrix for the outer part of the base of the palmate microtriches, we have followed Thompson et al. (1980).

Results

Surface ultrastructure

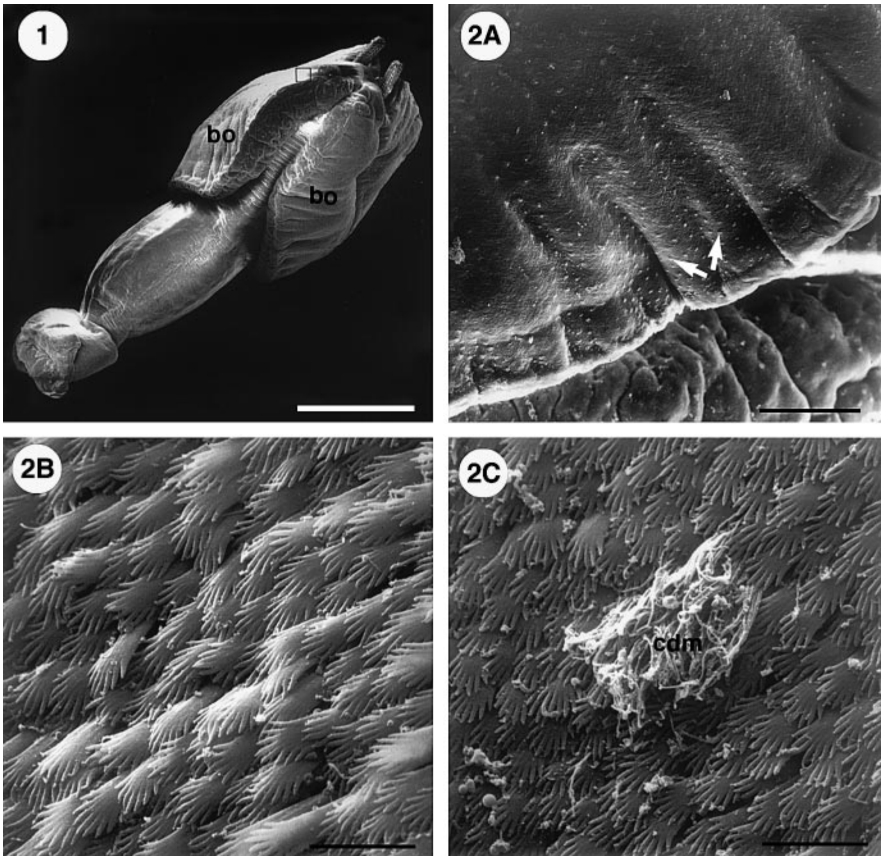
The surface of the plerocercoid of *B. sphyraenaicum* is dominated by two massive bothridia, which overlap approximately half of the scolex (Fig. 1). The surface of the bothridia bears densely overlapping palmate microtriches, each with seven or eight digitiform processes or "fingers", oriented towards the posterior of the worm (Fig. 2B–C). Extending above the plane of the palmate microtriches are regularly arranged tufts of "cap-dominated" (i.e. the cap comprised approximately 75% of the total length, and the base only 25%) filamentous microtriches, which adorn elevated sensory receptors (Fig. 2C, see below). The tufts are separated from each other by distances of 25–60 μm (Fig. 2A), lying closest together at the margins of the bothridia, and further apart in the centre of the bothridia.

Internal ultrastructure

Transmission electron microscopy revealed additional features of the highly specialised tegument (Fig. 3). These include (1) bases of the palmate microtriches inserted into depressions of the distal cytoplasm, and linked by connections; (2) abundant "equalised" (i.e. their cap and base each comprise 50% of the total length) filamentous microtriches borne on the undulations between the bases of the palmate microtriches, and (3) sensory receptors borne on papillae bearing tufts of cap-dominated filamentous microtriches (see above).

Palmate microtriches and their basal connections

The height of the palmate microtriches is approximately 8 μm. They comprise three distinct regions: a long electron-dense cap, a complex junction region and an elaborate base (Fig. 4A, B). Their outer surface is interpreted as a glycocalyx (Fig. 6D). The cap extends from the distal "fingers" through the "palm" until it reaches the junction region (Fig. 3), which is above the top of the undulations of the distal cytoplasm. The dense medulla of the cap is packed with abundant longitudinal microfilaments (Figs. 4B, 6D), and is covered by a narrow less electron dense cortex (Fig. 6D). The junction region between the cap and the base is shaped like an inverted U (Fig. 4A), and is angled so that the cap is tilted posteriorly (Fig. 4B). In the middle, a thin opaque lamina is evident (Fig. 4A, B). Below the junction region is the base, comprising a homogenous medium-dense area, the matrix (Fig. 4A, B), which extends from the anterior edge of the junction region down into the distal cytoplasm. The matrix is bevelled (as can be clearly seen in longitudinal sections, Fig. 4B), with its longer anterior wall extending in an S shape down into



