Ultrastructure of the proboscidial papillae in some *Glycera* species (Annelida: Polychaeta: Glyceridae)

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Abstract: The ultrastructure of the proboscidial papillae in five species of *Glycera*: *G. alba*, *G. lapidum*, *G. tesselata*, *G. tridactyla*, and *G. unicornis* is described based on transmission electron microscopy. The papillae are composed of four to five cells: one anterior mucous cell, one posterior serous cell and two to three multiciliated primary sensory cells which are presumed to be mechanoreceptors. The intracellular ciliary rootlets of the sensory cells are striated filamentous structures which might serve as skeletal elements. In two species (*G. lapidum* and *G. tesselata*) papillae sometimes bear lateral groups of cilia in addition to the cilia located apically. The physiological role of the papillae is discussed.

Résumé : *Ultrastructure des papilles de la trompe chez quelques espèces de* Glycera *(Annelida: Polychaeta: Glyceridae).* L'ultrastructure des papilles de la trompe de cinq espèces de *Glycera* : *G. alba, G. lapidum, G. tesselata, G. tridactyla* et *G. unicornis* est décrite. Les papilles comprennent quatre à cinq cellules : une cellule muqueuse antérieure, une cellule séreuse postérieure et deux à trois cellules sensorielles primaires multiciliées qui sont probablement des mécanorécepteurs. Les racines ciliaires intracellulaires des cellules sensorielles sont des faisceaux de filaments striés, jouant le rôle de cytosquelette. Dans deux espèces (*G. lapidum* et *G. tesselata*) les papilles portent parfois des groupes latéraux de cils en plus des cils apicaux. Le rôle physiologique des papilles est discuté.

Keywords : Annelida, Polychaeta, Glyceridae, *Glycera*, proboscidial papillae, ultrastructure.

Introduction

The Glyceridae have a symmetrically developed axial pharynx with a strong muscular region, which is typical for the Phyllodocida (Dales, 1962). This type of pharynx is often greatly protrusible and in such cases is called a proboscis (Dales, 1962; Purschke, 1988; Saulnier-Michel, 1992). The distal armature of the proboscis consists of four jaws which are associated with venomous glands and used in prey capture (Michel, 1972b; Ockelmann & Vahl, 1970). The peripheral nervous system and its connected sense organs have often been studied, whereas only a few investigations deal with the proboscis of the glycerids (e.g. Jourdan, 1891, 1892; Gravier, 1898a, b; Wallengren, 1901; Oppenheimer, 1902; Retzius, 1902; Raphaël, 1933; Michel, 1970a; Bantz & Michel, 1971, 1972). Most of these papers contained only histological data, whereas Bantz & Michel (1971, 1972) presented the first ultrastructural and histochemical results. According to Bantz & Michel (1971, 1972) the proboscidial papillae of *Glycera convoluta*

Keferstein, 1862 (syn. *G. tridactyla* Schmarda, 1861) bear keratinized fingernail-like structures and each papilla consists of one anterior mucous cell, one posterior serous cell and a few multiciliated primary sensory cells which are presumed to be mechanoreceptors.

Jourdan (1891) already presumed that the strongly innervated proboscis has probably a sensory function. Wallengren (1901) suggested that the proboscis is composed of a complex peripheral nervous system together with some sensory cells. The investigations of Jourdan (1891), Gravier (1898b) and Oppenheimer (1902) show that eighteen longitudinal nerves are embedded in the proboscis. From these longitudinal nerves, fibres spread outwards to form the peripheral nerve plexus. Each of the longitudinal nerves is correlated directly or indirectly with the proboscidial papillae via the nerve plexus. The proboscis is innervated by the stomatogastric nervous system (Michel & DeVillez, 1978).

When the proboscis is protruded, the proboscidial sheath covers it externally and the junction of the sheath and pharynx forms the physiological mouth opening (Michel, 1970b; Purschke, 1988; Saulnier-Michel, 1992). This zone is usually characterized by larger papillae which may carry some bipolar sensory cells and numerous branched, freely terminating nerve fibres (Retzius, 1902; Bantz & Michel, 1972). Gravier (1898b) suggested that these structures are 'eye-like' organs. However, according to Stolte (1932) they are probably only mechanoreceptors, which are responsible to raise the jaws during prey capture. The rest of the proboscidial sheath is covered with numerous papillae. These proboscidial papillae appear in a variety of types based on their shape, size and morphology of their posterior sides: papillae with a terminal fingernail structure (Michel, 1970a; Bantz & Michel, 1971, 1972), digitiform papillae, conical papillae and oval to globular papillae with or without different forms of ridges (Fiege & Böggemann, 1997). For the present study the different types of proboscidial papillae of five species of *Glycera* were examined by transmission electron microscopy (TEM) in order to look for additional species-specific characters to be used as taxonomic markers. *G. tridactyla* which has been investigated by Bantz & Michel (1971, 1972) was included for comparative reasons. The results are compared with previous data and the significance of these findings for functional morphology and systematics is discussed.

Material and methods

Specimens were collected during a cruise with R/V SENCKENBERG from a station in the North Sea (54°47.95'N, 1°27.01'E; *Glycera lapidum* Quatrefages, 1866), the intertidal zone of the Atlantic (Bretagne,

Carantec; *G. tridactyla*) and the French Mediterranean coast (Banyuls-sur-Mer; *G. alba* (O.F. Müller, 1776), *G. tesselata* Grube, 1863, *G. unicornis* Savigny, 1818). They were fixed and stored in 3% glutaraldehyde in 900 mOsmol sodium-cacodylate buffer pH 7.4, then rinsed with 1200 mOsmol sodium-cacodylate buffer pH 7.4 (6x20 min). Parts of the proboscis were postfixed for two hours at 20 °C in 1% OsO_4 in the same buffer, then rinsed in buffer (4x20 min) and dehydrated via a graded ethanol series.

