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FINE STRUCTURE OF PUSTULES OF *LABIDOSTOMA LUTEUM* KRAMER (ACARI, ACTINOTRICHIDA, LABIDOSTOMATIDAE) WITH FURTHER REMARKS ON THE COMPLEX CUTICLE OF THIS MITE

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ABSTRACT — Most Labidostomatidae bear lateral protuberances called pustules on their idiosoma, which have been considered as "enigmatic" structures. Here, the fine structure of the pustules of *Labidostoma luteum* is described using scanning and transmission electron microscopy. It is shown that the pustules represent peculiar exocrine glands which extrude their secretions through a specialized cuticular region which is shaped like the hat of a mushroom. This region includes a space located between the epicuticle and the procuticle and is regarded as a reservoir from which secretions likely are evacuated passing through the inner epicuticle. The inner epicuticle is incompletely penetrated by numerous tubular indentations. The peculiar structure of the pustules is shown to be a specialized region of the complex cuticle of the mite being provided with pore canals which terminate under cuticular indentations and a peculiar tunnel system. The latter is organized in cuticular ribs by spaces between inner epicuticle and procuticle. The function of the pustules and the tunnel system remains unknown, but inter- and/or intraspecific communication or a defensive role seem likely.

KEYWORDS — defense; epicuticle; gland; pore canals; procuticle; ultrastructure

INTRODUCTION

Labidostomatidae (Labidostomidae, Labidostommidae, Labidostommatidae, and Nicoletiellidae of authors) is a small family of mites regarded as a basal taxon within Prostigmata and comprising about 50 described species (Walter *et al.* 2009). These mites feed on small arthropods (Vistorin 1980) and reproduce by indirect spermatophore transfer (Schuster and Schuster 1969; Vistorin 1978) with *Labidostoma luteum* being parthenogenetic in its northern range (Betrand 1989; Walter *et al.* 2009). Labidostomatidae are peculiar because of a body armored almost completely by thick shields that are beautifully sculptured (e.g., Alberti *et al.* 1981; Vistorin 1981; Alberti and Coons 1999; Walter *et al.* 2009). Among other characteristics, these mites (the genus *Sellnickiella* is an exception; Walter *et al.* 2009) show behind the one pair of lateral eyes (lacking in some species; Bertrand and Coineau 1978/79) a more or less pronounced protuberance, called "pustule" (or "Seitenhöcker" by Thor 1931), which may be divided in a series of smaller cones on each side (Vitzthum 1940/43; Grandjean 1942a; Baker and Wharton 1952; Coineau 1964; Robaux 1977; Bertrand 1990) and is present already in the

larva (Grandjean 1942b). The pustules have been considered "enigmatic organs" (Walter *et al.* 2009) although it was shortly but clearly stated by Alberti and Coons (1999) that these structures represent glands substantiating the impression of Atyeo and Crossley (1961) who addressed these organs as "gland-like structures". Since larger dermal glands connected to the body surface in prostigmatid mites are rather exceptional and only freshwater mites generally possess a number of conspicuous glands, it seems reasonable to study these structures more closely.

MATERIALS AND METHODS

Specimens of *Labidostoma luteum* Kramer, 1879 were collected near Kiel (northern Germany) and Heidelberg (southwestern Germany) from leaf litter. For transmission electron microscopy (TEM) living specimens were cut into halves with a razor blade under a dissecting microscope and in a drop of cold fixative (ca. 4 °C). The specimens were transferred into a small vial containing the cold fixative, *i.e.* 3.5 % buffered glutaraldehyde (phosphate buffer: pH 7.4; 0.1 M) and placed into a refrigerator. After about 2h, the material was rinsed with buffer solution several times over 2h. Subsequently the tissues were transferred into a 2 % aqueous OsO_4-solution for another 2h. After rinsing again with buffer for 10min, tissues were dehydrated with graded ethanols (60 %, 70 %, 80 %, 95 %, absolute) and transferred into Araldite using propylenoxide as an intermedium. Polymerization occurred at 60 °C. Ultrathin (70 nm) and semithin (400 nm) sections were taken with a Leica Ultracut using a diamond knife. Semithin sections were used for general orientation with a conventional light microscope after staining according to Richardson *et al.* (1960). The ultrathin sections were stained with uranylacetate and lead citrate (Reynolds 1963) and studied in a JEOL Jem-1011transmission electron microscope (TEM). For scanning electron microscopy (SEM) material preserved in 70 % ethanol was used. The specimens were cleaned using ultrasound and then critical point dried. They were sputtered with Palladium-Gold and studied with a Zeiss EVO LS10 scanning electron microscope (see Alberti and Nuzzaci 1996 for more technical details).

