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Fine structure and phylogenetic significance of 'flexo-canal epidermal glands' in Chilopoda

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Abstract

In a comparative light and electron microscopic study, we examined isolated (scattered) epidermal glands, located on the head flanks of various scutigeromorph, lithobiomorph, craterostigmomorph, scolopendromorph and geophilomorph Chilopoda. We describe a distinct type of epidermal glands, named 'flexo-canal epidermal glands'. This type of epidermal gland is commonly found in all chilopod subtaxa, excluding Scutigeromorpha. The 'flexo-canal epidermal glands' exhibit a constant arrangement of one secretory cell, one intermediary secretory cell as well as one canal cell that release the secretion to the outside. Further characteristic features of 'flexo-canal epidermal glands' are: 1) their tendency to occur in small aggregations in the direct vicinity of sense organs, 2) a thin, elongated and strongly convoluted/meandering conducting canal running through the canal cell, 3) the presence of a more or less expanded central cavity surrounded by the canal cell, 4) the absence of widening areas in the reservoir (secretory cell) and basal part of the conducting canal (intermediary cell) and 5) the presence of apical loops interconnecting the intermediary cell and the secretory/canal cell. Epidermal glands of the 'flexo-canal' type are observed in many other euarthropod taxa, including Crustacea, Diplopoda and Hexapoda. It is assumed that 'flexo-canal epidermal glands' may have evolved once in the stem lineage of the Mandibulata. Their absence in Scutigeromorpha has to be considered a secondary loss and thus an apomorphy of this subtaxon.

Keywords: ultrastructure, cuticular canal, electron microscopy, canal cell, intermediary cell, secretory cell, evolutionary morphology, phylogeny, Mandibulata, Myriapoda

1. Introduction

The cuticle of centipedes (Chilopoda) is riddled with numerous pore openings that are associated with exocrine epidermal glands consisting only of a few cells. The high abundance of those small glandular organs in Chilopoda is known since the classical period of light microscopic examinations (e.g. Blower 1951, 1952). However, it was electron microscopy that unambiguously proved the glandular nature of the chilopod epidermis. For instance, scanning electron micrographs of various body regions revealed moderate or large quantities or scattered pore openings on the cuticle representing the superficially visible part of epidermal glands (e.g. Turcato et al. 1995). The cellular architecture of chilopod epidermal glands could be elucidated by transmission electron microscopy (TEM). Several types of epidermal glands have been described since then. Epidermal glands encompass the Tömösváry organ of *Lithobius forficatus* (Tichy 1973). Else, they are found on the antennae and around the basis of sensilla trichodea of *L. forficatus* (Keil 1975). Furthermore, epidermal glands were detected between the ommatidia in the compound eyes of *Scutigera coleoptrata* or within the ocellar fields of *L. forficatus* (Müller et al. 2003a, b). Additionally, they are situated in the direct vicinity of the coxal organs of various Pleurostigmophora, on the coxae of posterior trunk legs (*L. forficatus*) (Rosenberg 1985, 1994), and also frequently on the dorsal side of the head capsule (this paper). The organisation of epidermal glands is quite simple. The secretory cell releases its secretion distally into a more or less spacious extracellular cavity, the glandular reservoir, which continues into the tube-like conducting canal. This conducting canal is formed by an intermediary cell and one or several canal cell(s). The lower part of the conduced canal, formed by the intermediary cell, lacks a distinct and continuous cuticular sheath. Such cuticular lining of the conducting canal is almost only made by the canal cell(s). This cuticular sheathing of the conducting canal ends quite strictly at the level, where the (proximal) canal cell is connected to the intermediary cell. Proximal protrusions cause that the distalmost part of the apex of the intermediary cell is strengthened by a cuticle. According to the terminology recently defined by Hilken et al. (2005), three classes of epidermal glands in Chilopoda may be distinguished: 2-cell-glands (one secretory + one canal cell), 3-cell-glands (one secretory cell + one intermediary cell + one canal cell), and 4-cell-glands (one secretory cell + one intermediary cell + proximal and distal canal cell). Regarding phylogeny, the wide distribution of epidermal glands with intermediary cells let Hilken et al. (2005) argue to add such glands to the ground pattern of the Myriapoda. Among Chilopoda, epidermal glands do not always appear as isolated and loosely scattered organs. As ascertained from previous studies, epidermal glands may regularly form complex glands by aggregation, such as the epidermal maxilla-II-gland and the maxillary organ gland of *S. coleoptrata* (Hilken et al. 2003, 2005), the venom glands of *L. forficatus* (Rosenberg & Hilken 2006), or the vesicular glands of *S. coleoptrata* (Hilken & Rosenberg 2009). The glandular units of the maxilla-I gland, a salivary gland of *S. coleoptrata* show a composition comparable to the epidermal glands described above (Hilken & Rosenberg 2006a). The organisation of the glandular units, which compose the aggregated glands, is very similar to that of the isolated epidermal glands. Therefore, it has been assumed that these compound glands have derived from isolated epidermal glands (Hilken et al. 2005). Table 1 provides an overview of distribution and typology of isolated and compound epidermal glands so far identified in previous EM studies on Chilopoda. The entity of recent EM investigations on isolated or aggregated epidermal glands in Chilopoda well depicted a structural diversity

higher than to be sufficiently covered by given classification models. According to the short communications given by Müller et al. (2006, 2008), however, two different classes of epidermal glands may be distinguished by the structure of the canal cell and its conducting canal. Thus, the terms 'recto-canal epidermal glands' with a rather voluminous, untwisted (lat.: 'rectus') conducting canal and 'flexo-canal epidermal glands' with an extended, thin and heavily convoluted ('flexuous') conducting canal have been recommended to be used. The present study sets out to prove the applicability of the classification mentioned by Müller et al. (2006, 2008) with respect to 'flexo-canal epidermal glands'. In the following, the comparative fine structural organisation of 'flexo-canal epidermal glands' of Chilopoda is described including selected species of the Scutigeromorpha, Lithobiomorpha, Craterostigmomorpha, Scolopendromorpha, and Geophilomorpha. Finally, we try to give a perspective of how epidermal gland characters may contribute to the dispute about internal phylogeny of Euarthropoda recently flared up in the community of taxonomists (e.g. Edgecombe et al. 2003, Müller et al. 2003b, Pisani et al. 2004, Mallatt et al. 2004, Giribet et al. 2005, Stollewerk & Chipman 2006).

2. Materials and methods

For our studies on 'flexo-canal epidermal glands' we chose one or several species out of each chilopod subgroup. In each subgroup, we focused on adult specimens.

Scutigeromorpha

Specimens of *Scutigera coleoptrata* (Linnaeus, 1758) were found underneath stones, stone piles with spacious interstitium or rotten bark on the islands of Šipan (Croatia) and Ibiza (Spain) during different season periods of the years 2001 and 2004 to 2006.

Lithobiomorpha

Specimens of *Lithobius forficatus* (Linnaeus, 1758), *Lithobius dentatus* C. L. Koch, 1844 and *Lithobius mutabilis* L. Koch, 1862 were sampled in September 2003 in the soil of agricultural fields. Further specimens were found under rotten bark of degenerated forest trees as well as within woody litter material around Görlitz (Germany). We also studied specimens of *L. forficatus* collected under rotten tree bark in summer 2004 in a park in downtown Rostock (Germany). Specimens of *Eupolybothrus fasciatus* (Newport, 1844) were collected in June 2005 under woody litter in a forest at the eastern side of Monte Fogliano (Provinzia di Viterbo, Italy).

Craterostigmomorpha

Several specimens of *Craterostigmus tasmanianus* Pocock, 1902 were collected in August 2004 under woody litter in cool temperate rainforest near-by Wandle River (Northwestern Tasmania, 41°21'55'S 145°34'46'E, 580 m elevation).

Scolopendromorpha

Specimens of *Scolopendra cingulata* Latreille, 1789 and *Scolopendra oraniensis* H. Lucas, 1846 were caught in summer 2002 to 2004 in the immediate vicinity of Tuoro near Lago di Trasimeno (Italy) as well as on the islands of Šipan (Croatia) and Ibiza (Spain). *Cryptops hortensis* (Leach, 1815) was obtained from a compost heap in Bergheim outside of Cologne

(Germany) in September 2003 as well as under rotten leaves in summer 2004 in a park downtown Rostock (Germany).

Geophilomorpha

Strigamia crassipes (C.L. Koch, 1835) was gathered in May 2004 in a park in downtown Rostock (Germany) under woody litter, under stones and resting directly below the soil surface. *Stigmatogaster dimidiatus* (Meinert, 1870) was found underneath stones or in the soil from the upper supralittoral up to higher coastal areas characterised by Aleppo pine trees and *Juniperus* bushes in Cala Olivera (Ibiza, Spain) in March 2004 and 2005.

Following an anaesthetisation with carbon dioxide, all specimens of studied taxa were decapitated with a razor blade. Severed heads were fixed in full or split in halves along the mediosagittal plane. In *Stigmatogaster dimidiatus*, we also fixed some triplets of anterior trunk segments (15th to 20th segment). Heads and trunk segments were prefixed over night in a cold prefixative solution modified after Karnovsky (1965), containing 2 % glutaraldehyde, 2 % paraformaldehyde, 1.52 % NaOH, and 1.2 g d-glucose, dissolved in 2.25 % sodium hydrogen phosphate buffer (pH 7.4). After washing in the same buffer for six hours, the material was then postfixed for two hours in 1 % OsO_4 solution/sodium hydrogen phosphate buffer at room temperature and, following dehydration in a graded series of acetone, embedded in Araldite resin (FLUKA). With the objective of comparing identical areas of the chilopod head, we exclusively addressed the lateral flank regions of the head capsule, comprising the space posterior to the bases of the antennae, around the Tömösvary organ, around the compound eyes (Scutigeromorpha), around the ocellar fields (Lithobiomorpha, *Scolopendra* spp.) or around the single lateral ocelli (Craterostigmomorpha). Dorsally, we screened the epidermis up to the antennocellar suture. Posteriorly, we regarded those epidermal areas not distanced farther than 1 mm to the posterior margin of the compound eye/ocellar field. In blind species *Cryptops hortensis* and *Strigamia crassipes*, we investigated the entire lateral head sites because of the small dimensions of the entire head. In the trunk region of *S. dimidiatus*, we focused on the paratergal folds, where epidermal glands are particularly abundant. Serial ultrathin sections were stained with uranyl acetate and lead citrate for five minutes each and then examined under a Zeiss 902A transmission electron microscope (TEM), operated at 80 kV. A few of the TEM-images shown (see Figs 3C, 4B) were assembled with the aid of ITEM (software developed by Soft Imaging System, SIS) and consist of up to 15 single digital micrographs. For observations by scanning electron microscopy fixed head halves were critical-point dried, sputter-coated with gold, and examined at an accelerating voltage of 15–30 kV under a Zeiss DSM 960A scanning electron microscope (SEM).

