

themselves and the repercussion of human intervention on the coast and its near-shore morphology.

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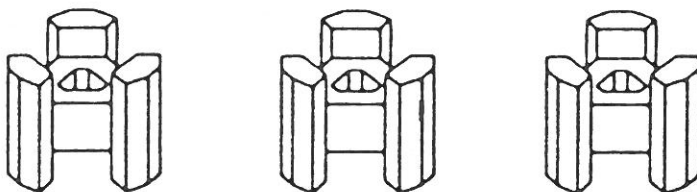
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## Anatomy and ultrastructure of the proboscis in *Mesorhynchus terminostylis* (Platyhelminthes, Rhabdocoela)

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**Key words:** ultrastructure, anatomy, Turbellaria, proboscis, epithelia

### Abstract

The ultrastructural organization of the proboscis in *Mesorhynchus terminostylis* is distinctly different from that in other members of the Polycystididae in which it is currently classified. The sheath epithelium is formed by three belts, all with intra-epithelial nuclei. The apical belt of the bipartite cone epithelium has a single intrabulbar nucleus, and the basal belt possesses five insunk nucleiferous cell parts behind the bulb. Six types of glands surface through the epithelia; the three types emerging through the cone epithelium can be homologized with those described for *Polycystis naegeli*. Only unciliary receptors are found in the epithelium. The musculature in the bulb has a very loose appearance, and the bulbar septum appears to be a bipartite basement membrane. The septum can be considered the basement membrane of the cone epithelium as if the contractile portion of the inner longitudinal muscles have invaded the epithelium and come to lie between the epithelial cells and the basement membrane. Thus the inner musculature of the bulb is entirely intraepithelial as is the case for *Psammorhynchus tubulipenis* and *Cytocystis clitellatus*. The systematic position of *M. terminostylis* remains uncertain but seems to lie between *Psammorhynchus* and *Cytocystis* on one hand and Koinocystididae and Polycystididae on the other.

### Introduction

The families of Eukalyptorhynchia were erected by Karling (1964, 1980), Schilke (1969), Brunet (1973), and Rieger & Sterrer (1975). The monotypic genus *Mesorhynchus* was created by Karling (1956) and assigned to the family Polycystididae because its genital structures are of the divisa type, typical for the Polycystididae. However, Karling (1956) pointed out that unlike other members of the Polycystididae, *Mesorhynchus* lacks four pharyngeal knobs (sclerotizations); also the presence of a large intrabulbar nucleus in

its proboscis is not typical of the Polycystididae. The systematic position of *Mesorhynchus* thus remains uncertain.

Ultrastructural studies of a variety of proboscises in the Eukalyptorhynchia have revealed discrete and apparently systematically significant differences in the organization of their epithelia, gland necks, sensory cells, and musculature (De Vocht, 1989, 1990; De Vocht & Schockaert, 1988). In order to obtain better insight into the phylogenetic relationships of *Mesorhynchus terminostylis*, I have investigated the ultrastructure of its proboscis.

### Materials and methods

Specimens of *M. terminostylis* Karling, 1956, were collected from muddy sediment harboring *Penatula* at 40 m depth near Gåsö in front of and in the mouth (58° 15' 68" N and 11° 27' 30" E) of the Gullmarfjord (Kristineberg), Sweden, in June, 1988. Animals were extracted by either sieving the fine mud through a 100- $\mu$ m-mesh screen and washing the remaining sediment and animals into a Petri dish or using the 'Übersand' method proposed by Armonies & Hellwig (1986). After identification, animals were relaxed in  $MgCl_2$  isotonic to seawater and prepared for electron microscopy as described by De Vocht (1990). Type material of *M. terminostylis* from the Swedish Museum of Natural History was studied as well by light microscopy.