For TEM observations proboscidial parts were embedded in a mixture of Araldite and Epon. Series of ultrathin sections were cut with a diamond knife on a Reichert-Jung Ultracut microtome, and collected on single slot grids (mesh 2x1 mm) coated with pioloform support films (0.3% pioloform in trichlormethane). The sections were stained with uranyl acetate for 25 min at 48 °C and with lead citrate for 6 min at 20 °C in a Leica Ultrostainer, and examined with a Zeiss EM 109 TEM.

For SEM observations proboscidial parts were critical-point dried using CO_2, mounted on aluminium stubs and subsequently coated with gold-palladium. Observations were performed with a CamScan CS 24 SEM.

Results

The proboscidial papillae of the genus *Glycera* show great differences in their external morphology among species, but their cellular structure seems to be rather similar. The proboscis of each species is densely covered with one predominant type of papillae. One or two additional types are present but constitute less than 10% of the total number. These other papillae are more or less distinctly distributed in longitudinal rows. In *G. alba* and *G. tridactyla* the main type of papillae shows a terminal fingernail structure, while in *G. lapidum* and *G. tesselata* their structure is digitiform with an undulating or straight median ridge. In *G. unicornis* the corresponding papillae are conical with three ridges. It was possible to study these three main types in the species mentioned above (Figs 1-5). The additional oval to globular type as found in *G. unicornis* (Fig. 5D) was also studied. The papillae differ in length and their basal cross sections are oval to slightly triangular and vary in diameter (Fig. 1B, Table 1).

Secretory supporting cells

The external layer of the papillae consists of two different glandular supporting cells. Both cells are linked to each other (Fig. 1B-C) and are connected by means of apical zonulae adherentes followed by septate junctions (Fig. 1C) and desmosomes (Fig. 1C). The oval to globular nuclei are always located basally and contain small irregularly scattered chromatin granules (Figs 3B; 5A, D).
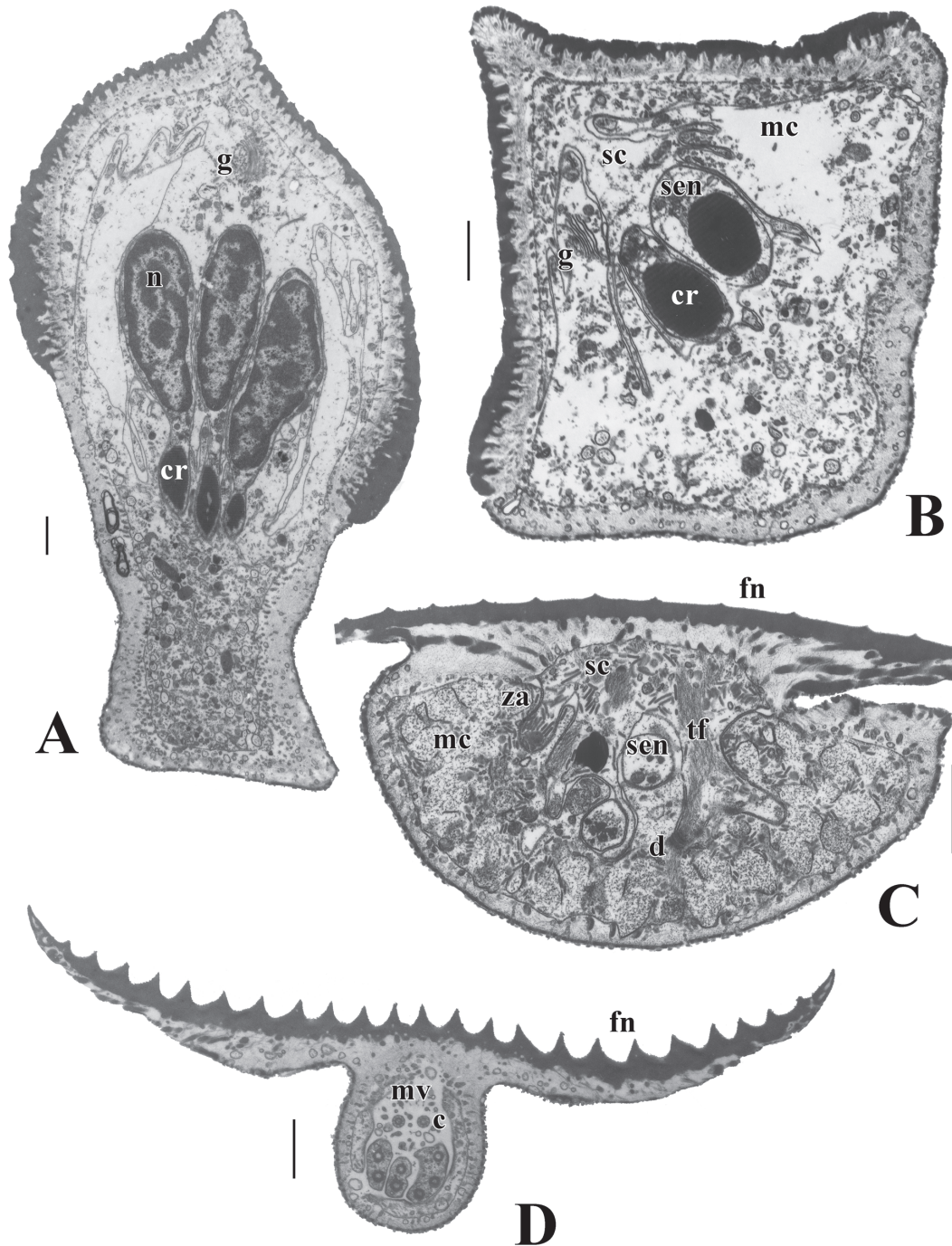
Figure 1. *Glycera alba*. **A** Longitudinal section through a fingernail papilla with three sensory cells and their ciliary rootlets. **B** Cross section in the basal part of a fingernail papilla with two sensory cells and their ciliary rootlets. **C** Cross section through the basal part of the terminal fingernail. **D** Cross section through the distal part of the terminal fingernail. (*c*) cilium; (*cr*) ciliary rootlet; (*d*) desmosome; (*fn*) fingernail; (*g*) Golgi apparatus; (*mc*) mucous cell; (*mv*) microvillus; (*n*) nucleus; (*sc*) serous cell; (*sen*) sensory cell; (*tf*) tonofilaments; (*za*) zonula adherens. Scale: A-D: 1 µm.