3. Results

3.1. Outer morphology and general description

‘Flexo-canal epidermal glands’ are moderately or very abundant in the cephalic and trunk epidermis of lithobiomorph, craterostigmomorph, scolopendromorph and geophilomorph centipedes (Fig. 3). In contrast, there is no evidence for their existence in the scutigeromorph *Scutigera coleoptrata*. In the following, characters typical for ‘flexo-canal epidermal glands’ of Chilopoda are described in detail. Our illustrations, however, by showing these

peculiarities can only exemplify some taxa, mostly only one as the representative of a chilopod subgroup or when showing a given differentiation state of an essential component as for instance the canal cell.

The tricellular 'flexo-canal epidermal glands' consist of one secretory cell, one intermediary cell and one canal cell (Figs 2; 3A–B, D). The secretory cell is located at the basis of the gland and mainly produces the secretion that is discharged into the distally located glandular reservoir. The intermediary cell connects the secretory cell to the canal cell and also seems to contribute to the making of the secretion. The canal cell lies distally and is apposed to the cuticle. The reservoir is in continuation with the following conducting canal formed by the intermediary cell and the canal cell. The small cuticular duct of the canal cell, here termed 'conducting canal', is strongly convoluted. It passes the cuticle and finally opens on its surface. At those parts of the head or trunk segments, which provide a spacious epidermis and where musculature does not attach to the cuticle, 'flexo-canal epidermal glands' often display the form of a tear with their constituting cells being wrapped around each other. The range from the base of the secretory cell to the cuticular surface usually measures about 30 µm. With decreasing thickness of the epidermis, the gland shape may however appear much more flattened and measure only 15 µm in length. In flattened formations, 'flexo-canal epidermal glands' tend to become asymmetrical. The longitudinal axis of flattened glands then shifts about 90°, the constituting cells sit next to each other rather than lying on top of each other. The conducting canal penetrates the cuticle in an angle of approximately 45° (normally, the angle amounts to 10°).

Based on SEM examinations of the cuticular surface, 'flexo-canal epidermal glands' are recognisable by the typical appearance of their pore openings. In *Lithobius* spp. (e.g. *Lithobius dentatus*: Figs 1A, A') and *Scolopendra* spp. (*Scolopendra oranienis*: Figs 1C, C'), the pore openings are simple breakthroughs in the cuticle and not delimited by a prominent ring-like structure. The diameter of a pore opening ranges from 0.5 to 0.8 µm. In many cases, the opening is blocked by a plug which most probably represents a rest of a recent expulsion of secretion (Figs 1A', C'). In *Eupolybothrus fasciatus* (Figs 1B, D), *Cryptops hortensis* (Figs 1E, F), *Strigamia crassipes* (Fig. 1G) and *Stigmatogaster dimidiatus* (not illustrated), the pore opening is around 0.6 µm in diameter and always lined by a distinct and homogeneous ring-like wall. Both types of pores are situated in furrows between scale-like polygons. The 'flexo-canal epidermal glands' not only end in those places, where three or four polygons make contact (corner points, see Figs 1A, G), but also all along those furrows where two polygons meet (Fig. 1C). In *Lithobius* spp., *E. fasciatus* as well as the *S. crassipes* and *S. dimidiatus*, 'flexo-canal epidermal glands' stand at a considerable distance to each other. Locally, we encountered more than five polygons between pore openings identical in construction. In *Craterostigmus tasmanianus*, *C. hortensis* and *Scolopendra* spp., abundance of 'flexo-canal epidermal glands' is much higher. Frequently, there are less than five polygons between structurally identical pore openings. Generally, the abundance of epidermal glands seems to be the highest in *S. crassipes* and *S. dimidiatus*. However, the ratio between 'flexo-canal epidermal glands' and 'recto-canal epidermal glands' appears to be inverted in comparison to those ratios found in Craterostigmomorpha and Scolopendromorpha. Gland-constituting cells are directly adjoined. A surrounding sheet of epidermal cells is rarely noticed.

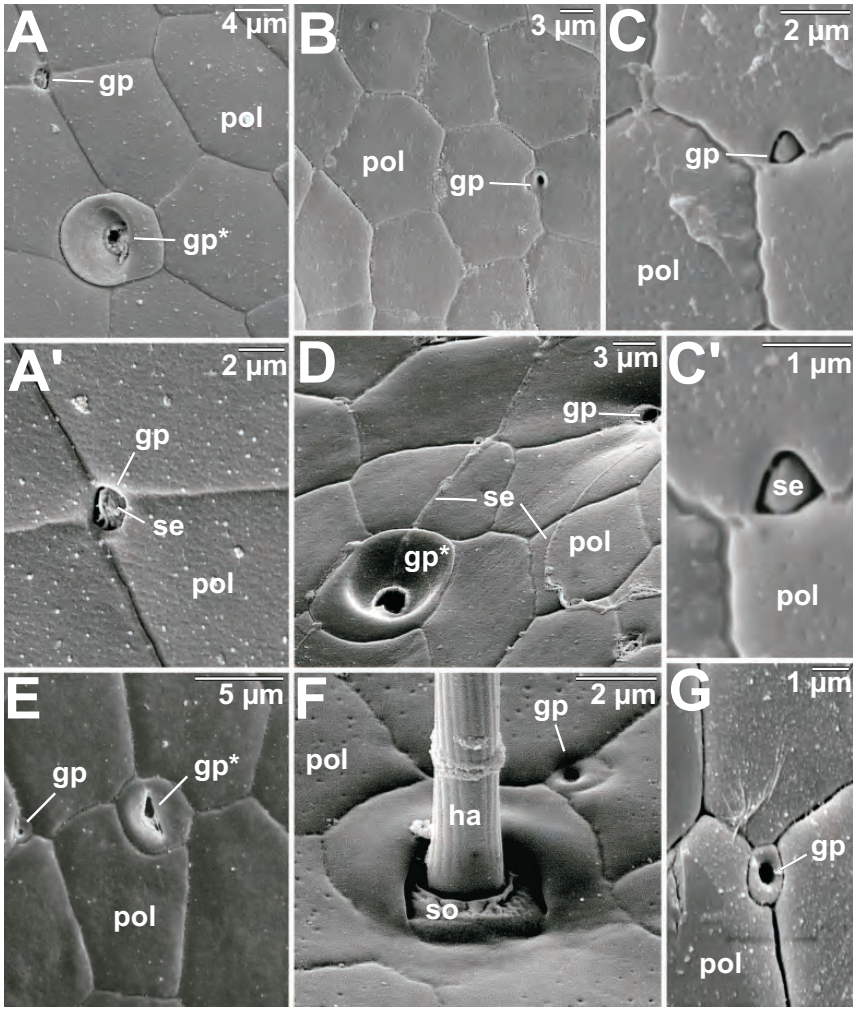


Fig. 1 A–G: SEM micrographs showing the simple, mostly breakthrough-like appearance of the pore openings of the 'flexo-canal epidermal glands' in pleurostigmophoran centipedes. The cuticle is diversified by polygonal sculpturation (*pol*). A: *Lithobius dentatus*. The pore opening is also shown in A' in a higher magnified view. A lump of secretion got stuck in the pore opening; B,D: *Eupolybothrus fasciatus*. Note the lines of secretion (*se*) lying on the cuticle putatively discharged by epidermal glands shown in D, C: *Scolopendra oraniensis*. The pore opening is shown in higher magnification in C' making visible a secretion plug in its middle; E–F: *Cryptops hortensis*. F shows a pore opening on the cuticle near the basis of a sensillum microtrichoideum; G: *Strigamia crassipes*. The images A, D and E give an impression of size differences between pores of 'flexo-canal epidermal glands' (*gp*) and 'recto-canal epidermal glands' (*gp**). *ha* hair of the sensillum microtrichoideum, *so* socket base of the sensillum microtrichoideum.

'Flexo-canal epidermal glands' principally occur as isolated organs. Occasionally, however, they show a tendency to form small aggregations, comprising up to five gland units per cluster (Fig. 4C). These aggregations are observed in the vicinity of sense organs as for instance epidermal sensilla (Fig. 1F), lateral ocelli (*Lithobius forficatus*: Müller et al. 2003a) or the Tömösvary organ (see Tichy 1973). Aggregation is accompanied by fusion of the distal, unconvoluted part of the conducting canals emitted by several canal cells. 2–5 clustered 'flexo-canal epidermal glands' thereby terminate in a single pore opening.

3.2. Fine structural organisation

3.2.1. Secretory cell

The secretory cell looks cup-shaped in spacious or sac-like in flattened regions of the epidermis (Fig. 2). Around its periphery, the secretory cell often emits small processes running distalwards and may thereby locally pierce or overlay the intermediary cell. This is especially the case in *Scolopendra* species and *Cryptops hortensis*, in which the up-running lobes of the secretory cell may completely encase the much smaller intermediary cell. Firm adhesion between the secretory cell and the intermediary cell is established by belt desmosomes (Maculae adhaerentes) between opposed apical loops. The secretory cell shows small, but clearly noticeable infoldings of the basal cell membrane that form a basal labyrinth. The electron opaque extracellular space between the infoldings appears widened (Fig. 6D). The basal matrix is only connected via tips of finger-like cytoplasmic processes. The strongly osmiophilic cytoplasm of the secretory cell is endowed with smooth and rough ER cisternae, particularly concentrated around the bottom (Figs 2, 6D). Golgi bodies, scattered and aggregated ribosomes, many polymorphous mitochondria of the cristae type and a few lysosomal bodies are found (Fig. 6D). The form of the nucleus varies from circular, elongated to U-shaped profiles. The caryoplasm contains only little amounts of heterochromatin but is often so electron dense that it barely contrasts against the cytoplasm (Fig. 3D). Most conspicuous is the dense packing of secretory granules (0.5–2.0 µm in diameter), whose inner matrices show a constant set-up but strongly differ amongst taxa examined. Simple granules filled up with a widely homogeneous, highly osmiophilic substance are observed in geophilomorph species (*Strigamia crassipes*, *Stigmatogaster dimidiatus*; see Fig. 3D). In lithobiomorph (*Lithobius* spp., *Eupolybothrus fasciatus*) and scolopendromorph (*Scolopendra* spp., *C. hortensis*) species, we spotted granules displaying a heterogeneous inner matrix. Peripheral areas of these granules are highly osmiophilic but enclose weakly or moderately osmiophilic disruptions in the centre (e.g. Figs 3C, 6C). According to their appearance, disintegrated centres of these secretory granules seem to be a result of sectioning (Figs 3A, 6C) or shrinking artefacts (Fig. 3C). In *Craterostigmus tasmanianus*, secretory granules show the largest diameters (0.5–2.0 µm in diameter) and have a spherical or bilobed outline. Their inner matrix looks very heterogeneous presenting a mosaic-like arrangement of moderate or highly electron dense inclusions. Sometimes, clustering of inclusions of equal electron density is observed (Figs 2, 3B, 6B, B''). The density and size of secretory granules grows when approaching the apical cell area. The secretory mass is discharged into a complex network of extracellular channels, called loculi. The entire apparatus of loculi is called the glandular reservoir (Fig. 6B). The walls of the glandular reservoir are always free of cuticle. To the centre, the channels converge with the common conducting canal built by the intermediary cell and the canal cell (Figs 2, 6B).