### Results

#### Epithelia

Epithelia of the proboscis of *M. terminostylis* comprised five circumferential belts in the specimens studied (Fig. 1). As in all previously investigated species of the Eukalyptorhynchia (see Schockaert & Bedini, 1977; De Vocht & Schockaert, 1988; De Vocht, 1989, 1990) two of these belts constituted the cone epithelium (i.e., this epithelium is bipartite). The remaining three belts formed the sheath epithelium as in Polycystididae and Cystioplanidae. These three belts were cellular. The basal belt of the cone epithelium was syncytial, while the apex was covered by a single cell. The proboscis epithelia were devoid of cilia, and junctions between cells included an apical-most zonula adhaerens (300 nm deep) and a more basal septate junction and maculae adhaerentes.

The distal belt of the sheath epithelium ( $S_1$ ) was formed by two cells, the median ( $S_2$ ) and proximal ( $S_3$ ) belts by four cells (Figs 2, 3). At the proboscis pore, the epithelium was only 2  $\mu$ m thick, but the major part of the distal belt as well as the median and proximal belts were 5  $\mu$ m thick. The epithelial surface bore long, slender microvilli

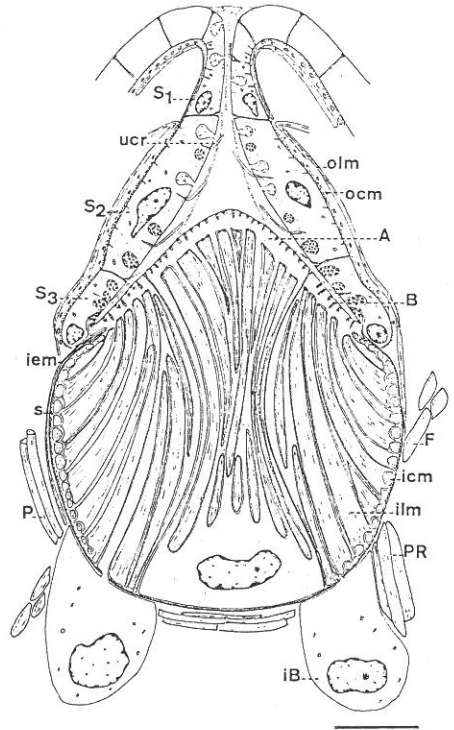


Fig. 1. Sagittal reconstruction of the proboscis of *Mesorhynchus terminostylis* from electron microscopic observations. Three cellular epithelial belts ( $S_1$ ,  $S_2$ ,  $S_3$ ) with intraepithelial nuclei form the sheath epithelium, while two belts ( $B$ ,  $A$ ) cover the cone. The syncytial basal belt has insunk nucleiferous cell parts ( $iB$ ); the nucleus of the apical cell lies inside the bulb. Gland necks and uniciliary receptors ( $ucr$ ) pierce the epithelia. Outer circular ( $ocm$ ) and longitudinal muscles ( $olm$ ) surround the sheath, and protractors ( $P$ ), fixators ( $F$ ), and retractors ( $PR$ ) insert on the bulbar septum ( $s$ ) which encloses the inner longitudinal ( $ilm$ ) and circular muscles ( $icm$ ). Intraepithelial muscles ( $iem$ ) are present only up to the juncture. Scale bar = 10  $\mu$ m.

(about 10 per linear  $\mu$ m), which were of progressively shorter length from the distal (820 nm), through the median (700 nm), to the proximal belt (500 nm). A distinct terminal web was not present, but a fine fibrillar layer was found in the apical third of these cells. The basal plasma mem-