Figure 1. *Glycera alba*. **A** coupe longitudinale d'une papille à onglet avec trois cellules sensorielles et leurs racines ciliaires. **B** coupe transversale de la partie basale d'une papille à onglet avec deux cellules sensorielles et leur racines ciliaires. **C** coupe transversale de la partie basale de l'onglet terminal. **D** coupe transversale de la partie distale de l'onglet terminal. (*c*) cil ; (*cr*) racine ciliaire ; (*d*) desmosome ; (*fn*) onglet ; (*g*) appareil de Golgi ; (*mc*) cellule muqueuse ; (*mv*) microvillosités ; (*n*) noyau ; (*sc*) cellule séreuse; (*sen*) cellule sensorielle ; (*tf*) tonofilaments ; (*za*) zonula adherens. Echelles : A-D : 1 µm.
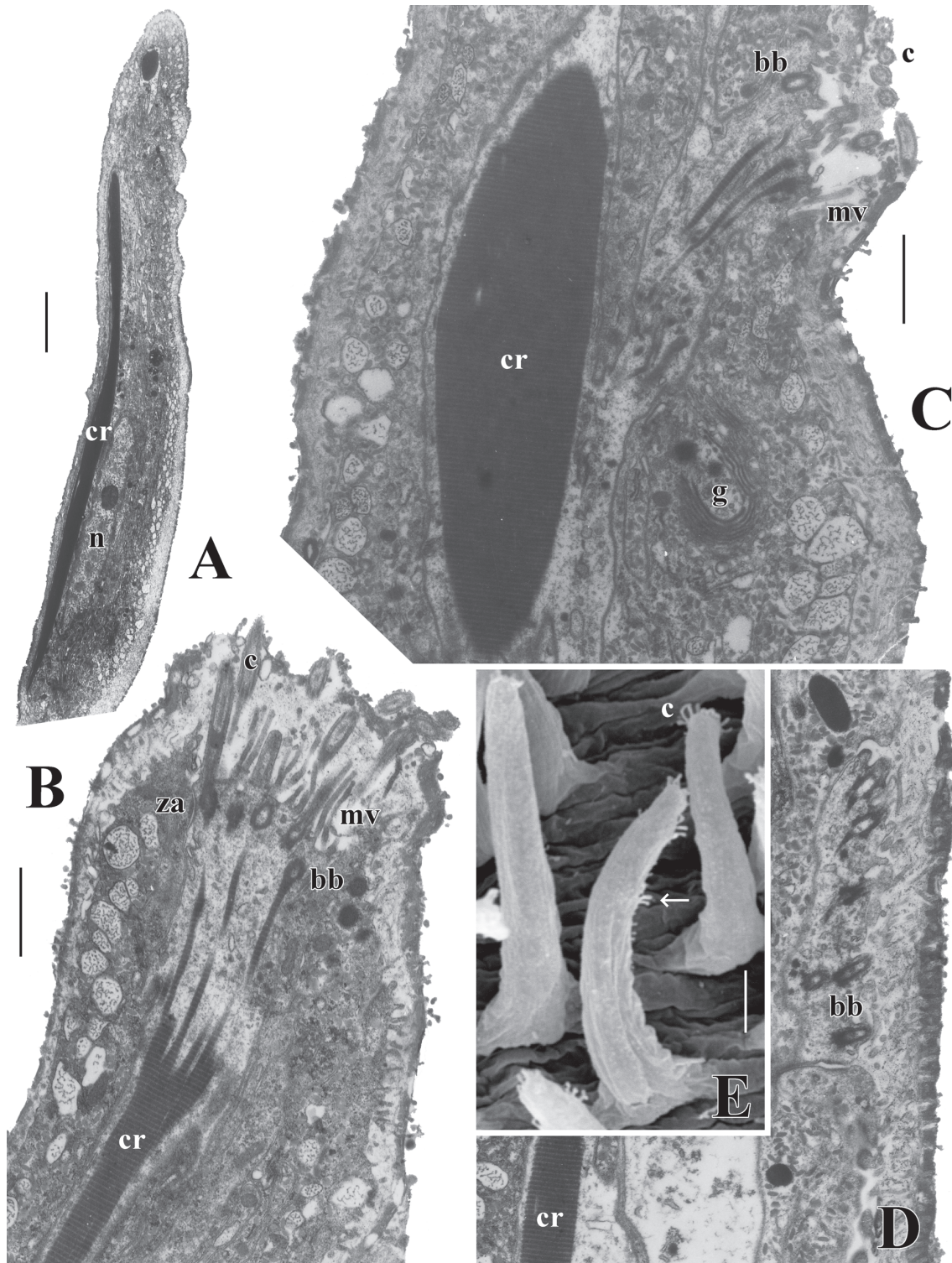
Figure 2. *Glycera lapidum*. **A** Longitudinal section through a digitiform papilla. **B** Apical part of a papilla. **C-D** Middle part of a papilla with lateral groups of cilia. **E** SEM figure of a papilla with lateral groups of cilia (*arrow*). (*bb*) basal body; (*c*) cilium; (*cr*) ciliary rootlet; (*g*) Golgi apparatus; (*mv*) microvillus; (*n*) nucleus; (*za*) zonula adherens. Scale: A, E: 5 μm; B-D: 1 μm.