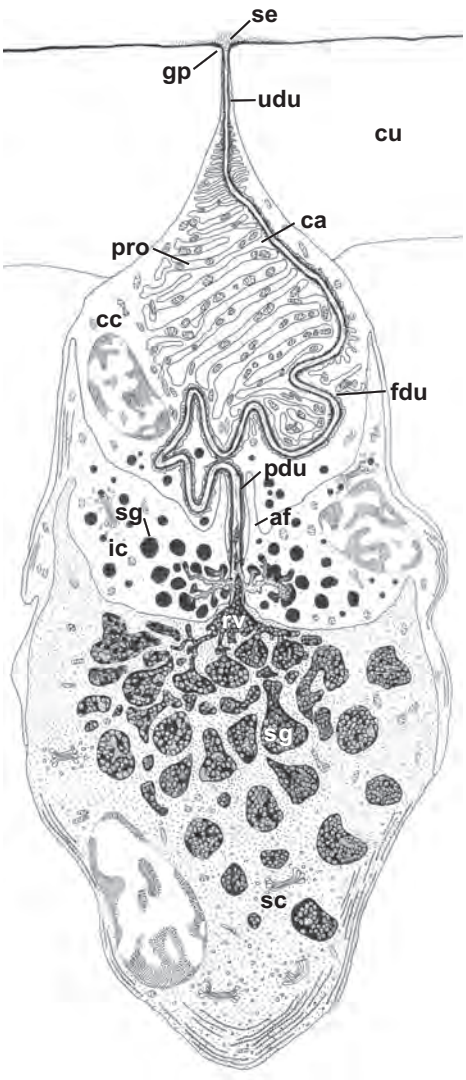
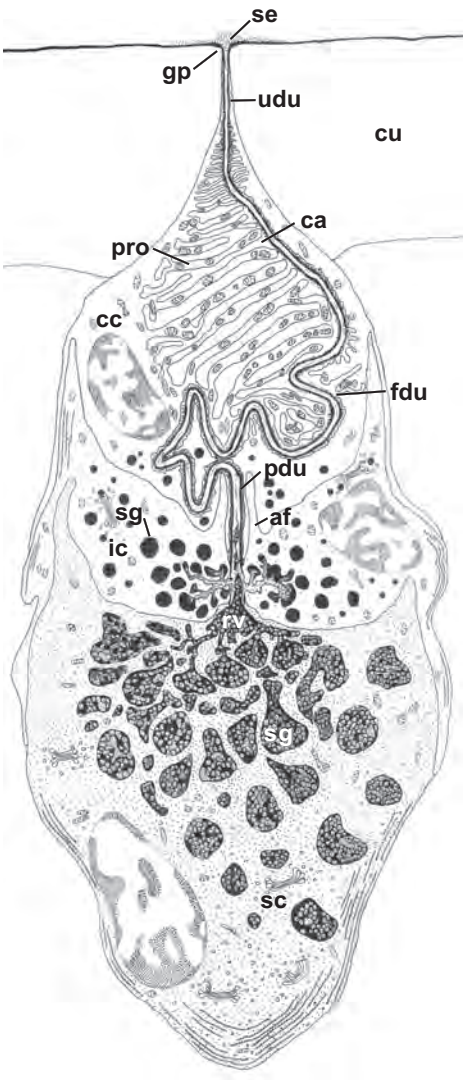


Fig. 2 Semischematic longitudinal scheme demonstrating the general organisation of a 'flexo-canal epidermal gland' in pleurostigmophoran centipedes by means of structures found in *Craterostigmus tasmanianus*. The meandering part of the conducting canal has been simplified for reason of clarity.

af apical, manchette-like projection of the intermediary cell, *ca* central cavity of the canal cell, *cc* canal cell, *cu* cuticle, *fdu* meandering (flexuous) part of the conducting canal, *gp* glandular pore, *ic* intermediary cell, *pdu* proximal part of the conducting canal, *pro* cytoplasmatic projections of the canal cell pointing into the extracellular cavity, *rv* glandular reservoir, *sc* secretory cell, *se* secretion mass, *sg* secretory granule, *udu* distal, untwisted and centred part of the conducting canal.



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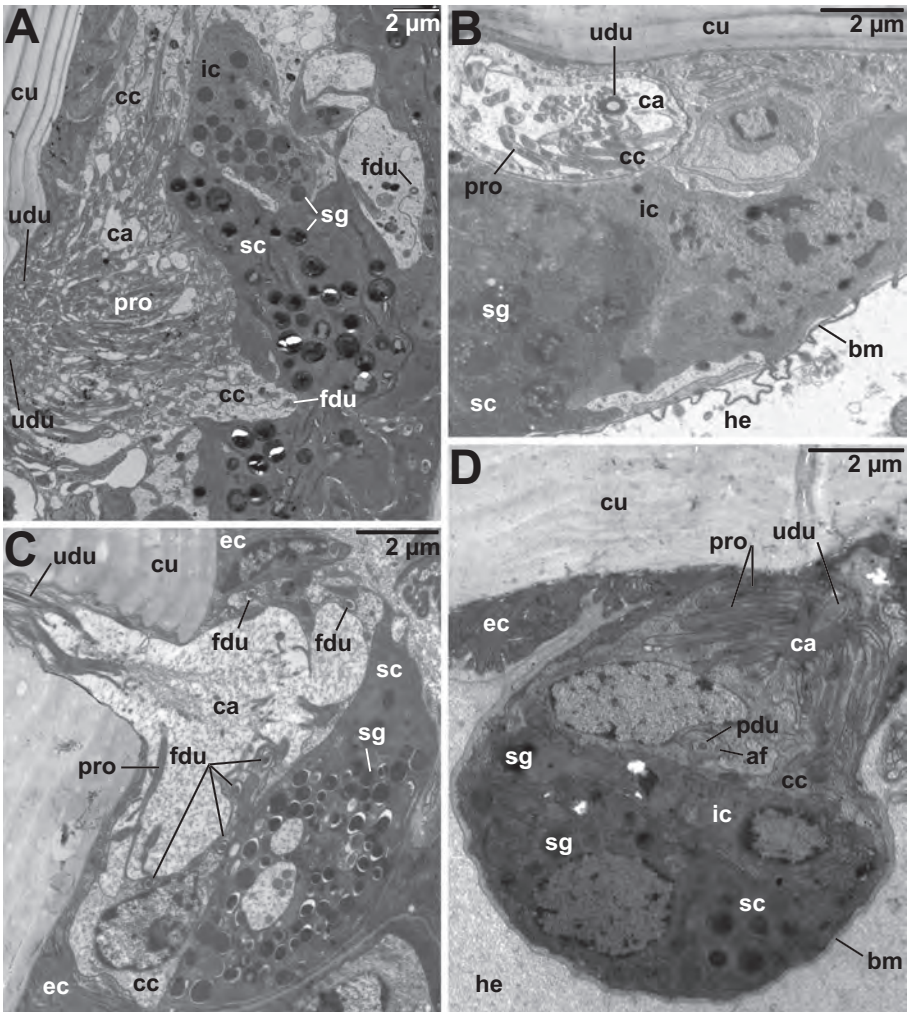

Fig. 3 A–D: TEM micrographs showing the cellular pattern in 'flexo-canal epidermal glands' of pleurostigmophoran centipedes; A: *Lithobius mutabilis*. Longitudinal view; B: *Craterostigmus tasmanianus*. Oblique section; C: *Scolopendra oraniensis*. Longitudinal view. The intermediary cell (*ic*) is not cut on this section level; D: *Stigmatogaster dimidiatus*. Longitudinal section.

af apical, manchette-like projection of the intermediary cell, *bm* basal matrix, *ca* central cavity of the canal cell, *cc* canal cell, *cu* cuticle, *ec* epidermal cell, *fdu* convoluted/meandering (flexuous) part of the conducting canal, *he* hemolymphatic space, *ic* intermediary cell, *pdu* proximal part of the conducting canal, *pro* cytoplasmatic projections of the canal cell pointing into the extracellular cavity, *sc* secretory cell, *sg* secretory granule, *udu* distal, untwisted and centred part of the conducting canal.

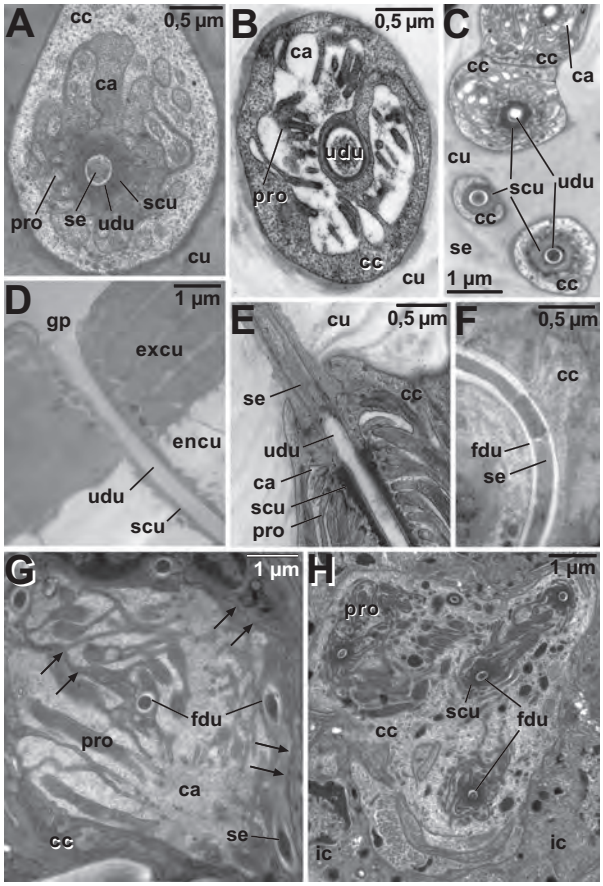

Fig. 4 A–H: TEM micrographs showing ultrastructural details of those cell types that contribute to the forming of ‘flexo-canal epidermal glands‘ in pleurostigmophoran centipedes: canal cell. A–C. Cross sections through distal part of the canal cell of solitary (A–B) or aggregated (C) epidermal glands housing the centered, untwisted part of the conducting canal; A: *Craterostigmus tasmanianus*; B: *Eupolybothrus fasciatus*; C: *Lithobius mutabilis*; D: *Scolopendra cingulata*. Distal part of a canal cell up showing the upper portion of the untwisted conducting canal terminating in the pore opening. Longitudinal section; E: *Lithobius dentatus*. Longitudinal view of distomedian part of a canal cell with ending of central cavity traversed by the centred, untwisted conducting canal; F: *S. cingulata*. Median region of a canal cell in cross section. Meandering conducting canal is cut along one transverse loop; G–H: Cross sections through the proximal part of a canal cell presenting two different forms of meandering conducting canal: *Scolopendra oraniensis*. Each two sections of the conducting canal are joined by a mesenterium-like structure indicated by double arrows (G). *C. tasmanianus*. Various cuttings of the conducting canal are visible free of mesenterium-like connections (H).

bm basal matrix, *ca* central cavity of the canal cell, *cc* canal cell, *cu* cuticle, *encu* endocuticle, *excu* exocuticle, *fdu* meandering (flexuous) part of the conducting canal, *gp* glandular pore, *ic* intermediary cell, *pro* cytoplasmatic projections of the canal cell pointing into the extracellular cavity, *scu* subcuticle, *udu* distal, untwisted and centred part of the conducting canal.