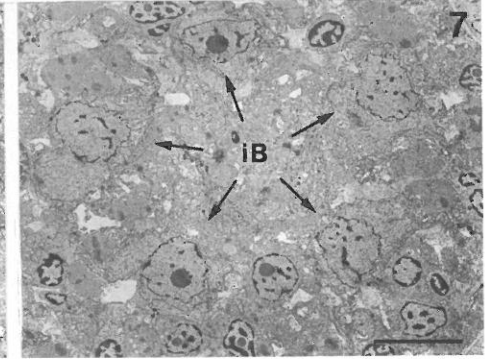
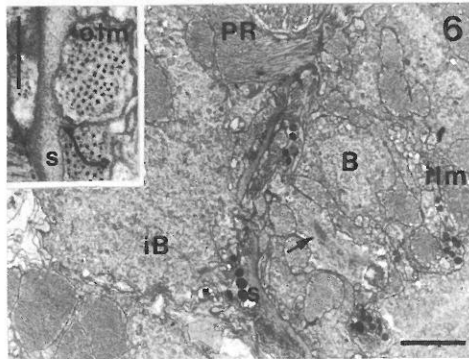
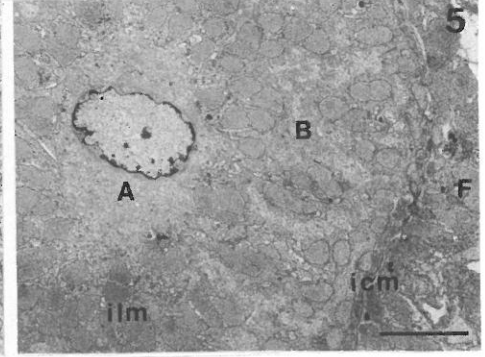
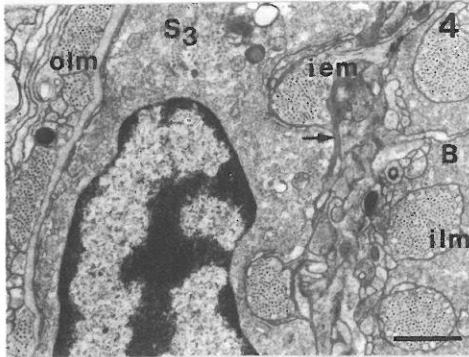
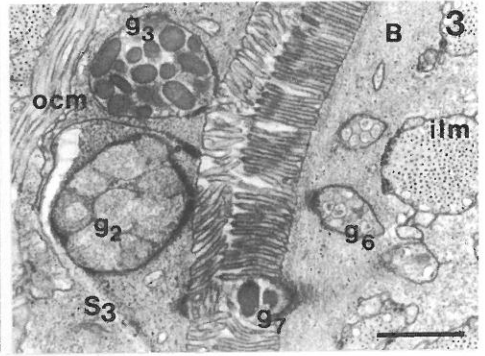
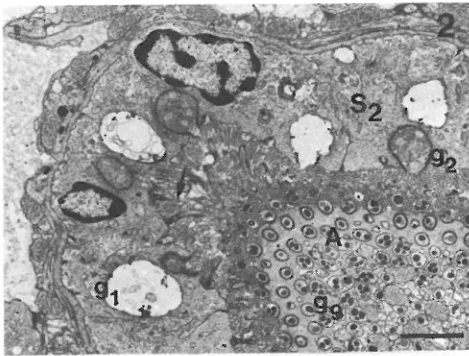
brane formed infoldings 300 to 400 nm high (Fig. 2). Mitochondria, a few Golgi apparatuses, and dense bodies were present in the granular cytoplasm. The distal and median belts had intraepithelial, bean-shaped nuclei, their ends pointing proximally (Fig. 2). The nuclei of the cells in the proximal belt were intraepithelial as well but situated just below the juncture of the sheath and the cone epithelium. The nuclei were progressively longer from the distal, over the median, to the proximal belt (7  $\mu\text{m}$ , 8.5  $\mu\text{m}$ , and 15  $\mu\text{m}$ , respectively). The underlying basement membrane was bipartite, 500–350 nm thick at the pore and around the distal belt and 350 nm down to 170 nm thick from the median belt on, and was continuous with the bipartite basement membrane of the epidermis at the pore. Below the sheath-cone juncture, the 170-nm-thick basement membrane was continuous with the bipartite bulbar septum. The posterior part of the proximal belt of the sheath epithelium was separated from the inner musculature by a thin (90 nm), electron-dense layer of extracellular matrix (Fig. 4, *arrow*) which was found around the intraepithelial muscle fibers as well (here, 10–20 nm thick). This layer was continuous with the 45-nm-thick apical layer of the septum. Where the positioning muscles, such as retractors, inserted on the septum, only a 90-nm electron-dense layer was present; this was continuous with the basal lamina of the septum (Fig. 6).

