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Ultrastructure of the proboscidial papillae in some Goniadidae species (Annelida: "Polychaeta")

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Abstract: The ultrastructure of the papillae present at the surface of the proboscis is described in six species of Goniadidae (*Glycinde multidens*, *Goniada hexadentes*, *Goniada maculata*, *Goniada vorax*, *Goniadella bobrezkii* and *Goniadides falcigera*). Scanning electron microscopical observations demonstrated that different types of proboscidial papillae are present. However, the ultrastructural investigations showed that these sclerotized papillae are quite homogeneous and are composed of three or four cells: two secretory supporting cells and one or two multiciliated primary sensory cells, which are presumed to be mechanoreceptors. In these cells, interior skeletal elements, like the large intracellular ciliary rootlets of the glycerids, are absent. The function of the papillae is discussed.

Résumé: *Ultrastructure des papilles de la trompe chez quelques espèces de Goniadidae (Annelida : Polychaeta).* L'ultrastructure des papilles présentes à la surface de la trompe de six espèces de Goniadidae: *Glycinde multidens*, *Goniada hexadentes*, *Goniada maculata*, *Goniada vorax*, *Goniadella bobrezkii* et *Goniadides falcigera* est décrite. Des observations au microscope électronique à balayage ont montré que différents types de papilles proboscidiales étaient présentes. Toutefois, l'étude de l'ultrastructure a mis en évidence que les papilles sclérifiées sont relativement homogènes et comprennent trois ou quatre cellules: deux cellules sécrétrices et une ou deux cellules sensorielles primaires multiciliées qui sont probablement des mécanorécepteurs. Dans ces cellules, certains éléments du cytosquelette des glycéridés manquent, comme par exemple les grandes racines ciliaires intracellulaires. Le rôle fonctionnel des papilles est discuté.

Keywords: Annelida; Polychaeta; Goniadidae; Proboscidial papillae; Ultrastructure.

Introduction

Glyceriformia Fauchald, 1977, composed of Glyceridae Grube, 1850 and Goniadidae Kinberg, 1865, have a large eversible, symmetrically developed axial pharynx, or proboscis (Dales, 1962; Purschke, 1988; Tzetlin & Purschke, 2005), with a strong muscular region. The proboscidial armature of the glycerids (Fig. 1A) consists of four jaws which are associated with venomous glands (Michel, 1970; Ockelmann & Vahl, 1970; Böggemann et al., 2000; Böggemann, 2002), whereas the jaw apparatus of the goniadids (Fig. 1B1-2) comprises a ring of macro- and/or micrognaths and sometimes additional chevrons (*Goniada* Audouin & Milne Edwards, 1833; *Goniadella* Hartman, 1950 and *Progoniada* Hartman, 1965). These are