RESULTS

In *Labidostoma luteum*, one pustule is located immediately behind each eye (Figure 1a). The SEM-images show a structure resembling the hat of a mushroom. In contrast to the surrounding cuticle including the eyes, the surface of the pustule is smooth (Figure 1b, c). Only in high magnification many tiny pores are detectable (Figure 1d). Figure 1e shows a pustule damaged by ultrasound. It reveals that under the smooth external cuticular layer a second layer is present, which has quite obvious perforations. Because of the cleaning with ultrasound the cerotegument (secretion layer) has largely disappeared.

The sections show that the pustule is made of a protuberance of the procuticle which towards its tip becomes thinner. Here the procuticle is perforated (Figures 2a,b, 3 and 7). The epicuticle is separated from the procuticle in the region of the pustule. Thus a space is formed between procuticle and epicuticle which is filled with a granular material. This space is only narrow immediately above the perforations of the procuticle but becomes wider towards the periphery of the pustule. In the apical area, a small connection between procuticle and epicuticle is retained (Figures 2d and 3a). The perforations of the procuticle are rather wide, but peripherally bridged by very thin, porose procuticular plates (Figures 3a,b), which are likely destroyed in the SEM-image (Figure 1d) through the ultrasound treatment. The contents of the space between procuticle and epicuticle is similar to the material found under the porose procuticular plate and appears similar thoughout (Figure 3b). The epicuticle overlying the mentioned space consists of an inner epicuticle (epicuticle s.str.) and a cerotegument of varying thickness (Alberti and Coons 1999). The inner epicuticle is penetrated by thin tubes containing a material continuous with the cerotegument. However, these tubes do not penetrate the inner epicuticle completely. A thin layer of inner epicuticle is proximally always present (Figures 3 and 8a).