The bipartite cone epithelium was formed by a basal syncytium and one apical cell (*B* & *A* in Fig. 1). The epithelium covering the cone was 1.0–1.5  $\mu\text{m}$  high with a fibrillar apical layer and dense bodies but was devoid of cell organelles. A part of the basal syncytium lined the posterior 3  $\mu\text{m}$  of the cavity. The cone epithelium bore slender, 700-nm long microvilli; those of the basal belt had dense tips (Fig. 3). No basement membrane separated the epithelium from the inner proboscis musculature. Granular cytoplasmic cell strands with mitochondria extended among the inner longitudinal muscles in the bulb. The nucleus-bearing part of the apical cell lay in the center of the bulb; it was widest in the posterior part where the nucleus (6.5  $\mu\text{m}$  diameter) lay. A

fibrillar layer of cytoplasm surrounded the nucleus (Fig. 5). Interdigitating cytoplasmic strands of the basal cone epithelium lay all around the apical cell in the bulb. Light and dense patches were present in the cytoplasm, the dense parts mainly near the plasma membrane surrounding the muscle fibers. Bundles of microfibrils (100–150 nm thick) ran from hemidesmosomes with the bulbar septum into the cytoplasm (Fig. 6, *arrow*). Strands of the basal cone epithelium penetrated narrow perforations in the bulbar septum (Fig. 6) to connect to five insunk nucleiferous cell parts behind the bulb, two dorsolaterally, two ventrolaterally, and one ventrally (Fig. 7). Their nuclei had a large nucleolus.

#### Glands

Type  $g_1$  gland necks in the distal and median belt of the sheath epithelium lost their contents during preparation of the specimens studied and contained only patches of membranes (Fig. 2). Type  $g_2$  gland necks, with moderately dense granular secretion granules (570 nm) were situated in the median and proximal belt of the sheath epithelium (Figs. 2, 3). Often the central part of the granules appeared less dense. Type  $g_3$  gland necks, with electron-dense secretion granules up to 500 nm long and 230 nm wide (Fig. 3), were present in the posterior part of the proximal belt of the sheath epithelium together with type  $g_2$  gland necks. The basal belt of the cone epithelium was pierced by two types of gland necks. Type  $g_6$  gland necks were rather inconspicuous because their 200 nm secretion granules with low electron density but centrally condensed contents (or empty) were only stored in the apical 1  $\mu\text{m}$  of the gland necks (Fig. 3). Type  $g_7$  gland necks were more numerous and contained ovoid electron-dense (or less-dense) secretion granules (up to 700 nm long) stored in narrow necks (Fig. 3). The cell covering the apical part of the cone was pierced by type  $g_9$  gland necks which had microtubules as terminal peripheral reinforcements (Fig. 2). The spherical-to-ovoid secretion granules, 200–400 nm in diameter, were usually elec-



tron dense but less-dense secretion granules were often present as in type  $g_7$  gland necks.

### Sensory cells

Two types of unciliary receptors were present in the proboscis epithelia of *M. terminostylis*. One type was present in the sheath epithelium, most frequently encountered in the median and proximal belt (Figs 1, 2) and relatively rarely in the distal belt. The terminal ends of the dendrites were connected to the epithelium by apical zonulae adhaerentes and more proximal septate junctions. The basal body was situated in a small terminus that protruded slightly above the epithelial surface; it was connected to a long, thin primary rootlet (up to  $3.5 \mu\text{m}$  long). From the basal body, cross-striated secondary rootlets radiated obliquely to zonulae adhaerentes. Unciliary receptors with short ciliary shafts and only primary rootlets were present in the cone epithelium.