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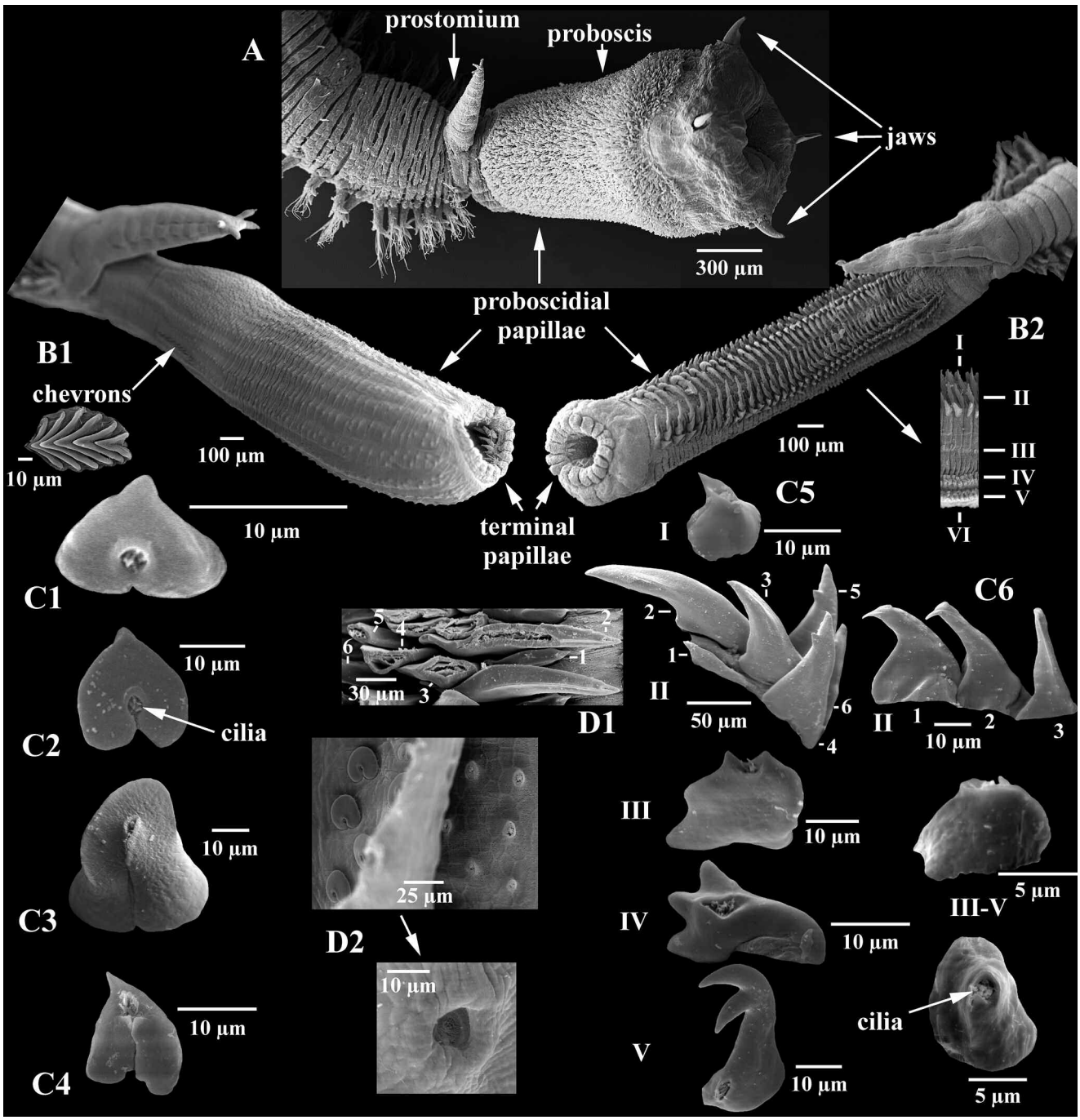


Figure 1. A. Glyceridae: Anterior end of *Glycera alba* with everted proboscis. **B1-D2.** Goniadidae. **B1.** Anterior end of *Goniada maculata* with everted proboscis and chevrons. **B2.** Anterior end of *Glycinde multidens* with everted proboscis and arrangement of area I-VI. **C1.** Proboscidial papillae of *Goniada hexadentes*; **C2.** *Goniada maculata*; **C3.** *Goniada vorax*; **C4.** *Goniadella bobrezkii*; **C5.** *Glycinde multidens* (C5 I-V: see text); **C6.** *Goniadides falcigera* (C6 II-V: see text). **D1.** Cross section through the proboscidial papillae of the latero-dorsal area II from *Glycinde*. **D2.** Proboscidial papillae of *Goniada* with (left side) or without cuticle (right side) and view under the detached cuticle (below).

Figure 1. A. Glyceridae: partie antérieure de *Glycera alba* avec la trompe sortie. **B1-D2.** Goniadidae. **B1.** Partie antérieure de *Goniada maculata* avec la trompe sortie et les chevrons. **B2.** Partie antérieure de *Glycinde multidens* avec la trompe sortie et l'arrangement de la région I-VI. **C1.** Papilles de la trompe chez *Goniada hexadentes* ; **C2.** *Goniada maculata* ; **C3.** *Goniada vorax* ; **C4.** *Goniadella bobrezkii* ; **C5.** *Glycinde multidens* (C5 I-V : voir texte) ; **C6.** *Goniadides falcigera* (C6 II-V : voir texte). **D1.** Coupe transversale des papilles de la région II chez *Glycinde*. **D2.** Papilles de la trompe chez *Goniada* avec (à gauche) ou sans cuticule (à droite) et vue sous la cuticule isolée (en bas).

v-shaped jaw elements (Fig. 1B1) arranged in two rows on either side of the proboscis with their tips facing towards the morphological mouth (Hartman, 1950; Böggemann, 2005; Tzetlin & Purschke, 2005). Furthermore, the proboscis in both groups is densely covered with numerous so called proboscidial papillae (Fig. 1A-B). These structures are of taxonomic importance as a diagnostic character, but they are usually only studied by light microscopy. However, more detailed investigations on the proboscidial papillae of Glyceridae were performed by Bantz & Michel (1971 & 1972), Böggemann et al. (2000) and Böggemann (2002), and those of Goniadidae have been analysed using scanning electron microscopy (Smith et al., 1995; Böggemann & Eibye-Jacobsen, 2002; Böggemann, 2005). For the present study the different types of proboscidial papillae of six species of the goniadids were examined by both scanning (Fig. 1) and especially transmission electron microscopy (Figs. 2-3) in order to clarify their structure and functional morphology, to look for additional species-specific characters and to allow comparison with the papillae of the closely related glycerids.