Figs. 1, 2 *Bombycirhynchus sphyraenaicum*, scanning electron micrographs of the scolex. **Fig. 1** Surface ultrastructure, showing two massive bothridia (*bo*). The region within the *square* is that examined at higher magnification (*bar* 1 mm). **Fig. 2A** Bothridial surface with tufts of cap-dominated filamentous microtriches (*arrows*) (*bar* 200 µm). **B** Palmate microtriches with seven or eight digitiform processes (*bar* 5 µm) (from Palm 1994, reproduced with permission of VCH, Weinheim). **C** A tuft of cap-dominated filamentous microtriches (*cdm*) (*bar* 5 µm)

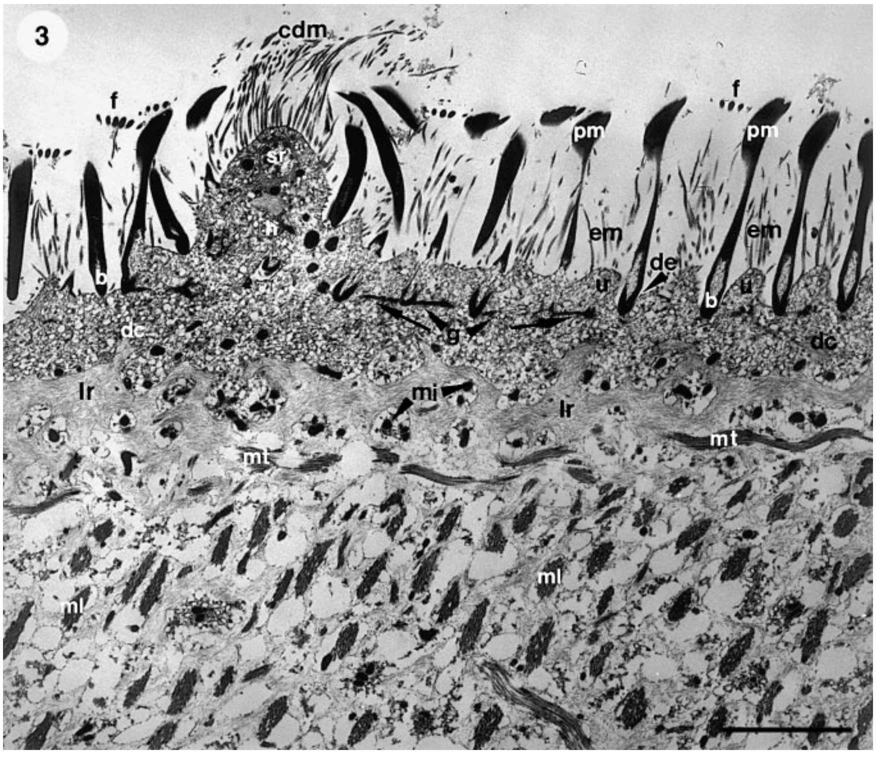
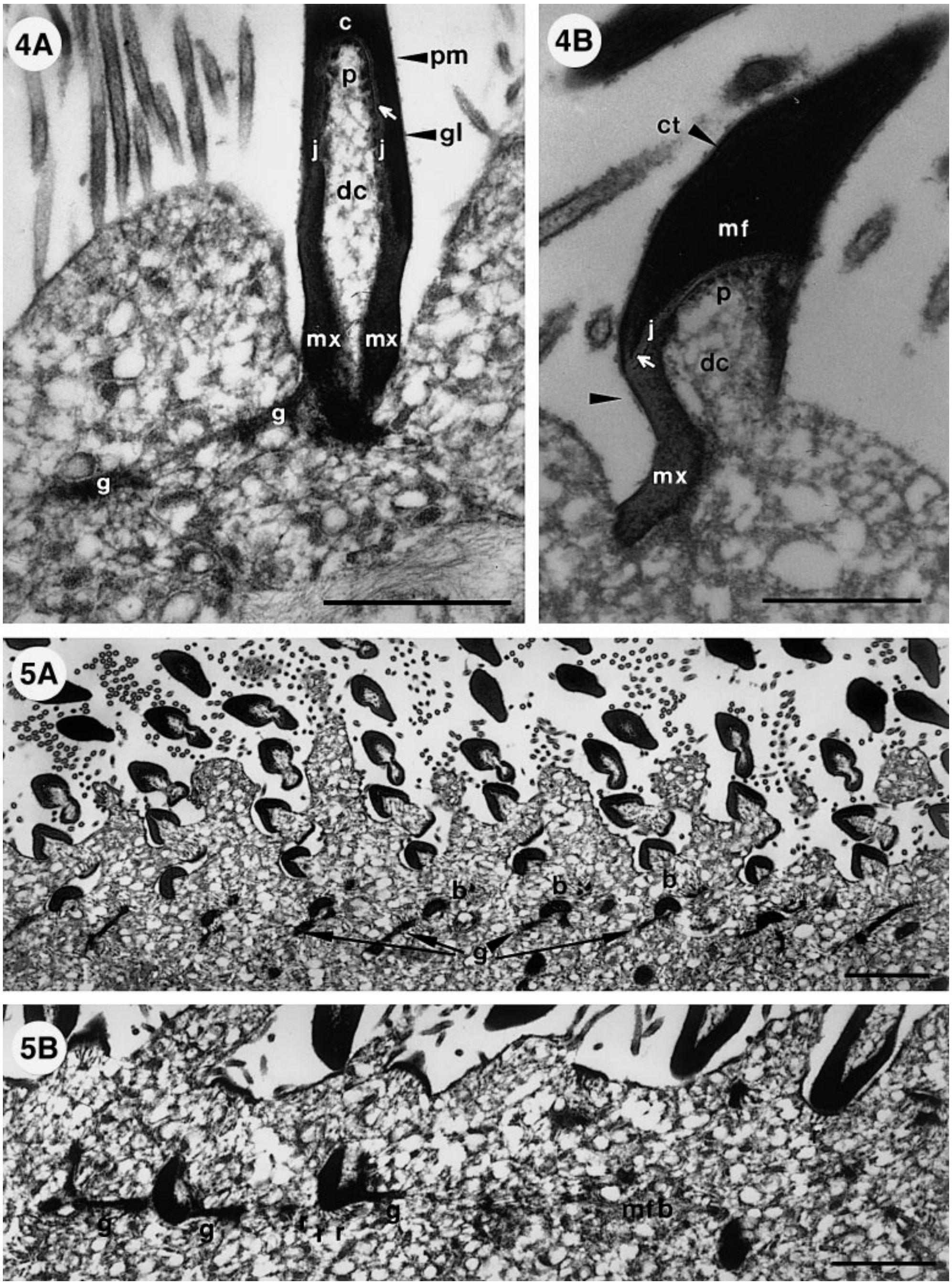