### Musculature

All muscle fibers had a peripheral sarcoplasmic reticulum; none were cross-striated.

The outer musculature of the proboscis comprised circular and longitudinal muscles surrounding the sheath and positioning muscles (i.e., protractor, retractor, and fixator muscles) mostly

inserting on the bulb. A circular muscle layer was present around the sheath epithelium from the median belt and the dilators of the sheath up to the posterior end of the proximal belt where the transition into inner circular muscles and bulbar septum lay. While no circular muscles were present around the distal belt of the sheath epithelium, more than twenty thin longitudinal muscle fibers were present here. They were situated immediately below the basement membrane and almost totally embedded in the basement membrane at the pore. From the median belt proximally, about 32 thick muscle fibers enclose the sheath. Apically the fibers were continuous with the dilators of the sheath and attached to the basement membrane; posteriorly, they were attached to the bulbar septum. They surrounded the bulb laterally together with the 34 or 35 intraepithelial muscles and about 30 thin fibers situated between the outer longitudinal and intraepithelial fibers just below the epithelium at the juncture. These muscle fibers were found from here to the posterior part of the bulb.

Three pairs of protractors inserting in a knot at the nodus, originated on the epidermal basement membrane in the anterior end. The ventrolateral pair was composed of three fibers each, the lateral pair of seven, and the dorsolateral pair of nine. More anteriorly some fibers split. Fixators inserted on the lateral side of the bulb and originated at the epidermal basement membrane. Four pairs of proboscis retractors inserted on the

Fig. 2. Cross section through median belt of sheath epithelium ( $S_2$ ) and apical cell on cone ( $A$ ). Type  $g_1$  and  $g_2$  gland necks and unciliary receptors (arrow) penetrate  $S_2$ ; type  $g_9$  gland necks and unciliary receptors penetrate  $A$ . Scale bar =  $2 \mu\text{m}$ .

Fig. 3. Cross section through proximal belt of sheath epithelium ( $S_3$ ) and basal cone epithelium ( $B$ ).  $S_3$  is surrounded by outer circular ( $ocm$ ) and outer longitudinal muscles and pierced by type  $g_2$  and  $g_3$  gland necks. Type  $g_6$  and  $g_7$  gland necks surface through  $B$  which bears long microvilli with condensations at the tips. Scale bar =  $1 \mu\text{m}$ .

Fig. 4. Cross section of nucleiferous cell parts of proximal belt of sheath epithelium ( $S_3$ ).  $B$ , intrabulbar part of basal cone epithelium;  $iem$ , intraepithelial muscles;  $ilm$ , inner longitudinal muscles;  $olm$ , outer longitudinal muscles; arrow, lipid droplets. Scale bar =  $1 \mu\text{m}$ .

Fig. 5. Cross section through posterior part of bulb with nucleiferous cell part of apical belt ( $A$ ) and peripheral strands of basal belt ( $B$ ) between inner longitudinal muscles ( $ilm$ ). Inner circular muscles ( $icm$ ) line inside of septum while fixators ( $F$ ) insert on its outer side. Scale bar =  $5 \mu\text{m}$ .

Fig. 6. Cross section through posterior part of bulb at a perforation in the septum. Scale bar =  $2 \mu\text{m}$ . Inset: septum at higher magnification showing apical electron-dense layer (left) and basal, less-dense layer. Scale bar =  $0.5 \mu\text{m}$ .  $iB$ , insunk cell part of the basal cone epithelium;  $ilm$ , inner longitudinal muscles;  $olm$ , outer longitudinal muscle;  $PR$ , insertion of a proboscis retractor.

Fig. 7. Cross section of posterior part of bulb showing the five insunk nucleiferous parts of the basal cone epithelium ( $iB$ ). Scale bar =  $10 \mu\text{m}$ .

lateroposterior part of the bulb and ran towards the posterior part of the body. Additional thin muscle fibers ran from the nodus posteriorly.