Materials and Methods

Specimens were collected during a cruise with R/V UTHÖRN from several sites: a station in the North Sea (Germany, Helgoland, 54°8.04'N, 7°57.48'E: *Goniada maculata* Örsted, 1843), the intertidal zone of the Atlantic Ocean (Brazil, Pontal do Sul: *Glycinde multidens* F. Müller, 1858; France, Bretagne, St. Efflam: *Goniadella bobrezkii* (Annenkova, 1929)), the Mediterranean Sea (France, Banyuls-sur-Mer: *Goniada hexadentes* Böggemann & Eibye-Jacobsen, 2002; *Goniada vorax* (Kinberg, 1865)), and the Indian Ocean (Seychelles, Mahé, Anse Forbans: *Goniadides falcigera* Hartmann-Schröder, 1962). They were fixed and stored in 2.5% glutardialdehyde in seawater. After dissection, parts of the proboscis were postfixed for one hour at 20°C in 1% OsO_4, then rinsed in 0.1 M phosphate buffer, and dehydrated via a graded ethanol series.

For TEM observations proboscidial parts were transferred to propylene oxide and 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 2×1 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 902 with a slow-scan digital camera.

For SEM observations proboscidial parts were critical-point dried using CO_2, mounted on aluminium stubs and subsequently coated with gold. Observations were performed with a Zeiss DSM 962 with digital camera.

Results

SEM investigations (Fig.1)

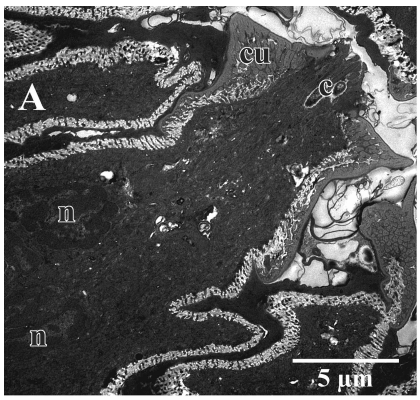
The proboscidial papillae of Goniadidae are usually provided with an exterior hard and thickened sclerotized layer (Fig. 1D1-2), which was found to include subapical, cup-like depressions containing tufts of short cilia (Fig. 1C1-6).

The proboscis of the observed *Goniada* and *Goniadella* species is densely covered with only slightly differing, more or less heart-shaped papillae of small size (Fig. 1C1-4). They are arranged irregularly or in more or less regular longitudinal rows (Fig. 1B1).

In contrast, the species of *Glycinde* F. Müller, 1858 and *Goniadides* Hartmann-Schröder, 1960 are provided with several different types of papillae (Hartman, 1950; Hubendick, 1952; Smith et al., 1995; Böggemann & Eibye-Jacobsen, 2002; Böggemann, 2005). They are arranged in distinct longitudinal rows (Fig. 1B2), and grouped into well defined areas (I to VI, dorsal to ventral; nomenclature following Hartman, 1950). Area I is single and mid-dorsal, areas II through V are paired and lie on either side of the proboscis. Area VI (the mid-ventral region) lacks papillae.

Glycinde multidens has up to three rows of small teapot-shaped papillae with laterally directed beak in area I (Fig. 1C5 I). Area II has six rows of papillae (Fig. 1C5 II) and is numbered from II-1 (dorsal) to II-6 (ventral). The tips of these papillae are mid-dorsally directed in the everted proboscis (Fig. 1B2). Area II-1 comprises short, unidentate papillae with broad base. The longer, fang-shaped papillae in areas II-2 to II-6 gradually decrease in length, with bases becoming slender and tips less curved; areas II-2 and II-3: unidentate; areas II-4 to II-6: bidentate, with decreasing distance between distal and subdistal tooth. The six longitudinal rows of papillae are always arranged in three successive transversal rows, each one with two papillae types: papillae of area II-1 together with papillae of area II-4, papillae of area II-3 together with papillae of area II-6 and papillae of area II-2 together with papillae of area II-5 (Fig. 1C5 II). Area III contains up to four rows of small, rectangular papillae with narrow base and more or less well-developed short lateral beaks (Fig. 1C5 III). Area IV is provided with one row of duckfoot-shaped papillae (Fig. 1C5 IV), and area V has one row of conical papillae with large base and curved tips, which in the median part of the proboscis are usually bifid (Fig. 1C5 V).