Fig. 3 *B. sphyraenaicum*, transmission electron micrograph of the bothridial tegument. Digitiform processes (*f*) of the palmate microtriches (*pm*) and their symmetrical bases (*b*) show that this is a transverse section. These bases are inserted into depressions (*de*) of the distal cytoplasm (*dc*), and are connected by girdles (*g*); equalised filamentous microtriches (*em*) are borne on undulations (*u*). A sensory receptor resembling a "haystack" (*h*) bears cap-dominated filamentous microtriches (*cdm*) and an apical sensory receptor (*sr*). The lamina reticularis (*lr*), and transverse (*mt*) and longitudinal muscles (*ml*) are located below the distal cytoplasm. Most of the mitochondria (*mi*) lie in chambers in the distal cytoplasm and lamina reticularis (*bar* 5 µm)



Figs. 4, 5 *B. sphyraenaicum*, transmission electron micrographs of the palmate microtriches. **Fig. 4** Transverse (**A**; *bar* 1 µm) and longitudinal (**B**; *bar* 0.5 µm) section. The palmate microtriche (*pm*) has a cap (*c*) packed with longitudinally oriented microfilaments (*mf*), and is covered by a narrow cortex (*ct*) and glycocalyx (*gl*). The junction region (*j*) has a narrow opaque lamina in the middle (*white arrow*), and bears finger-like projections (*p*) at its interface with the distal cytoplasm (*dc*). The base comprises the core of distal cytoplasm and the matrix (*mx*). In the transverse section, a girdle (*g*) is connected to the palmate microtriche. In the longitudinal section, the bevelled base of the palmate microtriche with the anterior wall (*black arrow*) is shown. **Fig. 5A, B** Girdles connecting the palmate microtriches. **A** Oblique section showing the girdles (*g*) connecting the bases (*b*) of the palmate microtriches (*bar* 2.0 µm). **B** Transverse section showing the radial array of fibres (*r*) around the proximal part of the bases of the palmate microtriches. A band of microfibrils (*mfb*) is continuous with the girdle (*g*). (*bar* 1.0 µm)

the distal cytoplasm. An extension of the distal cytoplasm is inserted into this oblique cuff of the matrix forming the core of the base (Fig. 4A, B). The interface between the junction region and the distal cytoplasm is adorned with small, electron-dense, finger-like projections (Fig. 4A, B).

The palmate microtriches are connected together by electron-dense connections, approximately 0.1 µm wide, passing transversely between their bases, some 1.5–2.0 µm below the surface of the distal cytoplasm (Figs. 3, 5A, B). Thus, the palmate microtriches are connected together in a series of transverse girdles passing around the bothridia. No longitudinal or oblique connections could be seen (Fig. 5A). Discrete radiating fibres could sometimes be seen around the basal end of the palmate microtriches (Fig. 5B). In some sections, a narrow band of microfibrils were seen, which appear continuous with the girdle connecting the palmate microtriches (Fig. 5B).