Figure 2. *Glycera lapidum*. **A** coupe longitudinale d'une papille digitiforme. **B** partie apicale d'une papille. **C-D** partie moyenne d'une papille avec groupe latéral de cils. **E** vue au MEB d'une papille avec des groupes latéraux de cils (*flèche*). (*bb*) corpuscule basal ; (*c*) cil ; (*cr*) racine ciliaire ; (*g*) appareil de Golgi ; (*mv*) microvillosité ; (*n*) noyau ; (*za*) zonula adherens. Echelles : A, E : 5 μm ; B-D : 1 μm.
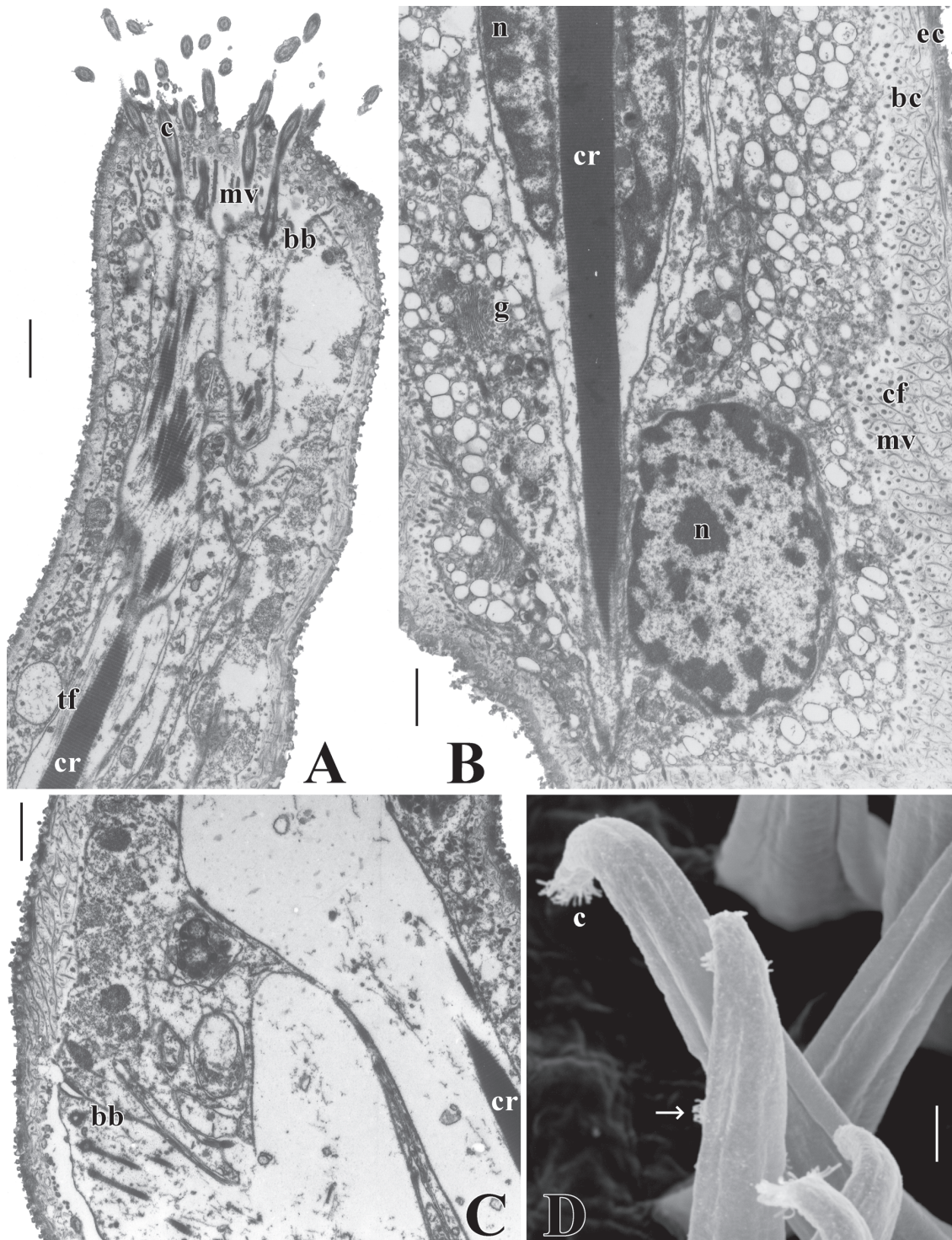
Figure 3. *Glycera tesselata*. **A** Apical part of a digitiform papilla with sensory cells cut at different levels. **B** Basal part of a papilla. **C** Middle part of a papilla with lateral groups of cilia. **D** SEM figure of a papilla with lateral groups of cilia (*arrow*). (*bb*) basal body; (*bc*) basal cuticle; (*c*) cilium; (*cf*) collagen fibres; (*cr*) ciliary rootlet; (*ec*) epicuticle; (*g*) Golgi apparatus; (*mv*) microvillus; (*n*) nucleus; (*tf*) tonofilaments. Scale: A-C: 1 µm, D: 5 µm.