In contrast to *Glycinde multidens*, *Goniadides falcigera* has no papillae in area I, and instead of six rows only three rows of long, unidentate, fang-shaped papillae are present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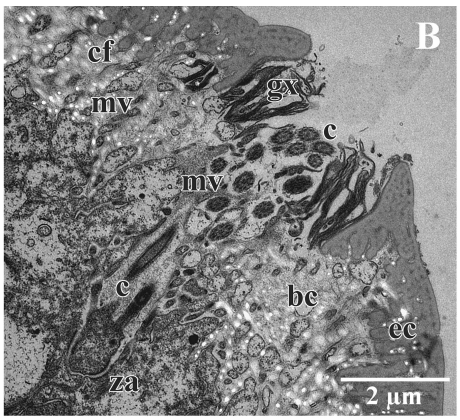
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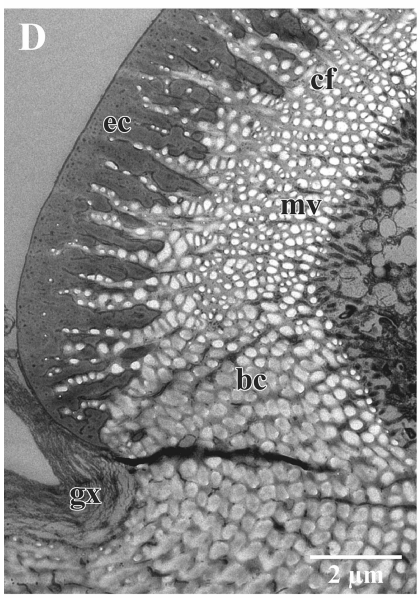
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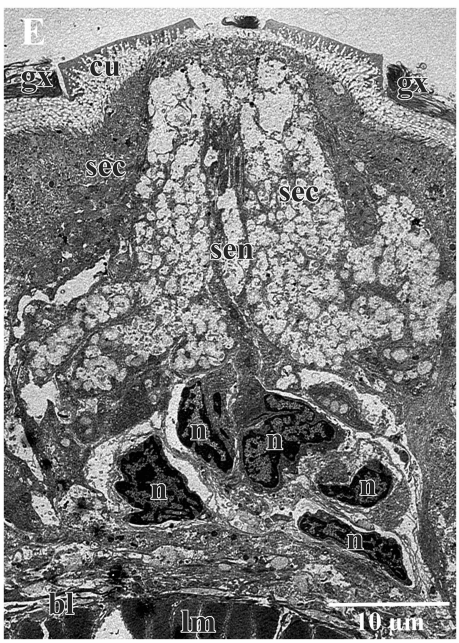
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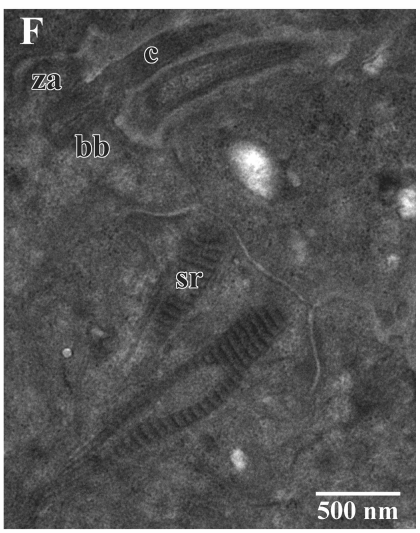
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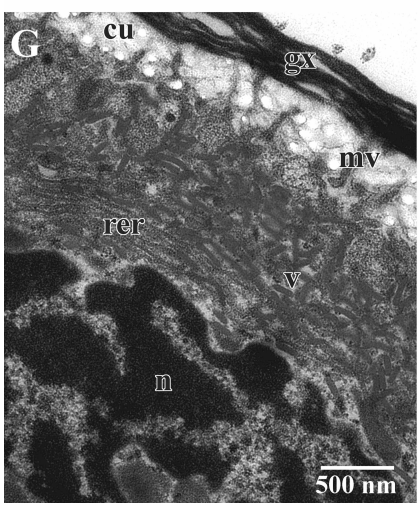
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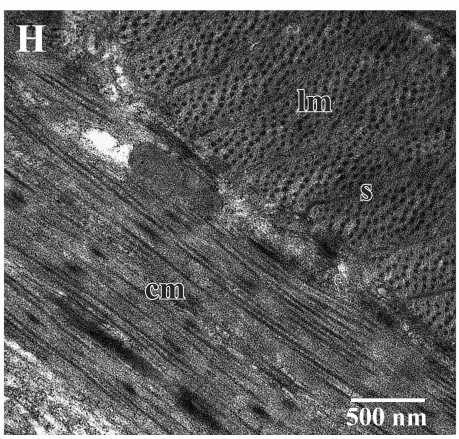
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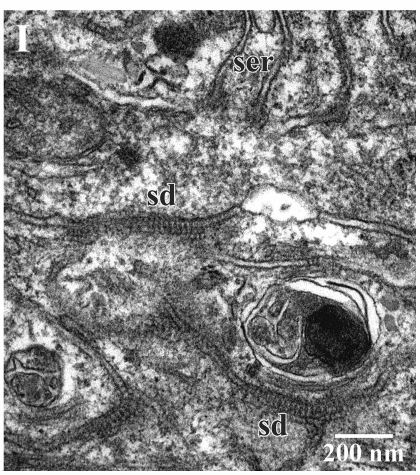
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in area II (Fig. 1C6 II), decreasing in length from II-1 to II-3 while their bases become slender and the tips less curved. Areas III through V each contain a single row of small, stout conical to globular papillae (Fig. 1C6 III-V).