Filamentous microtriches

Abundant filamentous microtriches are present, approximately 5–6 µm long and 0.1 µm wide at the base. The numerous microtriches borne on the tops of the

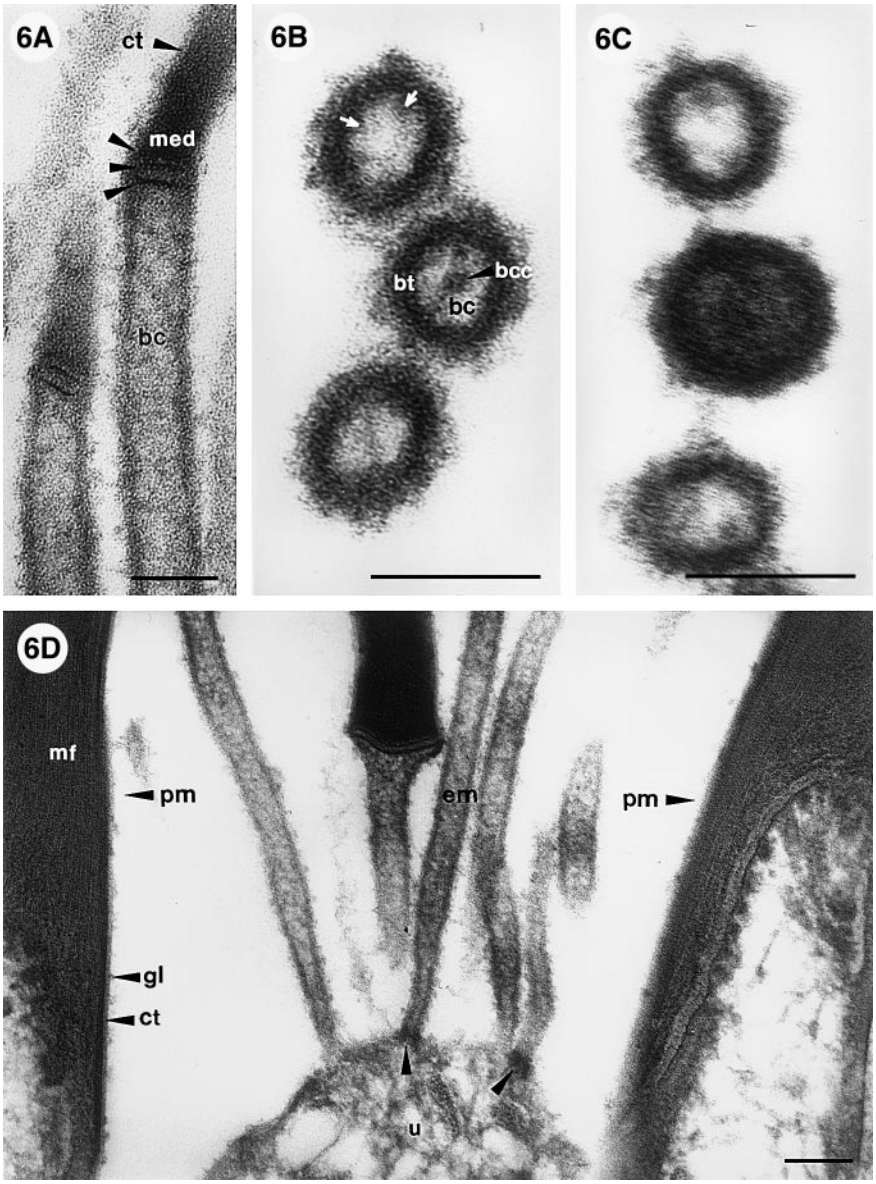


Fig. 6A–D *B. sphyraenaicum*, transmission electron micrographs of microtriches. **A** Longitudinal section through filamentous microtriches showing the electron-dense medulla (*med*) surrounded by a less dense cortex (*ct*). Circular components appear in the junction region (arrowheads). The base has an electron-lucent core (*bc*) (*bar* 0.1 µm). **B** Transverse section of three bases showing the electron-lucent core (*bc*). Circular electron-dense areas can be seen at the core/tunic interface (*white arrows*). An electron-dense centre (*bcc*) is linked to the tunic (*bar* 0.1 µm). **C** Transverse section of three bases, the middle one of which is electron opaque (*bar* 0.1 µm). **D** Longitudinal section, with a pair of palmate microtriches (*pm*) with microfilaments (*mf*), outer cortex (*ct*) and glycocalyx (*gl*). The equalised filamentous microtriches (*em*) on the undulation (*u*) insert with an electron-dense zone (arrow-head). Note the unusual microtriche with a wider cap than base (*bar* 0.2 µm)

undulations beneath the palmate microtriches (Fig. 3) were equalized (see above). In contrast, the microtriches at the apex of the papillae (Figs. 3, 7A–D) were cap dominated. The outer surface of the filamentous microtriches is interpreted as a glycocalyx.