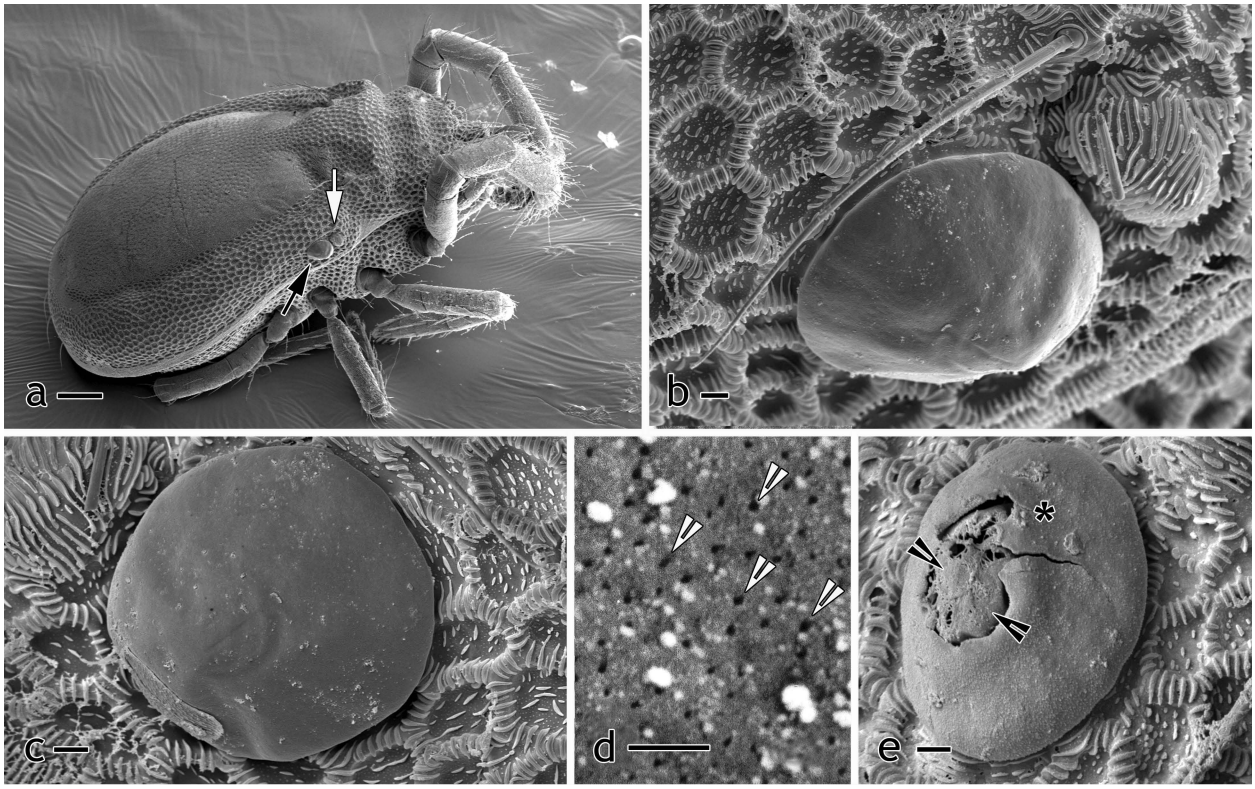


FIGURE 1: SEM images of *Labidostoma luteum* showing pustules. Specimens were cleaned using ultrasound and thus the cerotegument (secretion layer) is mostly removed. a – Dorsolateral view. Black arrow points to pustule, white arrow to eye. Note nicely sculptured cuticle. Scale bar: 50 μm; b – Detail showing pustule located immediately behind lateral eye. Note smooth surface of pustule contrasting with the surrounding structures. Scale bar: 5 μm; c – Direct view from above onto the pustule. No opening is visible. Scale bar: 5 μm; d – Direct view onto the surface of a pustule. In this high magnifiction numerous small pores (arrowheads) are visible. Scale bar: 0,5 μm; e – A slightly lateral view on a pustule damaged by ultrasound. Note that a peripheral layer, *i.e.* the epicuticle (asterisk), is partly destroyed revealing a further, deeper layer (arrowheads) which shows penetrations. Scale bar: 5 μm.

Thus, the pores seen in the SEM at high magnification (Figure 1e) indicate only the entrances of blind ending tubes or deep and narrow indentations. The thickness of the inner epicuticle varies being very thin at the tip of the pustule and becoming slightly thicker towards its periphery. The length of the tubes varies accordingly (Figure 3b,c).

Few elongated cells form the tissue beneath the pustule (Figures 2a,b,d, 4 and 7). Each cell has a nucleus which is located in its basal (proximal) region. It contains a distinct nucleolus and is surrounded by abundant rough endoplasmic reticulum (ER). The cisternae of the ER are inflated and contain a rather homogenous, moderately electron-dense material (Figure 4e,f). Within the areas with rough ER, groups of small electron-lucent vesicles occur, which likely represent Golgi bodies.

More distally, the cytoplasm becomes more heterogenous containing large electron-lucent vesicles which seem to form through confluence of smaller, probably Golgi-derived ones (Figures 2a,b,d and 4a-c). There are also dense inclusions, which at least partly are lysosomes (Figure 4d,e). Finally, in the upper third of the cell, distinct organelles are hard to detect and the cell contents becomes rather homogenous (except of electron-lucent vesicles). A distinct apical cell membrane does not exist. The cell contents is continuous with the material apparently delivered through the perforations of the procuticle into the space between procuticle and epicuticle (see above). The lateral cell borders of these cells are interconnected by smooth septate junc-