Figure 3. *Glycera tesselata*. **A** partie apicale d'une papille digitiforme avec des cellules sensorielles coupées à différents niveaux. **B** : partie basale d'une papille. **C** partie moyenne d'une papille avec des groupes latéraux de cils. **D** vue au MEB d'une papille avec des groupes latéraux de cils (*flèche*). (*bb*) corpuscule basal ; (*bc*) cuticule basale ; (*c*) cil ; (*cf*) fibres de collagène ; (*cr*) racine ciliaire ; (*ec*) épicuticule ; (*g*) appareil de Golgi ; (*mv*) microvillosité ; (*n*) noyau; (*tf*) tonofilaments. Echelles : A-C : 1 µm, D : 5 µm.
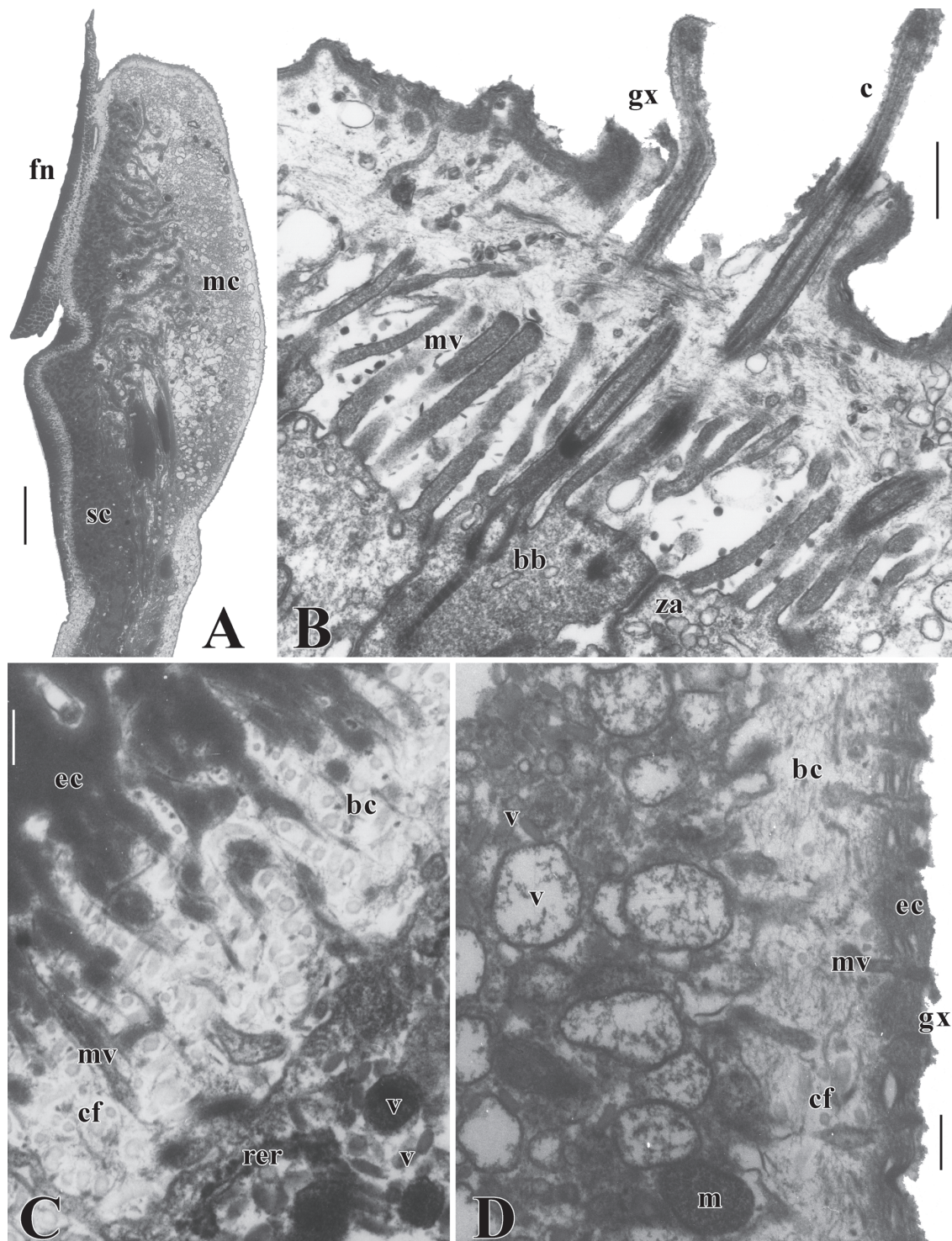
Figure 4. *Glycera tridactyla*. **A** Longitudinal section through a fingernail papilla. **B** Tip of a papilla. **C** Peripheral part of the posterior serous cell. **D** Peripheral part of the anterior mucous cell. (*bb*) basal body; (*bc*) basal cuticle; (*c*) cilium; (*cf*) collagen fibres; (*ec*) epicuticle; (*fn*) fingernail; (*gx*) glycocalix; (*m*) mitochondrion; (*mc*) mucous cell; (*mv*) microvillus; (*rer*) rough endoplasmic reticulum; (*sc*) serous cell; (*v*) vesicle; (*za*) zonula adherens. Scale: A: 5 μm, B: 0.5 μm, C-D: 0.2 μm.