The caps of the filamentous microtriches have a homogenous electron-dense medulla, surrounded by a less dense cortex (Figs. 6A, 7A, B). The junction region between the cap and the base usually appears bilaminate (Fig. 7B); however, in some section planes, three lamellae are seen, each consisting of a single row of circular components (Fig. 6A), each of which is 7 nm in diameter. The base of the filamentous microtriches has an electron-lucent core, surrounded by a cylindrical electron-dense core tunic (Fig. 6A–C). Some transverse sections of the bases showed an electron-dense centre, linked to the tunic, and also circular electron-dense areas at the core/tunic interface (Fig. 6B). Rare transverse sections of the base showed it to be electron opaque (Fig. 6C). The insertion of the filamentous microtriches into the distal cytoplasm was marked by dark zones and root-like extensions (Figs. 6D, 7B).

Putative sensory receptors

Sensory receptors are borne on papillae formed of the distal cytoplasm, extending nearly to the distal end of the palmate microtriches (Figs. 3, 7A). The papillae are covered with cap-dominated filamentous microtriches (see above), thus resembling a haystack. The sensory receptors at the apex of the papillae comprise a bulb, from which emerges a structure, 0.2–0.3 µm in diameter, resembling a cilium (Fig. 7A, D). This contains parallel longitudinal structures, thought to be microtubules (we were not able to confirm this having just a single worm