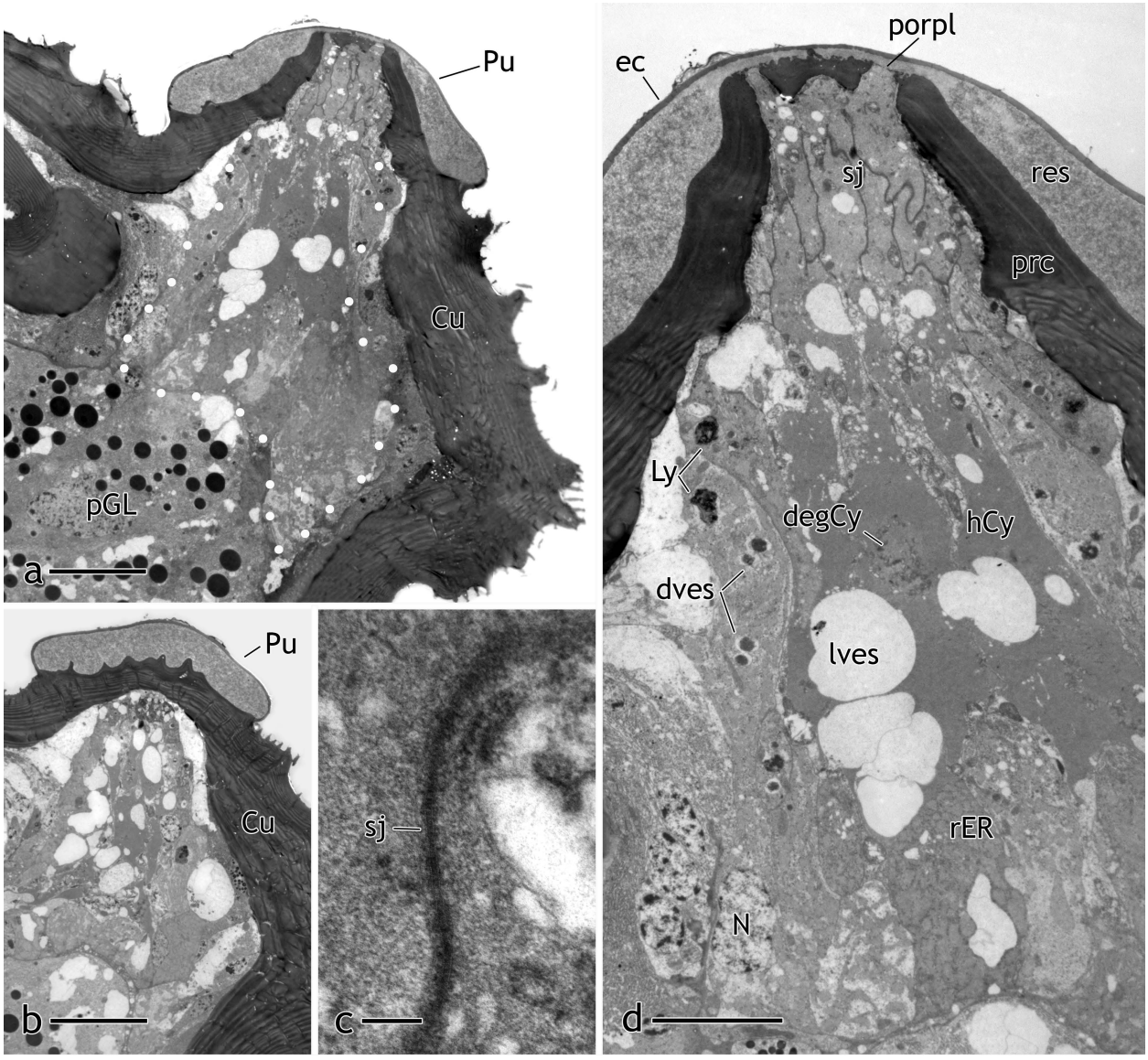


FIGURE 2: TEM images of sections through pustule. a – Overview of a section running through the middle of the pustule. Line of white dots indicates extension of glandular tissue of pustule. The figure is orientated in such a way that the apices of the cells point upwards. Consequently the dorsum of the animal is at right. Scale bar: 10 µm; b – A section through the periphery of the pustule. Scale bar: 10 µm; c – Septate junction between apices of two gland cells (compare Fig. 2d). Scale bar: 0.2 µm; d – Detail of Figure 2a showing the glandular tisssue of the pustule. Scale bar: 5 µm.
Abbr.: Cu, cuticle; degCy, degenerating cytoplasm; dves, electron-dense vesicle; ec, epicuticle; hCy, homogenous cytoplasm; lves, electron-lucent vesicle; Ly, lysosome; N, nucleus; pGL, podocephalic gland; porpl, porose plate of procuticle; prc, procuticle; Pu, pustule; res, reservoir space; sj, septate junction.