3.2.2. Intermediary cell

The intermediary cell connects the secretory cell to the canal cell and provides a passage for the secretion from the reservoir up to the conducting canal (e.g. Figs 2, 5C, 6B). The cell body appears mostly flattened and sometimes entirely wrapped by the secretory cell and/or the canal cell (e.g. Fig. 3D). Only around its nuclear region, the intermediary cell becomes so voluminous that it may crimp the secretory cell. The straight-running conducting canal, surrounded by the intermediary cell, is covered by a cuticle only in its distal part, whereas the proximal part is not cuticularised (Figs 5D, 6A, B, B'). Secretory granules produced by the intermediary cell are extruded into the conducting canal via radially spreading, complex network of extracellular cannels ('loculi') and get finally mixed with the secretion of the secretory cell (Fig. 6B). The cytoplasmic area around the conducting canal and the loculi is condensed by complex of microtubules and microfilamentous material. Where the intermediary cell and the canal/secretory cell adjoin each other to the duct, small evaginations interdigitate and are stably connected by septate junctions (Figs 5D, 6A, B,).

The cytoplasm of the intermediary cell is usually highly electron dense (e.g. Fig. 3A–D) and, besides a spherical, elongated and lobed nucleus with little portions of heterochromatin (Figs 3B, D, 6C), contains numerous organelles such as cisternae of smooth and rough endoplasmic reticulum (ER), Golgi vesicles, free ribosomes, polysomes, small empty vesicles, and many polymorphous mitochondria of the cristae type (Figs 3A–D, 4H, 5B–D, 6A–C). The presence of secretory granules (0.2–1.0 µm in diameter), indicate the ability of the intermediary cell to function as an accessory gland cell. The mostly spherical secretory granules can be distinguished from those of the secretory cell by the homogeneity of their highly osmiophilic inner matrix and by having principally smaller diameters. The latter feature is particularly striking in scolopendromorphs (Fig. 5C).

3.2.3. Canal cell

The canal cell represents the cell type that defines the class of 'flexo-canal epidermal glands'. Despite there is discernable variability on the ultrastructural level, each canal cell is characterised by a huge extracellular cavity and by a more or less strongly convoluted conducting canal. The canal cell directly abuts to the inner surface of the cuticle, with a rather short contact zone in tear-shaped glands (Fig. 2). When being in flattened, cubical gland configuration, however, the contact zone is always broad (e.g. Fig. 5A). The canal cell lines a huge central extracellular cavity and tapers into a small channel-like structure that penetrates the cuticle (Figs 3C, 5A). Around the bottom of the canal cell, there is a cytoplasmic process that reaches deeply into the intermediary cell (Fig. 5B). In its basal part, the cytoplasm of the canal cell houses most of the organelles including a mostly elongated nucleus including weak concentrations of heterochromatin, few Golgi stacks and cisternae of the endoplasmic reticulum (ER), locally accumulated free ribosomes, vesicles of varying shape and electron density (0.4 to 0.8 µm in diameter) as well as slim, elongated and multiply bent mitochondria of the cristae type (e.g. Figs 4G, H, 5A, B). The proximal part of the canal cell process looks depressed as it interlocks with a loop-like anchoring structure of the intermediary cell (Figs 5C, D, 6A,B). The basal cytoplasmic process of the canal cell carries the ovoid or circular cuticular conducting canal, which is approximately 4 µm in diameter. The canal is lined by a 30–40 nm thick multilayered cuticle. Due to its minute size and continuous cuticularisation, this part of the conducting canal may also be called the 'conducting canal'. In the basal area, the ductule is always straight ('unpaired') and firmly connected to the outer cell border via septate junctions (Figs 5C, D, 6A).

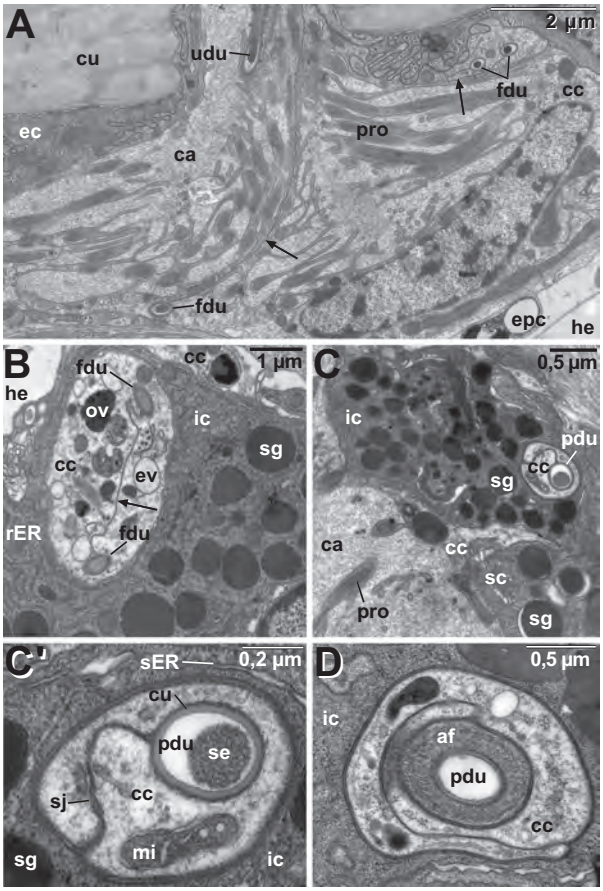

Fig. 5 A–D: TEM micrographs showing ultrastructural details of those cell types that contribute to the forming of 'flexo-canal epidermal glands' in pleurostigmophoran centipedes: canal cell and intermediary cell; A: *Scolopendra oraniensis*. Proximal region of one canal cell showing full extension of central cavity and meandering conducting canal observed from longitudinal perspective. Note the mesenterium-like connections between each two cuttings of meandering canal marked by *arrows* (also indicated in B); B: *Lithobius dentatus*. Basis of one canal cell cut transversally. The conducting canal appears convoluted; C: *S. oraniensis*. Transverse section more proximal to B containing apices of both intermediary and secretory cell. The proximal part of the conducting canal is erected and shown in higher detail in C'. D: *L. dentatus*. Most proximal region of the canal cell and the untwisted conducting canal. At this cross section level, the intermediary cell forms a ring-like projection around the proximal canal cell process housing the conducting canal.

af apical, manchette-like projection of the intermediary cell, *ca* central cavity of the canal cell, *cc* canal cell, *cu* cuticle, *ec* epidermal cell, *epc* external pigment cell, *ev* weakly electron dense ('empty') vesicle, *fdu* meandering (flexuous) part of the conducting canal, *he* hemolymphatic space, *ic* intermediary cell, *mi* mitochondrion, *ov* electron-dense ('osmiophilic') vesicle, *pdu* proximal part of the conducting canal, *pro* cytoplasmatic projections into the extracellular cavity, *rER* rough endoplasmatic reticulum, *rv* glandular reservoir, *sc* secretory cell, *se* secretion, *sER* smooth endoplasmatic reticulum, *sg* secretory granule, *sj* septate junctions, *udu* distal, untwisted and centred part of the conducting canal.

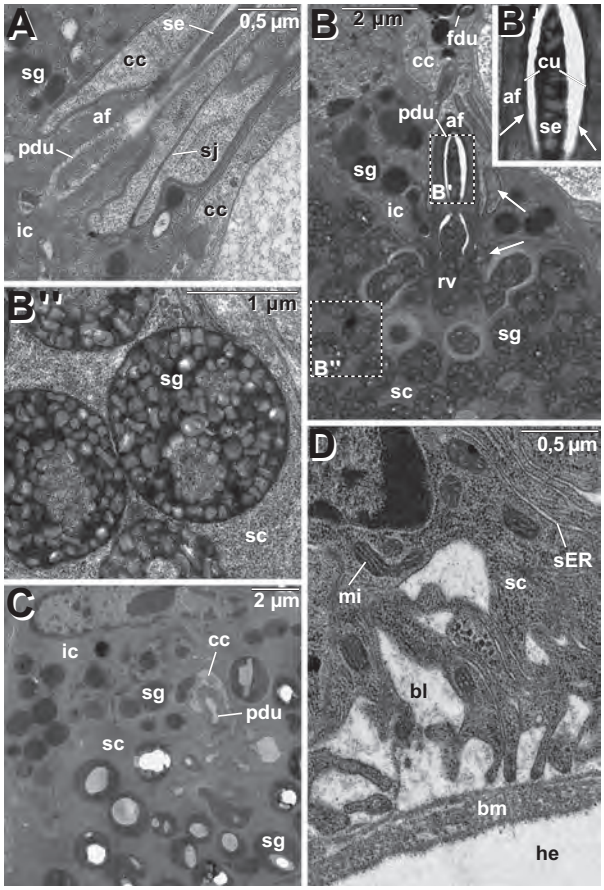

Fig. 6 A–D TEM micrographs showing ultrastructural details of those cell types that contribute to the forming of 'flexo-canal epidermal glands' in pleurostigmophoran centipedes: intermediary cell and secretory cell; A: *Scolopendra oraniensis*. Base of canal cell making contact to the apex of intermediary cell. Longitudinal section; B: *Craterostigmus tasmanianus*. Longitudinal view of the apices of the intermediary and secretory cell including the reservoir and the untwisted proximal part of the conducting canal. Note the anchoring loops of the intermediary cell (white arrows) intertwining with those of the canal cell and infoldings of the secretory cell. Note also both inserts providing a higher magnified view of the proximal, untwisted part of the ductule built by the intermediary cell and only partly lined by thick cuticle (beginning of thick wall cuticle indicated by white arrows) (B') as well as giving an insight into a sector of the cytoplasm of the secretory cell with some mosaic-like secretory granules (B''); C: *Lithobius dentatus*. Most proximal rest of canal cell surrounded by apex of intermediary cell as well as by massive body of the secretory cell. Oblique section; D: *C. tasmanianus*. Most proximal region of secretory cell forming a basal labyrinth. Longitudinal section.

af apical, manchette-like projection of the intermediary cell, *bl* basal labyrinth, *bm* basal matrix, *cc* canal cell, *cu* cuticle, *fdu* meandering (flexuous) part of the conducting canal, *he* hemolymphatic space, *ic* intermediary cell, *mi* mitochondrion, *pdu* proximal part of the conducting canal, *rv* glandular reservoir, *sc* secretory cell, *se* secretion, *sER* smooth endoplasmatic reticulum, *sg* secretory granule, *sj* septate junctions .