TEM investigations (Figs 2-3)

The interior of the proboscis consists of a thin layer of circular muscle fibres (1.7-6.5 µm; Fig. 2H), above which lie considerably larger bundles of longitudinal muscle fibres (8-32 µm; Figs 2E, H; 3A, C1). The latter are separated by more or less extensive sarcoplasmic zones and are covered by a thin basal lamina followed by a flattened epithelium provided with oval to globular nuclei (Fig. 2G). The cytoplasm of these cells is heavily stained and contains scattered organelles (e.g. rough endoplasmic reticulum) and numerous small rod-like vesicles (0.1-0.35 µm long, 27-52 nm wide; Fig. 2G). On the exterior the proboscis is covered by a flexible collagenous cuticle (0.2-11 µm) secreted by epidermal microvilli, which penetrate the whole cuticle with their tips protruding from the surface (Fig. 2G). The microvilli are mostly enclosed in a well-developed glycocalix which is composed of numerous electron-dense lamellar layers (0.03-2.2 µm; Fig. 2D-E, G).

However, instead of a glycocalix the epicuticle of the proboscidial papillae contains a scleroprotein which is not penetrated by microvilli (Figs 2A-B, D-E; 3A-F, H-I). Beneath this relatively thick electron-dense layer (0.3-8.8 µm) usually lies a basal cuticle (up to about 5 µm) which consists of a network of collagen fibres and microvilli (Figs 2B, D; 3B, I). In the longer papillae of *Glycinde multidens* and *Goniadides falcigera* the epicuticle is much more developed than the basal cuticle, especially in their terminal parts (Fig. 3D-F). The whole cuticle of the proboscidial papillae is produced by two peripheral glandular supporting cells. These cells are linked to each other by means of apical zonulae adherentes and septate desmosomes (Fig. 2I). The oval to globular nuclei are located basally and contain small, irregularly scattered chromatin granules (Figs 2A, E; 3A). The cytoplasm of both cells is heavily stained and contains some scattered organelles (Figs 2I, 3D1-2) in addition to numerous electron-dense granules, bundles of tonofilaments, and vesicles. The numerous small rod-like vesicles very likely are present in both cells (0.1-0.27 µm long, 36-55 nm wide; Fig. 3D1, D3); in addition, one cell has rounded vesicles (0.07-0.59 µm in diameter) with electron-dense material whereas the other contains larger vesicles (0.5-1.3 µm in diameter) with more or less electron-lucent substances (Fig. 3E). The latter vesicles usually can be found in the subapical parts of the papillae.

Surrounded by the two secretory cells, one to two sensory cells are located axially (Figs 2A, E; 3D1, E). The sensory cells are connected apically with each other and with the secretory supporting cells by zonulae adherentes followed by septate desmosomes (Figs 2C, F; 3G). The nuclei of the sensory cells are located more distally than those of the secretory cells and contain stained chromatin granules (Figs 2E; 3C1). The more electron-lucent cytoplasm is filled with only a few scattered organelles, some bundles of tonofilaments, and a few vesicles (Fig. 3I). The sensory cells are connected to a funnel-shaped opening, usually located at the tip of the papillae (Figs 2A-B; 3B, C2, f, H-I). Their distal part breaks up into a number of cilia, penetrating the cuticle (Figs. 2B-C, 3G). Each sensory cell gives rise to a varying number of up to six cilia, which always show the typical 9×2+2 microtubular pattern (Figs.2B; 3E-G). The cilia are encircled by numerous microvilli bearing a glycocalix distally (Figs 2B-C; 3E-F), and their basal body is connected to a short striated rootlet which ends blindly (Figs. 2C, F; 3G, I).