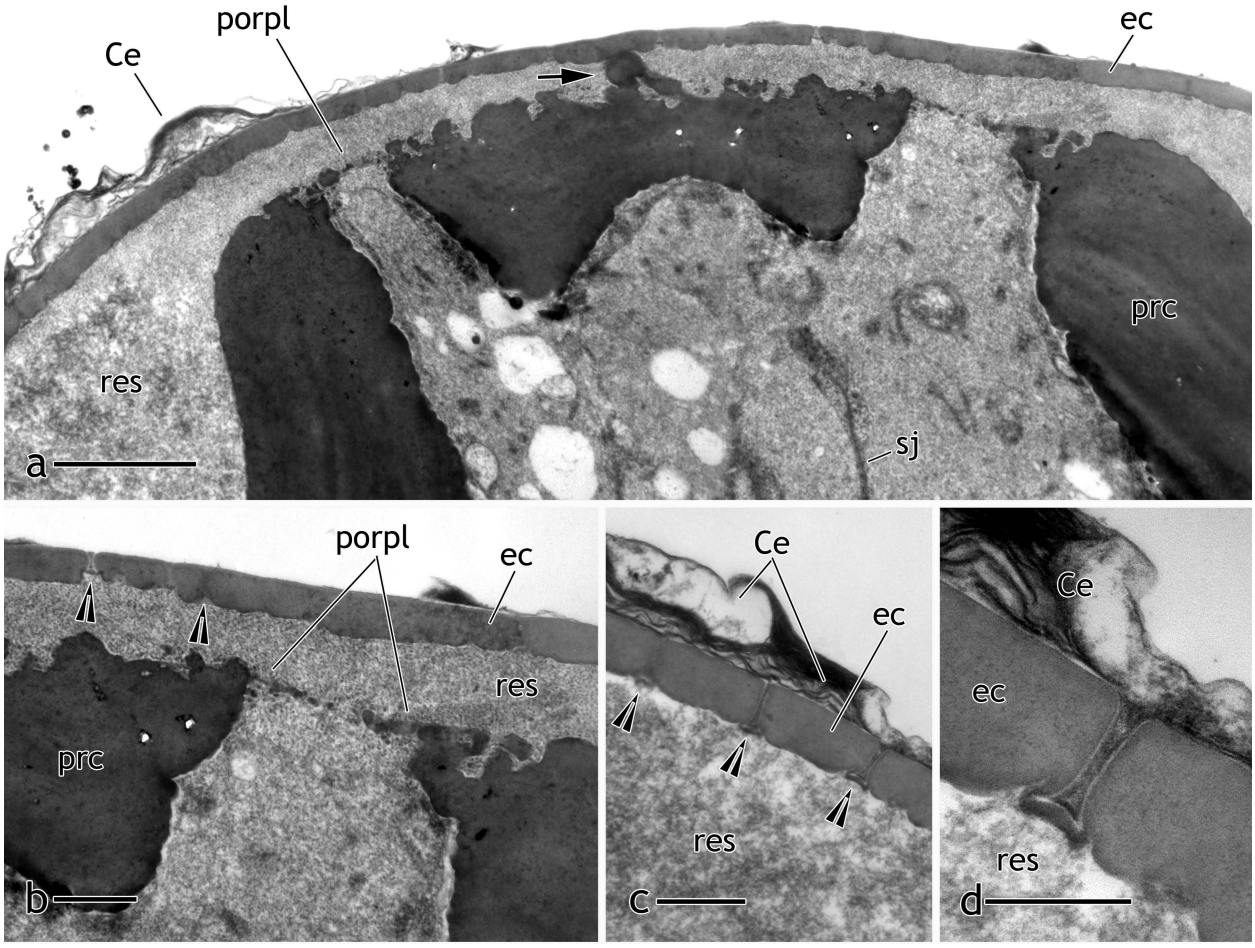


FIGURE 3: Details of apical (distal) parts of pustule. a – Overview showing very thin porose plate of procuticle covering the apical terminations of the glandular cells, the contents of which is delivered into the reservoir space located between epicuticle and procuticle. Note cerotegument. Arrow points to connection between procuticle and inner epicuticle. Scale bar: 1 μm; b – Detail of Figure 3a showing area of porose plate more closely. Arrowheads point to epicuticular indentations. Scale bar: 0.5 μm; c – Detail of a more peripheral area of the pustule. Note that the epicuticle is slightly thicker here and the indentations (arrowheads) are slightly longer. Scale bar: 0.5 μm; d – Detail of Fig. 3c showing epicuticular indentation in higher magnification. Note that the indentations do not penetrate the inner epicuticle completely. Scale bar: 0.2 μm.
Abbr.: Ce, cerotegument; ec, inner epicuticle; porpl, porose plate of procuticle; prc, procuticle; res, reservoir space; sj, septate junction.