Figure 4. *Glycera tridactyla*. **A** coupe longitudinale d'une papille à onglet. **B** sommet d'une papille. **C** partie périphérique d'une cellule séreuse postérieure. **D** partie périphérique d'une cellule muqueuse antérieure. (*bb*) corpuscule basal ; (*bc*) cuticule basale ; (*c*) cil ; (*cf*) fibres de collagène ; (*ec*) épicuticule ; (*fn*) onglet ; (*gx*) glycocalix ; (*m*) mitochondrie ; (*mc*) cellule muqueuse ; (*mv*) microvillosité ; (*rer*) réticulum endoplasmique rugueux ; (*sc*) cellule séreuse ; (*v*) vésicule; (*za*) zonula adherens. Echelles : A : 5 μm, B : 0.5 μm, C-D : 0.2 μm.
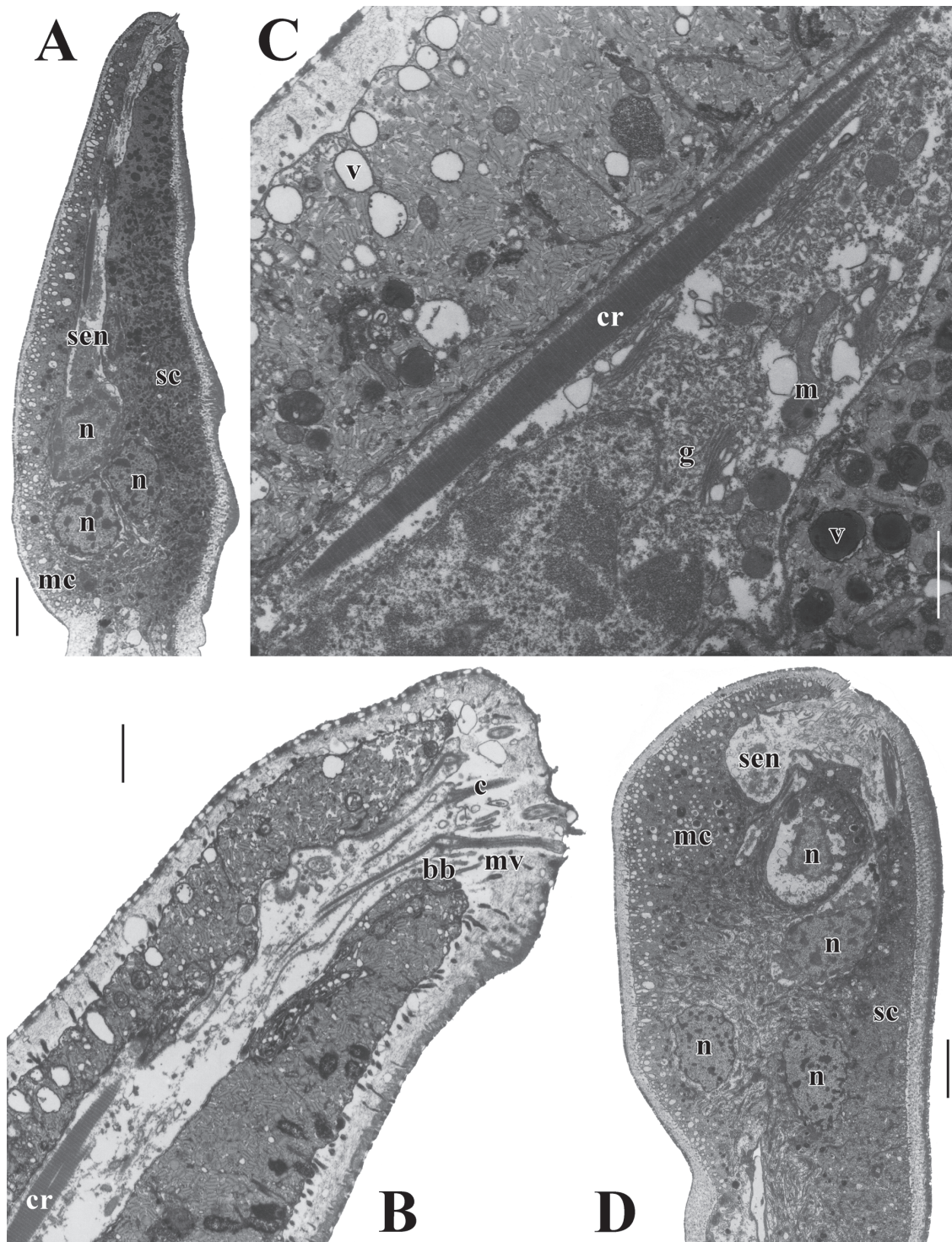
Figure 5. *Glycera unicornis*. **A** Longitudinal section through a conical papilla. **B** Tip of a main type papilla. **C** Middle part of a main type papilla with ciliary rootlet. **D** Longitudinal section through an oval to globular papilla. (*bb*) basal body; (*c*) cilium; (*cr*) ciliary rootlet; (*g*) Golgi apparatus; (*m*) mitochondrion; (*mc*) mucous cell; (*mv*) microvillus; (*n*) nucleus; (*sc*) serous cell; (*sen*) sensory cell; (*v*) vesicle. Scale: A, D: 5 µm; B-C: 1 µm.

Figure 5. *Glycera unicornis*. **A** coupe longitudinale d'une papille du type le plus fréquent. **B** partie moyenne d'une papille de type fréquent. **C** partie moyenne d'une papille de type fréquent avec racines ciliaires. **D** coupe longitudinale d'une papille de type ovale. (*bb*) corpuscule basal ; (*c*) cil ; (*cr*) racines ciliaires ; (*g*) appareil de Golgi ; (*m*) mitochondrie ; (*mc*) cellule muqueuse ; (*mv*) microvillosité ; (*n*) noyau ; (*sc*) cellule séreuse ; (*sen*) cellule sensorielle ; (*v*) vésicule. Echelles : A, D : 5 µm ; B-C : 1 µm.

The anterior mucus cell (Figs 1B; 4A, D; 5A, D) is covered on its external side by a thin cuticle and the posterior serous cell (Figs 1B; 4A, C; 5A, D; see Bantz & Michel (1971) for histochemical characterization of supporting cells) by a significantly thicker cuticle (Table 1).

The posterior cells of *G. alba* and *G. tridactyla* produce an additional fingernail-like structure on their distal part (Figs 1C-D, 4A).

The basal cuticle of both cells consists of a net of collagen fibres, which is best developed above the posterior cell (Figs 3B, 4C-D). This is covered by an epicuticle which, in the posterior serous cell, sometimes comprises a relatively thick electron-dense layer (*G. alba*: 0.2-0.5 µm, Fig. 1A-B; *G. tridactyla*: 0.3-1.2 µm, Fig. 4A, C; *G. unicornis*: 0.5-1.0 µm, Fig. 5A). Microvilli penetrate the whole cuticle, their tips protruding the surface (Figs 2B-D, 3A-C, 4D). With the exception of those regions of the posterior serous cells bearing the thick electron-dense layers, these microvilli mostly carry a well-developed glycocalix (Fig. 4D).

The cytoplasm of both cells is heavily stained and contains some scattered organelles (Figs 1B, 2C, 3B, 4C-D) in addition to numerous electron-dense granules, vesicles, and bundles of tonofilaments, some of which can be followed from the basal lamina terminating in desmosomes or in apical hemidesmosomes (Fig. 1C). The vesicles of the two cells show great differences (Figs 4A, C-D; 5A-D). In the anterior mucous cell the vesicles (ca. 0.2-0.5 µm in diameter) contain more or less electron-lucent material, whereas the vesicles of the posterior serous cell (0.15-0.35 µm in diameter) contain electron-dense substances. Besides these larger vesicles, both cells are filled with numerous smaller, rod-like vesicles (0.1-0.2 µm long, 20-40 nm wide; Figs 4C-D, 5B-C).