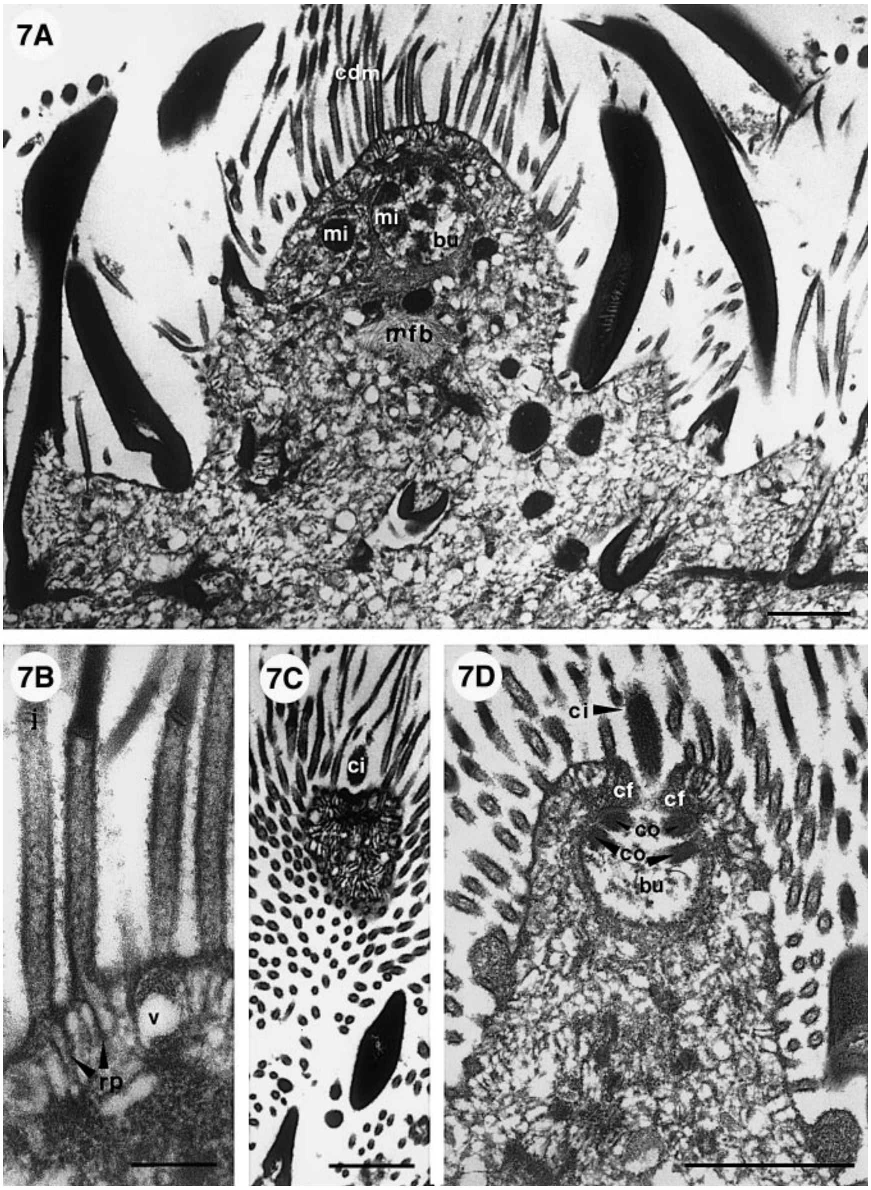


Fig. 7A–D *B. sphyraenaicum*, transmission electron micrographs of the sensory receptor. **A** Longitudinal section through a papilla with cap-dominated filamentous microtriches (*cdm*). It comprises a bulb (*bu*) with mitochondria (*mi*). The distal cytoplasm of the papilla is the same as that in the remainder of the tegument, including microfibrils (*mfb*) and mitochondria. Enlargement of part of Fig. 3 (*bar* 10 μm). **B** Longitudinal section of the interface of the cap-dominated filamentous microtriches and the papilla. Note the root-like projections (*rp*) extending into the distal cytoplasm. Note the vacuole-like structure (*v*) partly filled with electron-dense material and the bilaminate junction region (*j*) of the filamentous microtriches. Enlargement of part of Fig. 7A (*bar* 0.2 μm). **C** Oblique section of the apex of a sensory receptor showing the "cilium" (*ci*) and the crystalline appearance of the membranous cytoplasm (*bar* 1.0 μm). **D** Longitudinal section of the bulb (*bu*). Note the cuff (*cf*) surrounding the cilium (*ci*) and the two electron-dense collars (*co*). Homogenous vesicles are present on both sides of the papilla (*bar* 1.0 μm)

for the transmission electron microscopy study). Before entering the bulb, the "cilium", passed through an electron-dense cuff (Fig. 7D), at the base of which is a circular desmosome, connecting it with the bulb. Within the anterior part of the bulb, there are two similar-sized electron-dense collars, 0.1 μm wide (Fig. 7D). The bulb contains several mitochondria (Fig. 7A), the christae of which were visible at higher magnification. The posterior part of the bulb was seen to taper and pass into the tegumental cytoplasm.

The cytoplasm of the papillae is similar to that in the remainder of the tegument, including its covering with filamentous microtriches and the presence of microfibrils and mitochondria. Interestingly, electron-dense material like that of the cuff surrounds the bulb (Fig. 7A). Additionally, the cytoplasm at the apex of the papillae is densely membranous, giving it a somewhat crystalline appearance in some sections (Fig. 7B, C).

Subtegumental tissues and other structures

Beneath the distal cytoplasm lay the numerous microfibrils comprising the lamina reticularis, the interface being a series of undulations and interdigitations (Fig. 3). The majority of the tegumental mitochondria are found at this interface. Beneath this are the transverse muscles, and below this, numerous bundles of longitudinal muscles. The nuclei lie deep in the subtegument, some 30 μm beneath the surface of the distal cytoplasm. The highly vacuolated tissue indicates the suboptimal fixation and storage method resulting in the loss of some cytoplasm, inclusions and secretory material, as well as the absence of neuronal structures.

Occasionally, a slightly different kind of microtriche is visible (Fig. 6D). This has a similar base to that of the above-described filamentous microtriches; however, the cap and the junction region are much wider.

In some sections of the papillae, vesicles are present between the bases of the filamentous microtriches (Fig. 7D). Their contents are homogenous, and more electron dense and granular than the distal cytoplasm. Vacuole-like structures partly filled with a similar electron-dense material are evident on the periphery of the distal cytoplasm (see Fig. 7B).

Discussion

B. sphyraenaicum has a highly active bothridial tegument as demonstrated by the presence of amorphous secretions, originating from vacuole-like structures lying just beneath the surface. Lumsden (1966) reported certain vesicles in the cuticular matrix of the strobila of the trypanorhynch *Lacistorhynchus tenuis* and Featherston (1972) demonstrated similar secretions originating from between the microtriches of the gravid proglottids of *T. hydatigena*. For another trypanorhynch, possible secretory structures have been demonstrated before by Palm (1995), who reported pore fields on the tentacle surface of *Pseudolacistorhynchus noodti*.

Palmate microtriches

Palmate microtriches have been described from several other trypanorhynch species (Palm 1995), where they most often occur on the bothridial surfaces. The first transmission electron microscopical study of the bothridial tegument of *Otobothrium insigne* was carried out by Hildreth and Lumsden (1987). The authors described two types of microtriche on the pars bothridialis, type 1 with a similar ultrastructure to that we describe for the seven- to eight-fingered microtriches of *B. sphyraenaicum*. Palm (1995) reported three-fingered palmate microtriches from the bothridial surface of *O. insigne*, which most probably correspond to those studied by Hildreth and Lumsden (1987). It seems as if the number of digitiform processes of trypanorhynch palmate microtriches do not influence their general architecture, which is supported by the fact that the number of processes can vary at a single place on the bothridia (Palm 1995).