The median region is the most voluminous part of the canal cell. Here, the canal cell envelopes a huge extracellular space, traversed by the conducting canal. The extracellular cavity shows two degrees of complexity depending on the path of the winded ('flexuous'), always secretion-filled conducting canal (Fig. 4F). The lesser complex situation is found in examined geophilomorph species. The conducting canal looks convoluted (quill-like path). In cross and longitudinal sections, only 1–2 cuttings of the convoluted conducting canal are recognised traversing the central cavity. No meandering of the conducting canal is visible (Fig. 3D). The more sophisticated variant is based on the observation of up to eight cuttings of the conducting canal in a cross or longitudinal section through the median region of the canal cell and the extracellular cavity (meandering path) (Figs 2, 5A, 4G, H). The specific horizontal and vertical distribution of cuttings is caused by an extremely elongated conducting canal meandering through the canal cell. In lithobiomorph and scolopendromorph species, we observed cuttings of the conducting canal arranged in pairs. Each of those cutting pairs is interconnected by a membranous, mesenterium-like line that might be strained through the entire canal cell (Figs 3A, C, 4G, 5A, B). Such membranous connections are not noticeable in Craterostigmomorpha (Fig. 6H).

The central cavity moreover appears in two different cytophysiological states. It may look either inflated by presenting a maximally widened space filled with electron dense material (Figs 3C, 4B, G, 5 A) or much more compressed with its borders locally touching each other and leaving a fragmented cavity space (Figs 3D, 4A, H). The central cavity is filled with a loose meshwork of cytoplasmic projections that emanate from the apex of the canal cell and end near-by the conducting canal (Figs 4E–H 5A). In the inflated stage, the cytoplasmic projections form a loose meshwork with wide extracellular spaces (e.g. Figs 4B, 5A), whereas in more compressed state the cytoplasmic projections are in direct contact to each other (e.g. Figs 3D, 4A). The cytoplasmic projections are predominantly taken up by mitochondria, especially at those places where tubes build cross bridges.

The distal region of the canal cell mostly extends from the inner border of the cuticle up to the outer cuticular surface and terminates in the glandular pore (Fig. 4A–D). The volume of the central cavity shrivels as the canal cell tapers into a small channel-like structure resembling the tip of a syringe (Fig. 4E). This part of the canal cell contains a straight conducting canal in a central position (Fig. 4B, E). More distally, the central cavity diminishes in size and is replaced by a flourished system filled up with subcuticular material (Fig. 4A). Close to the pore region, only the conducting canal and its subcuticular coverage are visible (Fig. 4D).

4. Discussion

4.1. Homology and functional morphology of 'flexo-canal epidermal glands'

In present paper, the ultrastructure of 'flexo-canal epidermal glands' occurring on the heads of representatives of various chilopod taxa is compared. With the exception of Scutigeromorpha, we were able to discover these kinds of epidermal glands in all chilopod subtaxa. We found and list below six common features the 'flexo-canal epidermal glands' of all examined chilopod taxa share on the histological and ultrastructural level:

1) There is very little variation in cell numbers and cell types. In general, the tricellular organisation gives rise to the constant expression of one canal cell, one intermediary cell and one secretory cell. Tricellular epidermal glands have also been reported to exist in various euarthropod taxa, as for instance Crustacea (Talbot & Demers 1993), Hexapoda (Quennedey 1998) and Myriapoda (see Tab. 1). It seems unreasonable to dismiss quantity as a trivial aspect, since just in Myriapoda and among them especially in Chilopoda the tricellular architecture of an epidermal gland is only one amongst many. Hitherto described isolated epidermal glands or compound gland units that consist of four, five or even more cells may be assigned to the very diverse class of glands with broad and erect conducting canals ('recto-canal epidermal glands'), as for example the spermathecal gland units of the folding-trapdoor spider *Antrodiaetus unicolor* (see Michalik et al. 2005) or the tarsal glands, dermal glands or defence glands of the harvestman *Cyphophthalmus duricorius* (Martens 1979, Gutjahr et al. 2005) among Chelicerata or the rosette glands of the decapod *Palaemonetes pugio* (Doughtie and Rao 1982) decapod crustacean. Among Myriapoda, examples for tricellular arrangements can be found in the form of functional units within the maxillary organ gland, the epidermal maxilla-II-gland or the vesicular glands of the scutigeromorph chilopod *Scutigera coleoptrata* (Hilken et al. 2003, 2005, Hilken & Rosenberg 2009, for further examples see Tab.1) or the tegumental glands of the symphylan *Scutigerella silvatica* (Juberthie-Jupeau 1975). 'Recto-canal epidermal glands' do not only have increased cell numbers in an ordinary 'class-3-gland'-system but have also developed more than three different cell types. For instance, up to five different cell types can be identified in the isolated 'recto-canal epidermal glands' on the heads of various lithobiomorph, craterostigmomorph and scolopendromorph centipedes (see Tab. 1 and Müller et al. 2006, 2009 in prep.). In contrast, the small epidermal glands surrounding the Tömösvary organ as well as the interommatidial glands of Lithobiomorpha were described as bicellular, lacking an intermediary cell (Tichy 1973, Keil 1975, Müller et al. 2003a) (see Tab. 1). Because of its inconspicuousness, however, there is a well-founded suspicion that the intermediary cell might have been overlooked in bicellular 'flexo-canal epidermal glands'. While cell numbers and cell types appear to be fixed in Chilopoda, slight variations in cell numbers are possible in those epidermal glands present in closely related groups like the Diplopoda. The anal glands of *Rhapidostreptus virgator* (see Schlüter 1982) and the postgonopodial glands of *Glomeris marginata* (see Juberthie-Jupeau 1976, 1978) consist of three cell types and show a typically convoluted, slender conducting canal; the number of secretory cells, however, is doubled resulting in a total number of four cells per gland.

Tab. 1 Diversity and systematics of isolated and compound epidermal glands in Chilopoda investigated with electron-microscopic methods.[1]

Gland location	Author	Intermediary cell	Taxon/Species	Organisation degree	Class
Glands containing two cell types (secretory cell + canal cell)					
Small epidermal glands (between telepodite glands, at the base of sensilla trichoidea)	Keil (1975)	(-)	*Lithobius forficatus*	Isolated epidermal glands (1 secretory cell)	flexo-canal epidermal glands
Small epidermal glands (lining organ of Tömösvary)	Tichy (1973)	(-)	*Lithobius forficatus*	Isolated and aggregated epidermal glands (1 secretory cell)	flexo-canal epidermal glands
Interommatidial glands	Müller et al. (2003a)	(-)	*Lithobius forficatus*	Aggregated epidermal glands (1 secretory cell)	flexo-canal epidermal glands
Glands containing three cell types (secretory cell + intermediary cell + canal cell)					
'Telepodite glands' (on the antennae)	Keil (1975)	Present* (innere Hüllzelle')	*Lithobius forficatus*	Isolated epidermal glands (1 secretory cell)	erecto-canal epidermal glands
Epidermal glands 'Drüsenzellen' (associated with Tömösváry organ)	Tichy (1973)	Present* (see Figs.16+17)	*Lithobius forficatus*	Isolated or compound epidermal glands (1 secretory cell)	flexo-canal epidermal glands
Epidermal glands 'Epidermisdrüsen' (associated with coxal organs)	Rosenberg (1985)	Present* (see Fig.?)	Pleurostigmophora	Isolated epidermal glands (1 secretory cell)	flexo-canal epidermal glands?
epidermal coxal glands	Rosenberg (1994)	Present* (see Fig.3b)	*Lithobius forficatus*	Isolated epidermal glands (1 secretory cell)	flexo-canal epidermal glands
Interommatidial glands	Müller et al. (2003a)	Present	*Scutigera coleoptrata*	Isolated epidermal glands (1 secretory cell)	recto-canal epidermal gland
Telopodite glands (posterior legs)	Keil (1975)	Present* ('innere Hüllzelle', see Fig.12)	*Lithobius forficatus*	Isolated epidermal glands (2 secretory cells)	recto-canal epidermal glands
Sternal 'ventral' glands (on sternal plates)	Turcato & Minelli (1990), Turcato et al. (1995)	Present* (see Figs. 3,7)	Geophilomorpha	Isolated (or compound?) epidermal glands (1 secretory cell)	recto-canal epidermal glands
Periartrial gland	Carcupino (1996)	Present* (see Figs.33-34)	*Eupolybothrus fasciatus*	Isolated epidermal glands (2 secretory cells)	recto-canal epidermal glands

Tab. 1 cont.

Gland location	Author	Intermediary cell	Taxon/Species	Organisation degree	Class
Epidermal glands (on head flanks, in *Scutigera* around the compound eyes)	Müller et al. (2009 in prep.)	Present	Scutigeromorpha, Geophilomorpha	Isolated epidermal glands (1 secretory cell)	recto-canal epidermal glands
Epidermal glands (on head flanks, paratergites of trunk segments)	this study	Present	Pleurostigmophora	Isolated and compound epidermal glands (1 secretory cell)	flexo-canal epidermal glands
Glands containing four cell types					
(secretory cell + intermediary cell + distal canal cell + proximal canal cell) or					
(2 secretory cells + intermediary cell + canal cell)					
Epidermal maxilla-II-gland (at the basis of Maxilla II)	Hilken et al. (2005)	Present	*Scutigera coleoptrata*	Compound epidermal gland (each unit with 1 secretory cell)	recto-canal epidermal glands
Poison gland (in maxillipeds)	Rosenberg & Hilken (2006)	Present	*Lithobius forficatus*	Compound epidermal gland (each unit with 1 secretory cell)	flexo-canal epidermal glands
Epidermal glands (on head flanks, around ocellar field)	Müller et al. (2009 in prep.)	Present	Lithobiomorpha	Isolated epidermal glands (2 secretory cells)	recto-canal epidermal glands
Glands containing five cell types					
(2 secretory cells + intermediary cell + distal canal cell + proximal canal cell)					
Epidermal glands (on head flanks, near-by the eyes)	Müller et al. (2009 in prep.)	Present	Craterostigmomorpha, Scolopendromorpha	Isolated epidermal glands (2 secretory cells, 2–3 canal cells)	recto-canal epidermal glands
Maxillary organ gland	Hilken et al. (2003)	Present	*Scutigera coleoptrata*	Compound epidermal gland (each unit with 2 secretory cells, 2 canal cells)	recto-canal epidermal glands
Vesicular gland	Hilken & Rosenberg (2009)	Present	*Scutigera coleoptrata*	Compound epidermal gland (each unit with 2 secretory cells, 2 canal cells)	recto-canal epidermal glands

[1] Table represents a modified and expanded version of Hilken's et al. (2005) compilation of literature data dealing with this issue. A new classification of previously described gland types in accordance with 'recto-canal-' or 'flexo-canal epidermal glands' has been added to the list. Those glands marked with asterisks were guessed to include an intermediary cell, which had been illustrated but not expressively described in the reviewed literature.