Sensory cells

Surrounded by the two secretory cells, two to three sensory cells are axially located (Figs 1B-C, 5A). The species with longer, thinner papillae (*G. alba*, *G. lapidum*, *G. tesselata*) usually possess three sensory cells whereas those species with shorter, thicker papillae (*G. tridactyla* and *G. unicornis*), commonly have two sensory cells in each papilla. The sensory cells are connected apically with each other and with the secretory supporting cells by zonulae adherentes followed by septate junctions (Figs 2B, 4B). The nuclei of the sensory cells are located more distally than those of the secretory cells (Figs 3B; 5A, D). These are more elongated and their form is ellipsoidal or spindle-shaped and sometimes surround a prominent ciliary rootlet (Fig. 3B). The nuclei are less electron-dense than the more basally located nuclei of the secretory cells; however, the heavily stained chromatin granules are larger and more numerous. The sensory cells contain electron-lucent cytoplasm with

only a few scattered organelles (Fig. 5C), some bundles of tonofilaments (Fig. 3A), and a few vesicles (Fig. 5C).

A conspicuous electron-dense structure in each sensory cell is the ciliary rootlet, extending longitudinally through the whole cell (Fig. 2A). The rootled is connected with the cell membrane by tonofilaments (Fig. 3A). It is oval to globular in cross-section (0.5-2.5 µm in diameter) and takes up most of the cell body (Fig. 1B). The ciliary rootlet comprises a large bundle of filaments and shows the characteristic striation pattern (period 55-61 nm), consisting of electron-dense and electron-lucent bands of similar length (Figs 2B-D, 3A-C, 5C). Basally the ciliary rootlet splits up into smaller bundles ending blindly (Fig. 3B). At the apical end, the ciliary rootlet breaks up into a number of smaller rootlets, each ending in the basal body of a cilium (Figs 2B, 3A, 4B, 5B).

Each sensory cell gives rise to a varying number of cilia (2-8; Table 1), which always show the typical 9x2+2 microtubular pattern. The cilia penetrate the cuticle of the anterior mucous cell, projecting above the surface of the papillae, and are associated in a terminal tuft (Figs 2B, E; 3A, D; 5A-B). Their basal part is completely surrounded by the cuticle and each cilium is basally encircled by numerous short microvilli carrying a glycocalix distally (Figs 1D, 2B, 3A, 4B, 5B). In addition to the apical cilia in *G. lapidum* and *G. tesselata*, lateral groups of up to six cilia are present in certain papillae. The cilia are located in a bulge of one of the sensory cells and penetrate the posterior cuticle of the papilla (Figs 2C-D, 3C). The structure of these cilia is the same as those of the apical region. Numerous microvilli are situated between the cilia and their basal bodies are connected with ciliary rootlets. Scanning electron microscopy shows that only a few of the digitiform papillae carry such additional lateral groups of cilia (Figs 2E, 3D).

Discussion

Morphology of the papillae

The studies of Gravier (1898a) (on *G. convoluta* = syn. *G. tridactyla*), Wallengren (1901) (on *G. alba*, *G. goësii* Malmgren, 1867 = syn. *G. unicornis*), Oppenheimer (1902) (on *G. dibranchiata* Ehlers, 1868), Retzius (1902) (on *G. alba*, *G. goësii*), Stolte (1932) (on *G. unicornis*), Raphaël (1933) (on *G. convoluta*), Michel (1970a) and Bantz & Michel (1971, 1972) (on *G. convoluta*), showed that the proboscidial papillae of all species investigated are compound sensory organs, in which supporting cells are associated with receptor cells. Jourdan (1892) and Gravier (1898a) already distinguished between peripheral, epithelium-like cells and central sensory cells, carrying small nerve fibres apically, in the papillae. Stolte (1932) presumed that the epithelium-like cells might be secretory.

Table 1. Morphometric data of proboscidial papillae in *Glycera* species investigated
Tableau 1. Données morphométriques sur les papilles de la trompe chez différentes espèces de *Glycera*.

	G. alba	*G. lapidum*	*G. tesselata*	*G. tridactyla*	*G. unicornis*
Length of papillae [μm]	ca. 50	50-70	70-110	40-50	ca. 50 (main and additional type)
Diameter of basal cross-section [μm]	10-11	10-15	12-20	17-20	17-20 (main type) 21-27 (additional type)
Thickness of cuticle of anterior mucus cell [μm]	0.5-0.9	0.35-0.6	0.45-0.9	0.3-0.8	0.5-1.0 (main type) 0.6-1.2 (additional type)
Thickness of cuticle of posterior serous cell [μm]	0.9-1.5	0.4-1.6	0.9-2.2	1.4-2.6	0.9-3.0 (main type) 1.6-2.5 (additional type)
No. of cilia in sensory cells	up to 6	up to 7	up to 8	up to 5	up to 6 (main and additional type)
No. of cilia in papillae	7 to 16	12 to 16	16 to 24	7 to 13	8 to 16 (main and additional type)

Jourdan (1891) suggested that the sensory cells are connected with an opening at the tip of the papillae. Wallengren (1901) showed that the distal part of the sensory cell breaks up into a number of smaller fibres, which penetrate the cuticle, and terminate in cilia-like structures at the surface of the papillae.

Ultrastructural and histochemical investigations of the proboscidial papillae in *G. convoluta* (syn. *G. tridactyla*) showed that each papilla consists of one anterior mucous cell, one posterior serous cell and a few multiciliated primary sensory cells which are presumed to be mechanoreceptors (Bantz & Michel, 1971, 1972). Jourdan (1892) documented four sensory cells for *G. siphonostoma* (Delle Chiaje, 1822) (doubtful species either *G. fallax* Quatrefages, 1850 or *G. celtica* O'Connor, 1987) and Wallengren (1901) mentioned four to five sensory cells for *G. capitata* Ørsted, 1842. Bantz & Michel (1972) reported two to four sensory cells for *G. convoluta*.

The species presently studied show only two to three sensory cells. In all other aspects the present results confirm the previous electron microscopic investigations of Bantz & Michel (1971, 1972). Even the small rod-like vesicles, described by Bantz & Michel (1971), were found in the secretory cells of the investigated species.