We suggest that the palmate microtriches (their robust nature conferred by the densely packed microfilaments) of *B. sphyraenaicum* covering the bothridial surface serve for anchoring and traction as the worm penetrates the host tissues. Their bases are joined by connections, forming a series of girdles that pass transversely around the worm. Thus, the palmate microtriches might be coordinated, a prerequisite for their possible use as an anchoring and/or traction mechanism. As the girdles must be able to vary in circumference to accommodate the contraction and relaxation of the worm, we expect them to be made of contractile proteins, such as actin or paramyosin. Such muscle proteins are known from other platyhelminth teguments (Matsumoto et al. 1988). The posterior orientation of the palmate microtriches would allow unimpeded forward movement of the worm, thus assisting efficient penetration. The role of microtriches in anchoring and traction has been proposed previously, for example for spatulate microtriches by Berger and Mettrick (1971), and for the spine-like tips (caps) of filamentous microtriches (Rothman 1963). Palm (1997a) recently described a similar function for the hooklet microtriches on the bothridia of the trypanorhynch *Nybelinia edwinlintoni*, a worm which has no palmate microtriches. However, none of these authors mentioned internal supporting structures (such as the connections presented here) that could provide the coordination necessary for an effective mechanical function.

The morphology and movement mechanisms of a diversity of other invertebrate groups show striking similarities to the palmate microtriche system of *B. sphyraenaicum*. In the outer cortex of ciliated protozoa, the basal kinetosomes of the locomotory cilia are subtended by microtubular ribbons and fibrils, which can overlap to form a variety of complex networks (Lynn and Corliss 1991); an assemblage known as the infraciliature. Although the role of the microtubular networks of ciliates is debated, Sleigh and Silvester (1983) proposed that they provide an anchor for the cilium locomotor unit – a similar role to that which we now propose for the connections in *B. sphyraenaicum*. The cuticle of the nematodes *Ctenascarophis* and *Gnathostoma* is ornamented with distinctive palmate structures, and that of *Spinitectus* bears transverse denticulate rings (Anderson 1992; Chaubaud 1975; Zaman 1983). The presence of a complete digestive tract in these round worms eliminates the need for cuticular absorption and digestion; one may therefore infer that these cuticular ornamentations serve another role, the most obvious of which is to provide increased anchoring and traction.

It is interesting to note that the ultrastructure of the base of the palmate microtriches of *B. sphyraenaicum* is very similar to that of the blade-like, giant blade-like, peg-like and spine-like microtriches described from the scolex and immature proglottids of adult *Proteocephalus tidswelli* (Proteocephalidea) by Thompson et al. (1980). Of particular note is the possession by both species of a substantial matrix in the base, and the deep insertion of the bases into the distal cytoplasm, as can be seen on Figs. 3 and 4B. Thompson et al. (1980) suggest that the blade-like microtriches of *P. tidswelli* might have an ancillary mechanical function, serving as "spacers" between the absorptive surfaces of the parasite and the host.

Filamentous microtriches

Filamentous microtriches have been earlier reported from trypanorhynch cestodes: they can occur on the whole scolex surface (Palm 1995) as well as on the strobilar integument (Lumsden 1966). In contrast to the palmate microtriches, the ultrastructure of the microtriche type 2 reported by Hildreth and Lumsden (1987) from the bothridial surface of *O. insigne* differs to those described in the present study with its small distal cap. However, the authors found differences in basal and cap lengths of small filamentous microtriches on the pars proliferans, most having a long base and small dense tip, microtriches with a short base and long dense cap being much less common. This finding is similar to the cap-dominated and equalized filamentous microtriches on the bothridia of *B. sphyraenaicum*.

The bases of the equalized filamentous microtriches on the undulations and the cap-dominated filamentous microtriches on the papillae are proposed to serve for nutrition. Evidence for this is the extended base continuous with the distal cytoplasm, and the root-like extensions into it. A highly increased surface area, given by the undulations of the distal cytoplasm and the papillae, increases the nutritional surface. Such a nutritional function of microtriches has been widely reported, for example by MacKinnon and Burt (1983), Lumsden (1975a, b) and Lumsden and Hildreth (1983).

In addition to the nutritive function of the cap-dominated filamentous microtriches of *B. sphyraenaicum*, we propose that they also serve to support a possible mechanoreceptor function of the sensory receptors. Their long electron-dense caps, which partly extend above the tips of the palmate microtriches, might serve to transmit mechanical stimulations to the "cilium", extending from the bulb at the apex of each papilla. Such a mechanoreceptor function has not previously been attributed to filamentous microtriches. Interestingly, Braten (1968) has previously suggested that the caps of filamentous microtriches may have a different function from the bases, and Rothman (1963) and Hayunga (1991) proposed that the caps of filamentous microtriches of *Hymenolepis diminuta* (Cyclophyllidea) and *Hunterella nodulosa* (Caryophyllidea) serve for anchoring, and the bases for nutrient absorption.

Although filamentous microtriches are considered prototypical, being the commonest and simplest variant (Holy and Oaks 1986), their functions may be more complex than their simple morphology might indicate. Having such diverse functions as nutrition (absorption and digestion), anchoring and mechanoreception would explain morphological differences in filamentous microtriches, such as different proportions of cap to base length, that have been described by many authors. Other authors have reported dimorphic filamentous microtriches on different regions of various cestodes (MacKinnon and Burt 1983; Thompson et al. 1980). In our case, the two kinds of filamentous microtriches are adjacent in a single place on the bothridia.