2) Occurrence of small aggregations, no affinity towards forming compound glands. If joining each other, the units of 'flexo-canal epidermal glands' build clusters or ring-like formations. 'Flexo-canal epidermal glands' represent aggregations rather than compound glandular organs sensu Hilken et al. (2005), since, besides being associated with sense organs, there is no general evidence for an extra conducting canal joining neighbouring gland units. Compound glands of the 'recto-canal' type are much more complex and usually integrate several thousands of glandular units emitting their secretion into a common tube-like canal (Hilken et al. 2003, 2005, Hilken & Rosenberg 2006a, b, 2009, Rosenberg & Hilken 2006). Aggregated 'flexo-canal epidermal glands' may be responsible for impregnating the outer surface areas of sense organs such as compound eyes (Müller et al. 2003a), sensilla (this paper) and postantennal organs (Tichy 1973).

3) The canal cell forms a thin and strongly convoluted or meandering conducting canal. This specific path of the entire conducting canal is probably caused by a canal cell apex that turns around itself and builds deep infoldings during differentiation of the canal precursor cell. The arrangement of meandering loops along conducting canal in 'flexo-canal epidermal glands' of Lithobiomorpha and Scolopendromorpha is unique and represents a further degree of complexity when the ductule is formed during glandular genesis. The compartmentalisation and spatial stability of the canal cell is enhanced in those areas, where the strongly meandering conducting canal forms membranous connections between opposing parts of ductule loops. The formation of membranous lines between the ductule loops can be best explained by assuming that early apical infoldings are compressed in their centre. Of course, such developmental scenario has to be proven experimentally for chilopod epidermal glands.

Thin, strongly convoluted canals lined by a clearly visible cuticular intima and completely filled with secretion makes the most important difference in comparison to 'recto-canal epidermal glands', whose intermediary and canal cell(s) surround a shortened, erect conducting canal locally widened by cavities. Strongly convoluted, elongated and thinned conducting canals, similar or identical to the 'flexo-canal' type, have been noticed in epidermal glands present in some Crustacea (Decapoda: *Palaemonetes pugio*: Dougthie and Rao 1979; Peracarida: *Antromysis juberthiei*: Juberthie-Jupeau & Crouau 1977/78), Diplopoda (*Rhapidostreptus virgator*: Schlüter 1982; *Glomeris marginata* Juberthie-Jupeau 1976, 1978) and, after review of micrograph material, also in other body regions of the same chilopod taxa (cf. Tichy 1973, Keil 1975, see Tab. 1).

Regardless of variations in complexity, the elongated and convoluted and/or meandering conducting canal together with accompanying microvilliform projections of the canal cell are likely well adjusted to remove diffusive substances like water or small ions from the secretion floating through the conducting canal. Meandering path close-by all cytoplasmic areas of the canal cell may support or intensify this diffusion. The enormous absorbing capacity of the canal cell is further circumstantiated by dramatic volume changes going on in the central cavity. The absence of local widenings in the elongated and convoluted conducting canal of 'flexo-canal epidermal glands' may furthermore facilitate permanent secreting activity (cf. Schlüter 1979). This is supported by the fact that secretion masses were found at each level of the conducting canal. This stands in contrast to 'recto-canal epidermal glands', whose broad conducting canals are locally widened and compartmented by bulbous cavities. These huge cavities may provide storages of secretion, which might be drained on occasion. Large amounts of secretion can then be expelled to the outer environment at once.

4) The canal cell always contains an expanded central cavity. This more or less spacious (narrowed by microvilliform apical projections of the canal cell), physiologically dynamic system has never been depicted in epidermal glands with broad, erect conducting canals in Chilopoda (e.g. Müller et al. 2003a; Hilken et al. 2003, 2005, see also Tab.1.). In addition, the absence of an extracellular cavity is realised in euarthropod groups other than Chilopoda (compare e.g. Noirot & Quennedey 1974, 1991, Bitsch & Bitsch 1991, Talbot & Demers 1993, Quennedey 1998), regardless of its typological affiliation. 'Flexo-canal' type like glands in some peracarid and decapod Crustacea (Juberthie-Jupeau & Crouau 1977/78, Dougthie & Rao 1979) as well as those present in some glomerid and archispirostrepsid Diplopoda (Juberthie-Jupeau 1976, Schlüter 1982) lack a voluminous central cavity, but nevertheless show a distinct, electron dense interspace formed by pronounced dilation of the canal and penetrated by microvilli-like extensions of the apex of the canal cell. At least, Doughtie & Rao (1979) admitted the exceptional structure of the conducting canal in the 'flexo-canal'-like epidermal glands of *Palaemonetes pugio* by stating that canal cells with microvilliform dilations are lacking in 'class-3-glands' of insects (p. 290). It cannot be excluded that the appearance of the central cavity in 'flexo-canal'-like epidermal glands may pass through dramatic changes similar to those now found in Chilopoda. It seems likely that physiological states leading to swollen central cavities have not been described and illustrated by previous authors as a result of coincidence or assumption of irrelevance. Thus, homology of central cavity in epidermal glands with thin, elongated and convoluted conducting canals is still possible, even though considerable differences have been observed. Only in the interommatidial and vesicular glands of the archaeognath insects *Lepismachilis targionii*, *Machilis* spp. and *Petrobius brevistylis* (Bitsch & Palévody 1976, cf. Müller 2008), a spacious central cavity is noticed. However, the interommatidial glands of *Machilis* and *Petrobius* possess a forth cell type of sensory function, which produces a dendrite-like process heading towards the margin of the central cavity. These sensory cells are also present during the moulting process of 'flexo-canal' type epidermal glands of the diplopod *Rhapidostreptus virgator*, in the form of temporarily modified secretory cells developing cilia (Schlüter 1983). In some wingless insects, as for instance Collembola, Archaognatha and Zygentoma, such sensory cells are also involved in the maturation of epidermal glands during early development or moulting events, but are not transitory and retain in different numbers in the adult/intermoult state (see review of Bitsch & Bitsch 1991).

In a 'flexo-canal epidermal gland', the canal cell might play a pivotal role in accumulating and regulating the ion- and water-balance. The changes in size of the extracellular (central) cavity may indicate that this structure is involved in balancing the concentration of water within the convoluted conducting canal with the aid of cytoplasmic processes of the canal cell interspersed with numerous mitochondria.

5) Prominent apical loops together with adhering structures interconnect the intermediary cell and the secretory/canal cell. The association of apical loop anchoring structures and cell to cell adhesion structures (belt desmosomes, septate junctions) is different from the situation known from 'recto-canal epidermal glands'. There, solely belt desmosomes (Maculae adhaerentes) serve for the connection of the intermediary cell to the secretory cell(s) and canal cell, respectively (Müller et al. 2003a, Hilken et al. 2003, 2005, Hilken & Rosenberg 2006a, 2009, Rosenberg and Hilken 2006). The necessity to establish more advanced adhesion structures in 'flexo-canal epidermal glands' may be caused by the

enormous tractive power affecting the intermediary cell and canal cell related to the moulting cycle (cf. Juberthie-Jupeau & Crouau 1977/78). This is especially true for those glands equipped with a strongly meandering conducting canal, just as it was found in Lithobiomorpha, Craterostigmomorpha and Scolopendromorpha.

6) Heterogeneity of secretory granules produced by the secretory cell. Heterogeneous, mosaic-like secretory granules produced by secretory cells in 'flexo-canal epidermal glands' clearly show a typical mosaic-like structure in pleurostigmophoran centipedes, except Geophilomorpha. Similarly looking secretory granules seem to be accumulated in the epidermal glands of the mysidacean *A. juberthiei* (Juberthie-Jupeau & Crouau 1977/78) and the pheromone-producing postgonopodial glands of the diplopod *Glomeris marginata* (Juberthie-Jupeau 1976). The heterogeneous content of the secretory granules may evolve from a certain pathway of formation starting at the basis of the cell secretory cell and ending with their release in the reservoir.

4.2. 'Flexo-canal' vs. 'recto-canal epidermal glands' – purpose of a new classification

We listed up and commented in detail seven features potentially homologous among 'flexo-canal epidermal glands' in Chilopoda. In contrast, we separated the so-called 'recto-canal epidermal glands' from the former class by the following characters: 1) development of usually more than three cells build by more than three different cell types (caused by diversification and occasional multiplication of canal cells and/or secretory cells), 2) untwisted ('recto-'), relatively voluminous conducting canals, 3) presence of widened extracellular reservoir(s) formed by the secretory and/or intermediary cells, and 4) the tendency to build huge compound glandular organs by aggregation of glandular units, whose structure is well retraceable to isolated epidermal glands (Tab. 1 and Müller et al. 2006).

An ambitious and elaborated classification for epidermal glands of Chilopoda was recently provided by Hilken et al. (2005). This classification is based on characteristics others than the cell number alone, such as the specification of all cell types involved in the forming of the epidermal glands as well as the degree of their organisation. Based on these criteria, the discovery of further epidermal glands in Chilopoda have led to the definition of more and more subtypes (Hilken et al. 2003, 2005, see Tab.1). The increasing number of subtypes makes character coding, inevitable for conducting a solid cladistic analysis, more difficult, though. The finding of homologous character patterns and the estimation of the influence of functional coherence of certain structures in those epidermal glands seems to be considerably hampered.

What is the advantage of introducing a new terminology into the field of gland research in myriapodology? At least with respect to the Chilopoda, the new determination of 'flexo-canal' and 'recto-canal epidermal glands' reflects on the structural and functional diversity of epidermal glands. The new classification is mainly based on the ultrastructural set-up of the canal cell(s) and the conducting canal. The classification enables us to translate structures into a language sufficient and complex enough to draw homology concepts and, subsequently, to understand the evolutionary transformation of epidermal glands on various taxonomic levels of the Euarthropoda. The classical, purely cell number-oriented terminology defined by Noirot & Quennedey (1974, 1991), Sreng & Quennedey (1976) and Quennedey (1991, 1998) does not seem to be appropriate in regards to phylogenetic considerations. By distinguishing 'class-I-glands', 'class-II-glands' and 'class-III-glands', the Quennedey group focused on

insect epidermal glands. Due to distinct differences in the cuticle lining of the conducting canal down to the end apparatus, the homology of epidermal glands of insects and myriapods is doubtful (Hilken & Rosenberg 2009).