Ultrastructural differences, e.g. between spermatozoa or sensory organs, were often used for distinguishing closely related species and also to reconstruct their phylogeny (Pietsch & Westheide, 1985; Westheide et al., 1991;

Purschke et al., 1995). Previous investigations have shown that the proboscidial papillae provide a reliable species-specific character when studied by scanning electron microscopy (SEM) (Fiege & Böggemann, 1997).

However this investigation has shown that the different types of proboscidial papillae (papillae with a terminal fingernail structure, digitiform papillae, conical papillae and oval to globular papillae) in the species investigated are ultrastructurally quite homogeneous. Indeed, differences of papillae in size, number of sensory cells, and various cellular components were recorded (Table 1), but no species-specific characters isolated as taxonomic markers.

Ciliary rootlet

The proboscis of the closely related Goniadidae also bears papillae, but they appear to be sclerotized (Smith et al., 1995). In the papillae of the Glyceridae however, the prominent ciliary rootlet might serve as a supporting structure, in addition to the sensory function. This assumption is supported by the fact that the shorter, thicker papillae usually possess only two sensory cells with a ciliary rootlet (*G. tridactyla*, *G. unicornis*) whilst the longer, thinner papillae possess mostly three sensory cells (*G. alba*, *G. lapidum*, *G. tesselata*).

Similar intracellular supporting structures occur rarely within the Polychaeta. They are present for example in the penis papillae of *Microphthalmus* cf. *similis* Bobretzky, 1870 (Westheide, 1979) and in the ventral pharyngeal

organs of the Protodrilidae as well as some Nerillidae and Saccocirridae (Jouin, 1978; Purschke, 1985; Purschke & Jouin, 1988), but these rods end blindly, have no connection to cilia, and serve no sensory function.

Although sensory cells with large ciliary rootlets have been described in certain species, such sensory cells appear to be unique in polychaetous Annelida and none shows the features typical for *Glycera* spp. (Bantz & Michel, 1972; for polychaete sensory structures see Storch & Schlötzer-Schrehardt, 1988 and Verger-Bocquet, 1992). For instance, in the R2 cells of the lugworm *Arenicola marina* (Linné, 1758) the ciliary rootlets of the cilia are not fused to form a single compact rod-like structure of comparable size and they are apically surrounded by an electron-dense sheath (Jouin et al., 1985).

Scanning electron microscopical observations of the hard and thickened proboscidial papillae of the goniadid *Glycinde armigera* Moore, 1911 revealed subapical, cuplike depressions on all papillae containing also tufts of cilia (Smith et al., 1995). However, nothing is known concerning the presence of ciliary rootlets similar to those occurring in *Glycera* spp. A hypothesis regarding their role as supporting structures requires further examination using TEM.

Location of cilia

The cilia in *Glycinde armigera* are short and do not project beyond the rim of the cup-like depression (Smith et al., 1995) indicating a protective function of the subapical cup. In all the *Glycera* spp. investigated, the sensory cilia always project into the surrounding medium (Bantz & Michel, 1971, 1972; Smith et al., 1995; Fiege & Böggemann, 1997).

Until now it has been supposed that the cilia penetrate the cuticle only at the tip of the papillae (Bantz & Michel, 1972). But Retzius (1902) already mentioned some sensory cells of *G. alba* and *G. goësii* (syn. *G. unicornis*), where their distal ends are more or less branched and reach the surface in different places. The illustrations given by Retzius (1902: Tafel IX; Figs 6a-c, 21-23, 25) clearly show that the laterally located groups of cilia in *G. lapidum* and in *G. tesselata* can also be found in other species, but probably only in regions without the thick electron-dense layer on the posterior cell, since it seems impossible that they can penetrate this structure.

Usually sensory cells of polychaetes are bipolar primary sensory cells (Storch & Schlötzer-Schrehardt, 1988; Verger-Bocquet, 1992), i.e. each sensory cell bears only one receptive (dendritic) process. This process is more or less distinct from the perikaryon. There are only few cases where multipolar sensory cells have been described. Since the lateral and distal groups of cilia in this paper clearly emerge from dendritic processes of one perikaryon, it is supposed that they are of the multipolar type. Outside the taxon *Glycera*, sensory cells with two dendritic processes have only been described in *Lumbrineris longifolia* Imajima & Higuchi, 1975 (Eunicida) by Hayashi & Yamane (1997). However, in this species the dendrites are monociliary.

Possible functions of proboscidial papillae

A possible function of the proboscidial papillae during prey capture might be to secure a firm grip by increasing friction (Ockelmann & Vahl, 1970). The terminal fingernail structures of some species (*G. alba*, *G. tridactyla*), which are hardened by keratine (Bantz & Michel, 1971), appear to be adaptive for this task while the proboscis is retracted. The anterior mucus cells possibly serve to envelope the prey supporting its transfer to the digestive tract and protecting the proboscis from damage. The characteristic morphology of the posterior cells may represent 'distance holders' in the retracted proboscis, which simplify the release of the mucus into the lumen.

The proboscis of the Glyceridae is also used to burrow into the sediment (Ockelmann & Vahl, 1970). During the eversion of the organ the posterior cells of the papillae come in direct contact with the sediment, and it is hypothetical that the thick, keratinized cuticle may act as a protective layer against abrasion. The mucus of the anterior cells consolidates the wall of the burrow (Ockelmann & Vahl, 1970).

Wallengren (1901) and Retzius (1902) supposed that the sensory cells are mechano- or chemoreceptors. After experiments on living specimens, Stolte (1932) presumed that they are chemoreceptors. Bantz & Michel (1972) state that they function solely as mechanoreceptors, and are used to examine the sediment with regard to composition and grain size. Another, perhaps more plausible function, might be the localization of the prey just before capture. During prey capture the proboscis everts possibly preventing the use of other sensory structures on the prostomium. The authors believe that observations on living specimens are needed to fully clarify the function of the sensory cells.

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