The inner musculature included circular and longitudinal muscles. The longitudinal muscles had a loose appearance in that they did not form bundles but rather extended individually through the cone epithelium, separated by strands of the cone epithelium (Fig. 5). No nuclei of the inner musculature could be found. The inner circular-muscle layer was composed of thin (700 nm) fibers that surrounded the inner longitudinal muscles from a position at the nodus almost up to the juncture. In the anterior part of the bulb, the circular muscles lay within the matrix of the bulbar septum. Anteriorly, the longitudinal muscles attached to the cone epithelium by desmosomes; posteriorly they connected to the bulbar septum by hemidesmosomes.

The intraepithelial muscles of the proboscis pierced the transition zone of sheath epithelial basement membrane and bulbar septum and entered the posterior part of the proximal belt of the sheath epithelium (Fig. 4). They adhered to the basal belt of cone epithelium just above the juncture by narrow desmosomes which connected to the apical fibrillar layer of the epithelium (Fig. 6, inset).

## Discussion

### General anatomy

Salient features of the proboscis of *M. terminostylis* are these: sheath epithelium comprising three belts, bipartite cone epithelium, loose musculature in bulb, and intrabulbar nucleus being that of apical cone epithelium. Five insunk nucleiferous cell parts of the basal cone epithelium pass through the proboscis bulb and lie behind it. The presence of three epithelial belts in the epithelium lining the proboscis cavity and a bipartite cone epithelium is characteristic also of the proboscis in *Polycystis naegelii* and in Cystiplanidae (Schockaert & Bedini, 1977; De Vocht, 1989). However, the belts are cellular, unlike the two or three syn-

cytial belts in *Po. naegelii* and Cystiplanidae; and the proximal belt has intraepithelial nuclei, more resembling the condition in many koinocystidids (Brunet, 1972; Karling *et al.*, 1972). That the cone epithelium is formed by two belts appears to be general for all Eukalypatorhynchia (see De Vocht, 1989, 1990).

### Ultrastructure

The basement membrane of the sheath epithelium of *M. terminostylis* is continuous with the bulbar septum which, by its bipartite structure, appears to be the basement membrane of the cone epithelium. By this interpretation, only the basal epithelium has insunk nuclei, and the inner longitudinal muscles are intraepithelial, perhaps originating from positioning muscles inserting on the bulbar septum. These inner muscles appear to be devoid of nuclei. Such a proboscis, with the inner bulb musculature being essentially intraepithelial, stands sharply distinct from proboscises in which the bulb musculature lies entirely below the cone epithelium. The intraepithelial bulb is known for *Psammorhynchus tubulipenis* and *Cytocystis clitellatus* as well as *M. terminostylis*; the subepithelial bulb is known for *Cicerina remanei* and *Po. naegelii*.

Microvilli in the sheath epithelium of *M. terminostylis* are longer in the distal than in the proximal belt, as is true also of Cystiplanidae (De Vocht, 1989). The microvilli in the cone epithelium are longer than in other species of Eukalypatorhynchia. *M. terminostylis* is the only species known to have longer microvilli in the cone than in the sheath epithelium (Fig. 3).

Bundles of microfibrils, like those in the intrabulbar strands of the cone epithelium in *M. terminostylis*, were encountered in the cone epithelium of *Ci. remanei* (see De Vocht & Schockaert, 1988). A syncytial belt at the base of the cone is characteristic of *Ci. remanei*, *Po. naegelii*, Cystiplanidae, *Ps. tubulipenis* and *Cy. clitellatus* (see De Vocht & Schockaert, 1988; Schockaert & Bedini, 1977; De Vocht, 1989, 1990). Only *Toia calceiformis* and *Nannorhynchides herdlaensis* are