4.3. Significance of epidermal glands for phylogenetic reconstruction

Not least due to present paper, there is growing evidence that epidermal glands in Euarthropoda typically contain intermediary cells connecting the secretory cell to the canal cell. Reviewing previous literature, equivalents and probable homologues of the intermediary cell can be hypothesised to exist in epidermal glands of Chelicerata (e.g. Opiliones: 'collar cell' in defence glands: Gutjahr et al. 2005, 'enveloping cell' in tarsal gland: Martens 1979), Crustacea (e.g. Notostraca: 'Halszelle' in epidermal glands: Rieder 1977; Malacostraca: 'hillock cell' in exocrine dermal glands: Doughtie & Rao 1979, 'intermediate cell' in uropod and lateral plate gland units: Weirich & Ziegler 1997), Symphyla ('cellule interne du canal' in tegumental glands: Juberthie-Jupeau 1975), Diplopoda (e.g. 'intermediary cell' in postgonopodial gland units: Juberthie-Jupeau 1976, 'Übergangszelle' in pyloric gland units: Schlüter 1980, 'intermediary cell' in anal gland units: Schlüter 1982, 1983) and Hexapoda (e.g. 'cellule canaliculaire' in various epidermal glands of 'Apterygota': Bitsch & Bitsch 1991, 'intercalary class III gland cell' or 'second canal cell' in class-3 epidermal glands of Pterygota: Noirot & Quennedey 1991, Quennedey 1998). Except for the Pterygota, the intermediary cells encircle a conducting canal. In most cases, a cuticle is only developed in the most distal part of this lower region of the conducting canal. This is exactly in line with the situation observed in Chilopoda. The majority of isolated or compound epidermal glands so far examined in Euarthropoda have canal cells with short, erect and broad cuticular ducts. They may be put in the class of 'recto-canal epidermal glands'. To discuss the evolution of both gland types, the disparity of the intermediary cell among euarthropds and the evolutionary transformation of the intermediary cell in insect glands would be far beyond the scope of this paper. Either way, it seems now reasonable to assume that tricellular epidermal glands consisting, of one secretory cell, one intermediary cell and one canal cell belong to the ground pattern of the Euarthropoda. Considering their wide distribution in Euarthropoda, it is appears more parsimonious to suggest the 'flexo-canal epidermal glands' to have derived from 'recto-canal epidermal glands'.

Epidermal glands similar to the 'flexo-canal type' are observed in some other euarthropod taxa, including Mysidacea (Crustacea), Diplopoda and Archaeognatha (Hexapoda) (Bitsch & Palévody 1976; Juberthie-Jupeau 1976, 1978; Juberthie-Jupeau & Crouau 1977/78; Schlüter 1980, cf. Müller 2008). However, descriptions of these 'flexo-canal' type-like glands never entirely fit the pattern of characters we defined above for Chilopoda. To date, the most striking and convincing argument for homology of 'flexo-canal' type-like epidermal glands in above-listed taxa is the possession of a canal cell forming a thin, elongated and strongly convoluted/meandering conducting canal. Among all found potential homologues, the antennal glands of Mysidacea (Juberthie-Jupeau & Crouau 1977/78) apparently show the highest degree of similarity to 'flexo-canal epidermal glands' in Chilopoda (tricellular pattern, convoluted ductule, heterogenous secretory granules). All in all, based on ultrastructural data, one could infer homology of 'flexo-canal' type-like glands and single evolution of this gland class in the stem lineage of Mandibulata. However, we are aware of the fact that this assumption very preliminary and still contestable. First, the number of structural variations

found in crustaceans, diplopods and hexapods is considerable in relation to the chilopod pattern. The common expression of a thin, elongated and strongly convoluted conducting canal might have happened several times independently driven by 'forced evolution', namely to evolve permanently active epidermal glands. However, adaptations to terrestrial lifestyle cannot be used for explanation since Mysidacea are aquatic animals. Second, we have to cope with the derived position of those taxa with 'flexo-canal' type-like epidermal glands. Mysidacea are highly derived malacostracan crustaceans (Richter & Scholtz 2001, their Fig. 7). Among Diplopoda, only the Pentazonia, including Glomerida, are known to have a comparably basal position in the chilognath clade, as a sister group of the Helminthomorpha; the Spirostreptida are highly derived chilognaths, belonging to the Juliformia (Sierwald & Bond 2007, their Fig. 6). At the basis of the Progoneata and Tetraconata (Crustacea + Hexapoda), we are confronted with a huge gap of knowledge concerning the presence and architecture of epidermal glands. Thus, an assumption of homology appears questionable unless future re-investigations on the glands of above-listed taxa are conducted or analyses enlightening the epidermal gland structures in phylogenetic key taxa, similar to Penicillata, Remipedia, Symphyla, Ellipura, and also Xiphosura are provided. To evaluate this additional apomorphy of the Mandibula would be of great phylogenetic importance, as this taxon was challenged in recent years by molecular systematics (e.g. Pisani et al. 2004, Mallatt et al. 2004). As a countermove, Mandibulata received additional support by new evolutionary morphological studies (e.g. eye structures: Müller et al. 2003b, 2007; mandible structures: Edgecombe et al. 2003) or combined molecular and morphological analyses (Giribet et al. 2005). Perhaps, epidermal gland data will likewise find acceptance as a new, complex morphological tool to resolve gross euarthropod relationships. There are astonishing congruencies to compound eyes, which like compound glands are made up of numerous functional units, the ommatidia. Ommatidia and in particular certain cell types forming them are approved characters to successively reconstruct the phylogeny of the Euarthropoda (e.g. Paulus 1979, Müller et al. 2003b, 2007, Bitsch & Bitsch 2005, Müller 2008). Isolated and compound euarthropod epidermal glands, although simpler organised than a typical mandibulate ommatidium, may be considered at least equally important because they are present in both terrestrial and aquatic taxa.

If one assumes the 'flexo-canal epidermal glands' to be homologous across Mandibulata, one has to draw the conclusion that their apparent absence in Scutigeromorpha is due to a secondary loss (additional apomorphy of this taxon). However, this implies homology of the 4-cell-units in the pyloric and anal glands of spirostreptid, glomerid and polydesmid Diplopoda (see Juberthie-Jupeau 1976, 1978, Schlüter 1980, 1982) with the tricellular 'flexo-canal epidermal glands' of Chilopoda. An augmentation of secretory cells might have taken place in the stem lineage of Diplopoda quite easily when glandulogenesis is prolonged due to further mitoses. At present state of knowledge, it cannot be entirely excluded that epidermal glands of the 'flexo-canal type' have evolved independently in the stem lineage of the phylogenetically well supported Pleurostigmophora (e.g. Borucki 1996, Giribet & Edgecombe 2006, Edgecombe & Giribet 2004, 2007). But more likely, 'flexo-canal epidermal glands' in Pleurostigmophora have been retained from a mandibulate or myriapod ground pattern. A combination of evolutionarily transformed and retained characters led to specific set of characters typical for 'flexo-canal epidermal glands' in Pleurostigmophora.

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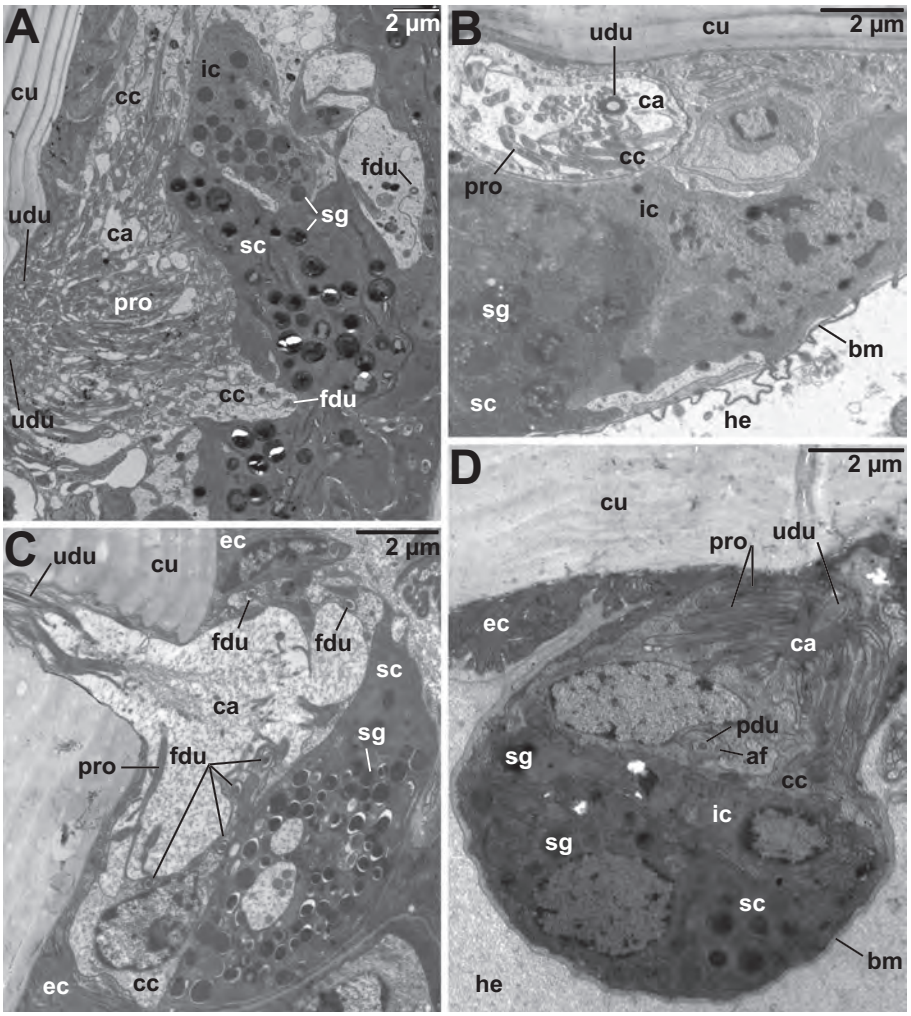

Fig. 3 A–D: TEM micrographs showing the cellular pattern in 'flexo-canal epidermal glands' of pleurostigmophoran centipedes; A: *Lithobius mutabilis*. Longitudinal view; B: *Craterostigmus tasmanianus*. Oblique section; C: *Scolopendra oraniensis*. Longitudinal view. The intermediary cell (*ic*) is not cut on this section level; D: *Stigmatogaster dimidiatus*. Longitudinal section.

af apical, manchette-like projection of the intermediary cell, *bm* basal matrix, *ca* central cavity of the canal cell, *cc* canal cell, *cu* cuticle, *ec* epidermal cell, *fdu* convoluted/meandering (flexuous) part of the conducting canal, *he* hemolymphatic space, *ic* intermediary cell, *pdu* proximal part of the conducting canal, *pro* cytoplasmatic projections of the canal cell pointing into the extracellular cavity, *sc* secretory cell, *sg* secretory granule, *udu* distal, untwisted and centred part of the conducting canal.