Putative sensory receptors

Although the roles of some of the cestode tegumentary structures have been established, their functional specialisation for sensory reception is not well understood. Recently, Halton et al. (1994) and Crangle et al. (1995) identified a rich bothridial innervation of the trypanorhynch *Grillotia erinaceus*, a prerequisite for sensory reception by the bothridial surface. Halton et al. (1994) reported nerve endings at the bothridial margins, where uniciliated structures reminiscent of sense organs could be seen by scanning electron microscopy. This suggested that the associated serotonin-immunoreactive innervation in that region may be sensory in nature. However, though several putative sense organs have been described in flatworms, their real sensory nature has not yet been established. Experimental and behavioural studies are still lacking.

For the first time within trypanorhynch cestodes, regularly arranged and microtriche-adorned papillae on the bothridial surface bearing sensory-receptor-like structures are reported. Their morphology corresponds to that of numerous papillae with associated sensilla which were detected on the scolex of the anoplocephalid *Monoecocestus americanus* by Blair and Burt (1976). Interestingly, in some papillae the authors found more than a single sensory organ as well as a microtubule arrangement of either 9 + 9 or 9 + 10 in the cilium emerging from the bulb. The sensory-receptor-like structures are similar to the ciliated sensory mechanoreceptors described for flatworms by other authors. Uniciliated sensory receptors, proposed to be for tactile reception, have been reported from *Hymenolepis microstoma*, Cyclophyllidea, by Webb and Davey (1974) and *Bothriocephalus scorpii*, Pseudophyllidea, by Jones (1975). They are also known from other platyhelminth groups, such as monogeneans and aspidogastreans (Rohde 1993). "Peg organs" were reported from the monogenean *Acanthocotyle lobianchi*, where a cilium is surrounded by a cone of epidermis which projects beyond the general body surface, the enclosed cilium projecting beyond this (Lyons 1973). The author attributed a mechanoreceptor function to these organs, which were numerous on the whole body, similar to the high number of sensory papillae on the bothridia of *B. sphyraenaicum* and on the scolex of *M. americanus* (Blair and Burt 1976). It is interesting to note that Okino and Hatsushika (1994) detected non-ciliated receptors within numerous microtriche-adorned papillae around the genital atrium of *Spirometra erinacei* (Cestoda: Pseudophyllidea), to which they attributed an important role as sensory receptors in the orientation of cross-insemination.

Although the function of any sensilla in platyhelminths, in the absence of physiological data, is speculation, the functions may be inferred by comparison with sensory structures of known function from other animals, as done by Webb and Davey (1974). In the case of *B. sphyraenaicum*, the elevated location of the putative sensory receptors on the papillae, with the cap-dominated filamentous microtriches and possibly also the "cilium" protruding above the level of the palmate microtriches, supports a mechanoreceptor function, receiving stimuli unhindered by the palmate microtriches. This exposed position in *B. sphyraenaicum* is similar to that of the sensilla reported by Blair and Burt (1976), the long filamentous sensory processes by Hess and Guggenheim (1977) and the uniciliated structures by Halton et al. (1994), but contrasts with the protected position of the tactile sensory endings in *H. microstoma* and in *Raillietina cesticillus* as reported by Webb and Davey (1974) and Blitz and Smyth (1973). Microfilaments in the cytoplasm of the papillae, however, indicate that the "cilium" position can be varied. It might receive direct stimulation and/or it might receive stimulation from adjacent cap-dominated filamentous microtriches (see above), the latter thus acting as transducers (Webb and Davey 1974). In this case, an enlarged surface area receptive to stimulation provided by the filamentous microtriches might increase the sensitivity. Stimulus direction might be detected due to differences in activation of numerous receptors covering the whole bothridial surface. This would explain their abundance and regular arrangement.

Within the trypanorhynchs, sensory structures have been reported around the genital atrium of *L. tenuis* by Pintner (1932), and as "Sinnesbläschen" at the bothridial margins of *F. saccatus* as well as "nervöse Endapparate" (pear shaped and elevated above the surface) from the surface of its blastocyst (Pintner 1903). Another bothridial structure thought to have a sensory function is the "ciliated pit" (sensory fossette), a mostly U-shaped structure on the bothridial borders (restricted to the superfamily Otobothrioidea sensu Palm 1995). These ciliated pits can be evaginated, extending beyond the plane of palmate microtriches covering the bothridial surface (Palm et al. 1993). Their position on the bothridial borders resembles that of the uniciliated structures shown by Halton et al. (1994). We suggest therefore that the ciliated pits and the sensory receptors on the tegumental papillae might perform a similar mechanoreceptor function. However, the functional morphology of these organs still warrants examination (Palm 1997b).

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