known to have a cellular basal cone epithelium (unpublished observations). Such a syncytial basal cone epithelium is widespread in Eukalyptorhynchia. The proboscis of *M. terminostylis* can be derived from a koinocystidid type of proboscis or *vice versa* by a change between an intrabulbar and a sunken position for the nuclei of the basal-cone epithelium. Intrabulbar nuclei are known for Koinocystididae in general (Brunet, 1972; Karling, 1980), for *Ps. tubulipenis* (Karling, 1964), for *Cy. clitellatus* (Karling, 1953), for some species of Cicerinidae and Gnathorhynchidae (Meixner, 1938; Karling, 1964, 1983), and for *Lekanorhynchus remanei* Meixner, 1938, a species with uncertain taxonomic position (Meixner, 1938). Formerly, these nuclei were regarded as nuclei of muscle cells, but they are undoubtedly nuclei of the epithelium. Not only are nuclei of the cone epithelium found inside the bulb, but also nuclei of the proximal belt of the sheath epithelium (De Vocht, 1990). In the latter case, a ring of nuclei at the juncture is lacking. In Koinocystididae, such a ring is present, and all intrabulbar nuclei belong to the cone epithelium.

Relatively few types of glands pierce the proboscis epithelia. Type  $g_6$ ,  $g_7$ ,  $g_8$ , and  $g_9$  gland necks in *Po. naegeli* (see Schockaert & Bedini, 1977) are probably homologous to type  $g_2$ ,  $g_7$ ,  $g_6$ , and  $g_9$  gland necks respectively in *M. terminostylis*. Type  $g_9$  necks are typical for the apical cone epithelium in all eukalyptorhynchids; the type  $g_6$  and  $g_7$  necks in the basal cone epithelium of *M. terminostylis* are also seen in *Po. naegeli*, Cystiplanidae, and *Cy. clitellatus* as well (Schockaert & Bedini, 1977; De Vocht, 1989, 1990).

All sensory cells found in the proboscis of *M. terminostylis* are uniciliary receptors. The receptors in the sheath epithelium are homologous to those found in the sheath epithelium of Cystiplanidae, *Ps. tubulipenis*, and *Cy. clitellatus* (see De Vocht, 1989, 1990). The receptors in the cone epithelium are present in other species as well (type IV of Reuter, 1975; Schockaert & Bedini, 1977; De Vocht, 1989, 1990).

The myofibrils of the muscle fibers are loosely arranged, unlike the dense pseudostriated myofibrils of Cystiplanidae (see De Vocht, 1989).

Small intraepithelial muscles penetrating below the juncture are present in Polycystididae and Cystiplanidae as well as *M. terminostylis*; these reach anteriorly to the apical cone epithelium where they penetrate the basement membrane.

Three belts constitute the sheath epithelium in *M. terminostylis*, just as in the Polycystididae, Cystiplanidae, and Koinocystididae (Schockaert & Bedini, 1977; De Vocht, 1989). By contrast, a bipartite sheath epithelium is known for Cicerinidae, Psammorhynchidae, and Cytocystidae (see De Vocht & Schockaert, 1988; De Vocht, 1990). Concerning the organization of the cone epithelium, however, *M. terminostylis* is quite like *Ps. tubulipenis* and *Cy. clitellatus*, but the absence of insunk sensory organs excludes a close relationship.

The organization of the proboscis permits us to exclude *M. terminostylis* from the family Polycystididae although an incorporation into any other existing family is not indicated. Creating a new taxon with higher rank for *M. terminostylis* as for *Ps. tubulipenis* and *Cy. clitellatus* could be a taxonomic solution but still leaves open the question of kinship. The presence of three belts in the sheath epithelium, the absence of insunk multiciliary receptors, and the presence of intraepithelial muscles and of fixators indicate a close relationship with the families Polycystididae, Cystiplanidae, and Koinocystididae. The presence of three belts in the sheath epithelium can be used as synapomorphic character for these families combined. The bipartite organization of the cone epithelium, an organization occurring outside this group of families as well, might be considered a plesiomorphic character state or the result of parallel evolution.

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