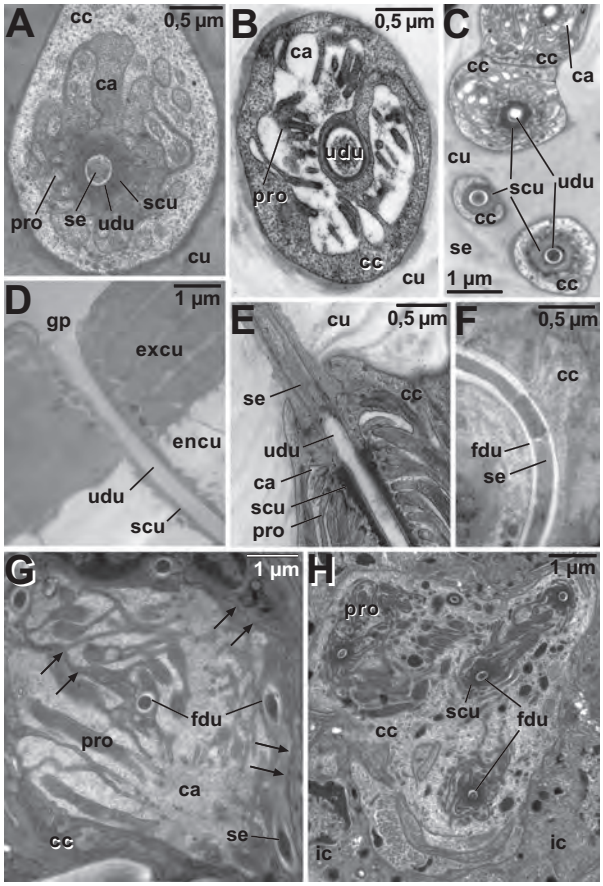

Fig. 4 A–H: TEM micrographs showing ultrastructural details of those cell types that contribute to the forming of 'flexo-canal epidermal glands' in pleurostigmophoran centipedes: canal cell. A–C. Cross sections through distal part of the canal cell of solitary (A–B) or aggregated (C) epidermal glands housing the centered, untwisted part of the conducting canal; A: *Craterostigmus tasmanianus*; B: *Eupolybothrus fasciatus*; C: *Lithobius mutabilis*; D: *Scolopendra cingulata*. Distal part of a canal cell up showing the upper portion of the untwisted conducting canal terminating in the pore opening. Longitudinal section; E: *Lithobius dentatus*. Longitudinal view of distomedian part of a canal cell with ending of central cavity traversed by the centred, untwisted conducting canal; F: *S. cingulata*. Median region of a canal cell in cross section. Meandering conducting canal is cut along one transverse loop; G–H: Cross sections through the proximal part of a canal cell presenting two different forms of meandering conducting canal: *Scolopendra oraniensis*. Each two sections of the conducting canal are joined by a mesenterium-like structure indicated by double arrows (G). *C. tasmanianus*. Various cuttings of the conducting canal are visible free of mesenterium-like connections (H).

bm basal matrix, *ca* central cavity of the canal cell, *cc* canal cell, *cu* cuticle, *encu* endocuticle, *excu* exocuticle, *fdu* meandering (flexuous) part of the conducting canal, *gp* glandular pore, *ic* intermediary cell, *pro* cytoplasmatic projections of the canal cell pointing into the extracellular cavity, *scu* subcuticle, *udu* distal, untwisted and centred part of the conducting canal.

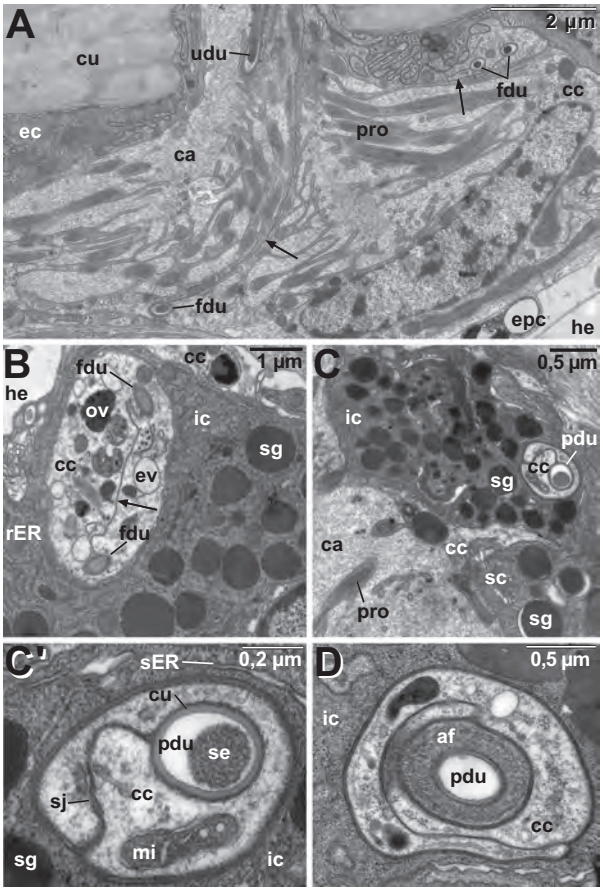

Fig. 5 A–D: TEM micrographs showing ultrastructural details of those cell types that contribute to the forming of 'flexo-canal epidermal glands' in pleurostigmophoran centipedes: canal cell and intermediary cell; A: *Scolopendra oraniensis*. Proximal region of one canal cell showing full extension of central cavity and meandering conducting canal observed from longitudinal perspective. Note the mesenterium-like connections between each two cuttings of meandering canal marked by *arrows* (also indicated in B); B: *Lithobius dentatus*. Basis of one canal cell cut transversally. The conducting canal appears convoluted; C: *S. oraniensis*. Transverse section more proximal to B containing apices of both intermediary and secretory cell. The proximal part of the conducting canal is erected and shown in higher detail in C'. D: *L. dentatus*. Most proximal region of the canal cell and the untwisted conducting canal. At this cross section level, the intermediary cell forms a ring-like projection around the proximal canal cell process housing the conducting canal.

af apical, manchette-like projection of the intermediary cell, *ca* central cavity of the canal cell, *cc* canal cell, *cu* cuticle, *ec* epidermal cell, *epc* external pigment cell, *ev* weakly electron dense ('empty') vesicle, *fdu* meandering (flexuous) part of the conducting canal, *he* hemolymphatic space, *ic* intermediary cell, *mi* mitochondrion, *ov* electron-dense ('osmiophilic') vesicle, *pdu* proximal part of the conducting canal, *pro* cytoplasmatic projections into the extracellular cavity, *rER* rough endoplasmatic reticulum, *rv* glandular reservoir, *sc* secretory cell, *se* secretion, *sER* smooth endoplasmatic reticulum, *sg* secretory granule, *sj* septate junctions, *udu* distal, untwisted and centred part of the conducting canal.

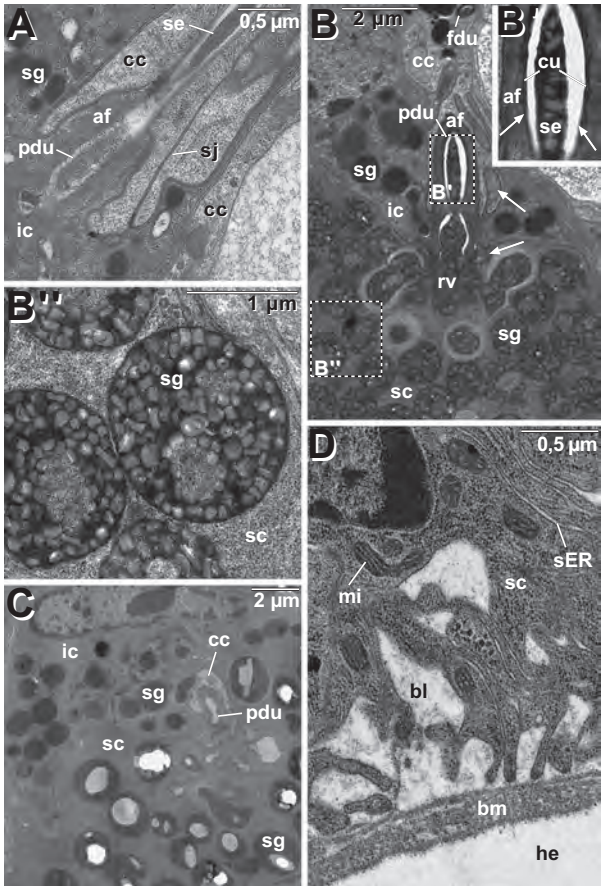

Fig. 6 A–D TEM micrographs showing ultrastructural details of those cell types that contribute to the forming of 'flexo-canal epidermal glands' in pleurostigmophoran centipedes: intermediary cell and secretory cell; A: *Scolopendra oraniensis*. Base of canal cell making contact to the apex of intermediary cell. Longitudinal section; B: *Craterostigmus tasmanianus*. Longitudinal view of the apices of the intermediary and secretory cell including the reservoir and the untwisted proximal part of the conducting canal. Note the anchoring loops of the intermediary cell (white arrows) intertwining with those of the canal cell and infoldings of the secretory cell. Note also both inserts providing a higher magnified view of the proximal, untwisted part of the ductule built by the intermediary cell and only partly lined by thick cuticle (beginning of thick wall cuticle indicated by white arrows) (B') as well as giving an insight into a sector of the cytoplasm of the secretory cell with some mosaic-like secretory granules (B''); C: *Lithobius dentatus*. Most proximal rest of canal cell surrounded by apex of intermediary cell as well as by massive body of the secretory cell. Oblique section; D: *C. tasmanianus*. Most proximal region of secretory cell forming a basal labyrinth. Longitudinal section.

af apical, manchette-like projection of the intermediary cell, *bl* basal labyrinth, *bm* basal matrix, *cc* canal cell, *cu* cuticle, *fdu* meandering (flexuous) part of the conducting canal, *he* hemolymphatic space, *ic* intermediary cell, *mi* mitochondrion, *pdu* proximal part of the conducting canal, *rv* glandular reservoir, *sc* secretory cell, *se* secretion, *sER* smooth endoplasmatic reticulum, *sg* secretory granule, *sj* septate junctions .