Figure 2. A. *Goniadella bobrezkii*: longitudinal section through a papilla. **B-C.** *Goniada maculata*. **B.** Apical part of a papilla. **C.** Tip of a papilla. **D.** *Goniada vorax*: cuticle of a secretory cell. **E.** *Goniada maculata*: longitudinal section through a papilla. **F.** *Goniadella bobrezkii*: apical part of a sensory cell. **G-H.** *Goniada hexadentes*. **G.** Peripheral part of the proboscidial epithelium. **H.** Muscles. **I.** *Goniada maculata*: connection zone of the two secretory cells. (*bb*) basal body; (*bc*) basal cuticle; (*bl*) basal lamina; (*c*) cilium; (*cf*) collagen fibres; (*cm*) circular muscles; (*cu*) cuticle; (*ec*) epicuticle; (*gx*) glycocalix; (*lm*) longitudinal muscles; (*mv*) microvilli; (*n*) nucleus; (*rer*) rough endoplasmic reticulum; (*s*) sarcoplasmic reticulum; (*sd*) septate desmosome; (*sec*) secretory cell; (*sen*) sensory cell; (*ser*) smooth endoplasmic reticulum; (*sr*) striated rootlet; (*v*) vesicles; (*za*) zonula adherens.

Figure 2. A. *Goniadella bobrezkii* : coupe longitudinale d'une papille. **B-C.** *Goniada maculata*. **B.** Partie apicale d'une papille. **C.** Sommet d'une papille. **D.** *Goniada vorax* : cuticule au dessus d'une cellule sécrétrice. **E.** *Goniada maculata* : coupe longitudinale d'une papille. **F.** *Goniadella bobrezkii*: partie apicale d'une cellule sensorielle. **G-H.** *Goniada hexadentes*. **G.** Partie périphérique de l'épithélium de la gaine de la trompe. **H.** Muscles. **I.** *Goniada maculata* : zone de contact de deux cellules sécrétrices. (*bb*) corpuscule basal ; (*bc*) cuticule basale ; (*bl*) lame basale ; (*c*) cil ; (*cf*) fibres de collagène ; (*cm*) muscles circulaires ; (*cu*) cuticule ; (*ec*) épicuticule ; (*gx*) glycocalix ; (*lm*) muscles longitudinaux ; (*mv*) microvillosités ; (*n*) noyau ; (*rer*) réticulum endoplasmique rugueux; (*s*) réticulum sarcoplasmique ; (*sd*) desmosome septé ; (*sec*) cellule sécrétrice ; (*sen*) cellule sensorielle ; (*ser*) réticulum endoplasmique lisse ; (*sr*) racine ciliaire; (*v*) vésicules; (*za*) zonula adherens.

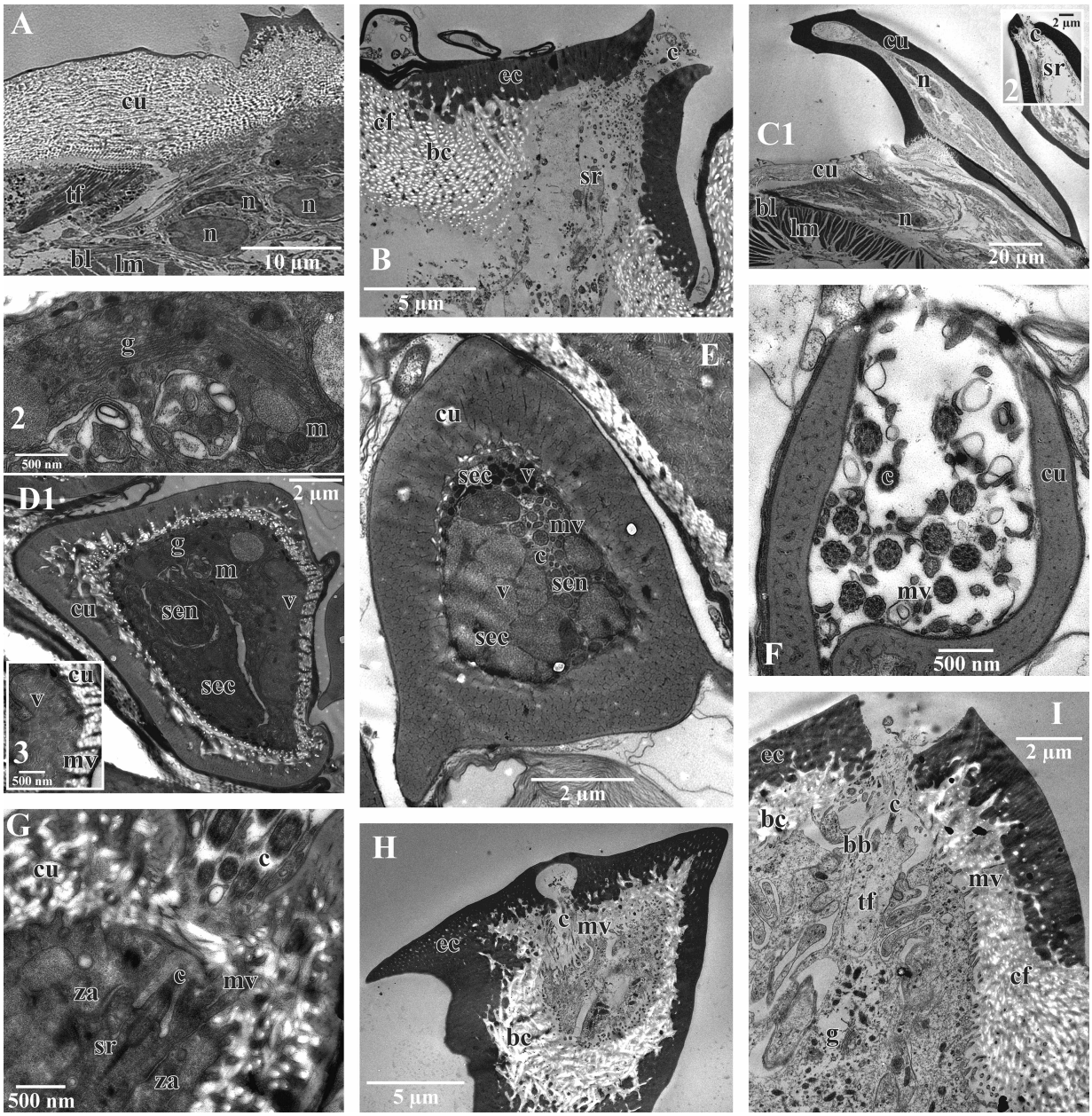

Figure 3. A-C2. *Glycinde multidens*. **A.** Longitudinal section through area I. **B.** Papilla in area I. **C1.** Longitudinal section through area II. **C2.** Apical part of a papilla in area II. **D1-G.** *Goniadides falcigera*. **D1.** Cross section through the basal part of a papilla in area II. **D2-3.** Details of the secretory cells. **E.** Cross section through the subapical part of a papilla in area II. **F.** Cross section through the apical part of a papilla in area II. **G.** Tip of a papilla in area III-V. **H-I.** *Glycinde multidens*. **H.** Longitudinal section through a papilla in area III. **I.** Cross section through the basal part of a papilla in area V. (*bb*) basal body; (*bc*) basal cuticle; (*bl*) basal lamina; (*c*) cilium; (*cf*) collagen fibres; (*cu*) cuticle; (*ec*) epicuticle; (*g*) Golgi apparatus; (*lm*) longitudinal muscles; (*m*) mitochondrion; (*mv*) microvilli; (*n*) nucleus; (*sec*) secretory cell; (*sen*) sensory cell; (*sr*) striated rootlet; (*tf*) tonofilaments; (*v*) vesicles; (*za*) zonula adherens.

Figure 3. A-C2. *Glycinde multidens* **A.** Coupe longitudinale de la région I. **B.** Papille de la région I. **C1.** Coupe longitudinale de la région II. **C2.** Partie apicale d'une papille de la région II. **D1-G.** *Goniadides falcigera*. **D1.** Coupe transversale de la partie basale d'une papille de la région II. **D2-3.** Détails des cellules sécrétrices. **E.** Coupe transversale de la partie subapicale d'une papille de la région II. **F.** Coupe transversale de la partie apicale d'une papille de la région II. **G.** Sommet d'une papille de la région III-V. **H-I.** *Glycinde multidens*. **H.** Coupe longitudinale d'une papille de la région III. **I.** Coupe transversale de la partie basale d'une papille de la région V. (*bb*) corpuscule basal ; (*bc*) cuticule basale ; (*bl*) lame basale; (*c*) cil ; (*cf*) fibres de collagène ; (*cu*) cuticule ; (*ec*) épicuticule ; (*g*) appareil de Golgi ; (*lm*) muscles longitudinaux ; (*m*) mitochondrie ; (*mv*) microvillosités ; (*n*) noyau ; (*sec*) cellule sécrétrice ; (*sen*) cellule sensorielle ; (*sr*) racine ciliaire ; (*tf*) tonofilaments ; (*v*) vésicules ; (*za*) zonula adherens.

Discussion

The terminal part of the goniadid proboscis, which forms the physiological mouth opening, is characterized by large soft papillae, each of which containing either a row of sensory cells (Retzius, 1902) or freely terminating nerve fibres (Wallengren, 1901). Stolte (1932) suggested that these terminal papillae in the similar glycerids are mechanoreceptors, which are responsible for raising the jaws during prey capture. In Goniadidae, usually a ring of eighteen terminal papillae is present, which correspond to the embedded eighteen longitudinal muscular bands and the eighteen longitudinal nerves found in the proboscis (Hartman, 1950).

From the longitudinal nerves, fibres spread outwards to form the peripheral nerve plexus which is correlated with the proboscidial papillae (Wallengren, 1901). These usually hard and thickened sclerotized structures of the Goniadidae revealed subapical, cuplike depressions on generally all papillae, containing tufts of short cilia which do not project beyond the border (Smith et al., 1995). Their recessed position could provide protection for the cilia, which would otherwise be exposed to the rigors of burrowing and food gathering (Smith et al., 1995). However, some dorso-basal, ventro-basal and a few papillae of area I sometimes lack cilia, and a small number of *Bathyglycinde* Fauchald, 1972 species have additional soft papillae with hardened terminal fingernail structures which are also present in some glycerids (Böggemann, 2005). In contrast to Glyceridae, the papillae of Goniadidae are usually orientated anteriorly with the ciliated depressions towards the physiological mouth opening; only the duckfoot-shaped papillae of area IV point in the opposite direction, and the tips of the papillae of area II are mid-dorsally directed in the everted proboscis of *Bathyglycinde*, *Glycinde* and *Goniadides* species.

The ultrastructural investigations showed that the papillae are quite homogeneous and that no species-specific characters are present. The papillae are always composed of two peripheral secretory supporting cells and one or two central multiciliated primary sensory cells, which predominantly agree with the structure of the glycerid papillae. The comparable secretory supporting cells of Glyceridae are identified by Bantz & Michel (1971 & 1972) as mucous and serous cells. The structure of these cells in Goniadidae is rather similar to those described by Bantz & Michel (1971) and Böggemann et al. (2000) for glycerids and even the small rod-like vesicles were found in the secretory cells of the investigated species. However, large ciliary rootlets similar to those occurring in the sensory cells of Glyceridae (Böggemann et al., 2000) are not present in Goniadidae. This supports the hypothesis that the prominent ciliary rootlets of the softer glycerid papillae may serve as internal skeletal elements in addition to their sensory function (Böggemann et al., 2000). Such a supportive structure seems not to be necessary in the goniadid papillae, which are usually externally sclerotized on all sides. These organs appear to be really unique for Glyceridae and, therefore, they are another good character that distinguish them from their probable sister group Goniadidae.

The proboscidial papillae probably aid in grasping and holding the prey during swallowing and might support the proboscis with traction in the initial phase of burrowing (Smith et al., 1995). Especially the dorsal radula-like papillae of area II (Grube, 1870; Hartman, 1950; Hilbig, 1994) in the *Glycinde* and *Goniadides* species appear to be adaptive for this task and might act as grappling hooks for the retracting proboscis. The ciliated sensory cells of the proboscidial papillae, which are presumed to bear mechanoreceptors, might be used to locate the prey just before capture, because during prey capture the proboscis everts and this might prevent the use of other sensory structures (like nuchal organs or ciliated prostomial appendages and depressions) on the prostomium (Böggemann et al., 2000; Böggemann, 2002). The serous cells presumably develop the external sclerotized cuticle, and the presumed mucus cells might serve to envelope the prey with secretion in order to protect the proboscis and the digestive tract from damage or stabilize the burrow system with mucus.

In summary, the different proboscidial papillae of the Goniadidae show great differences in their external morphology, but the types seem to be derived from each other and might be all evolved from small heart-shaped papillae (Böggemann, 2005). This is especially likely because the ultrastructure of all examined papillae seems to be rather similar. However, their external structure divided the Goniadidae into two groups: species with more or less heart-shaped papillae of small size (Fig. 1B1, C1-4; e.g. *Goniada*, *Goniadella*) and species with radula-like papillae (Fig. 1B2, C5-6; e.g. *Glycinde* and *Goniadides*). Furthermore, the ultrastructure of the papillae have a phylogenetic significance to separate goniadids with their sclerotized papillae from glycerids with their prominent intracellular ciliary rootlets. Therefore, the common ancestor of Glyceridae and Goniadidae was most likely provided with ciliated proboscidial papillae.

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