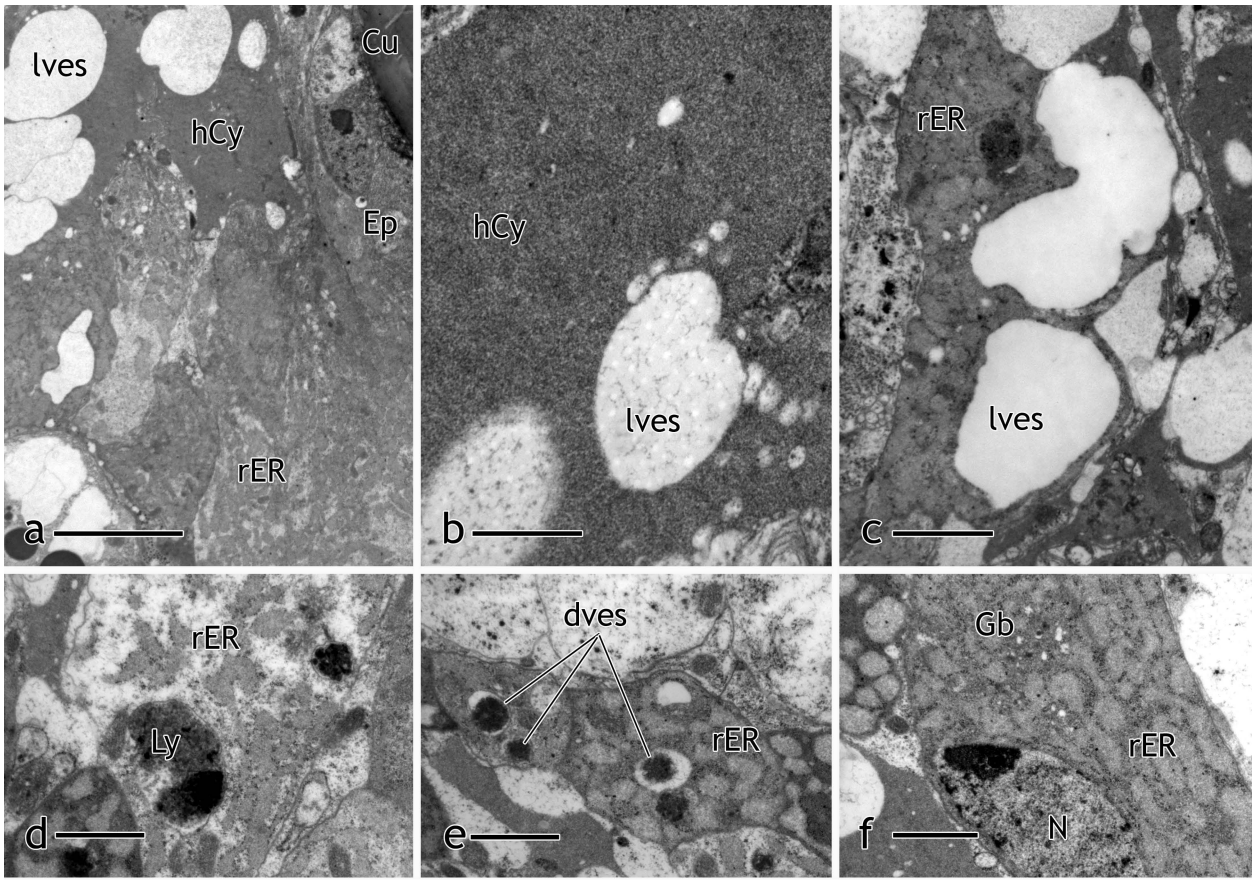


FIGURE 4: Details from the glandular tissue of the pustule. a – Area where the cytoplasm becomes homogenous. Scale bar: 0.5 μm; b – Homogenous cytoplasm. Note large electron-lucent vesicle surrounded by small similar vesicles. Scale bar: 0.5 μm; c – Another aspect with irregularly shaped electron-lucent vesicles likely formed by fusion. Scale bar: 2 μm; d – A region with electron lucent areas in the cytoplasm, inflated rough ER and lysosomes. Scale bar: 1 μm; e – Cytoplasm with dense inclusions. Scale bar: 1 μm; f – Nuclear region with inflated rough ER and indistinct field of small vesicles likely representing a Golgi body. Scale bar: 1 μm.
Abbr.: dves, electron-dense vesicle; Ep, epidermis; Gb, Golgi body; hCY, homogenous cytoplasm; N, nucleus; lves, electron-lucent vesicle; Ly, lysosome; rER, rough endoplasmic reticulum.

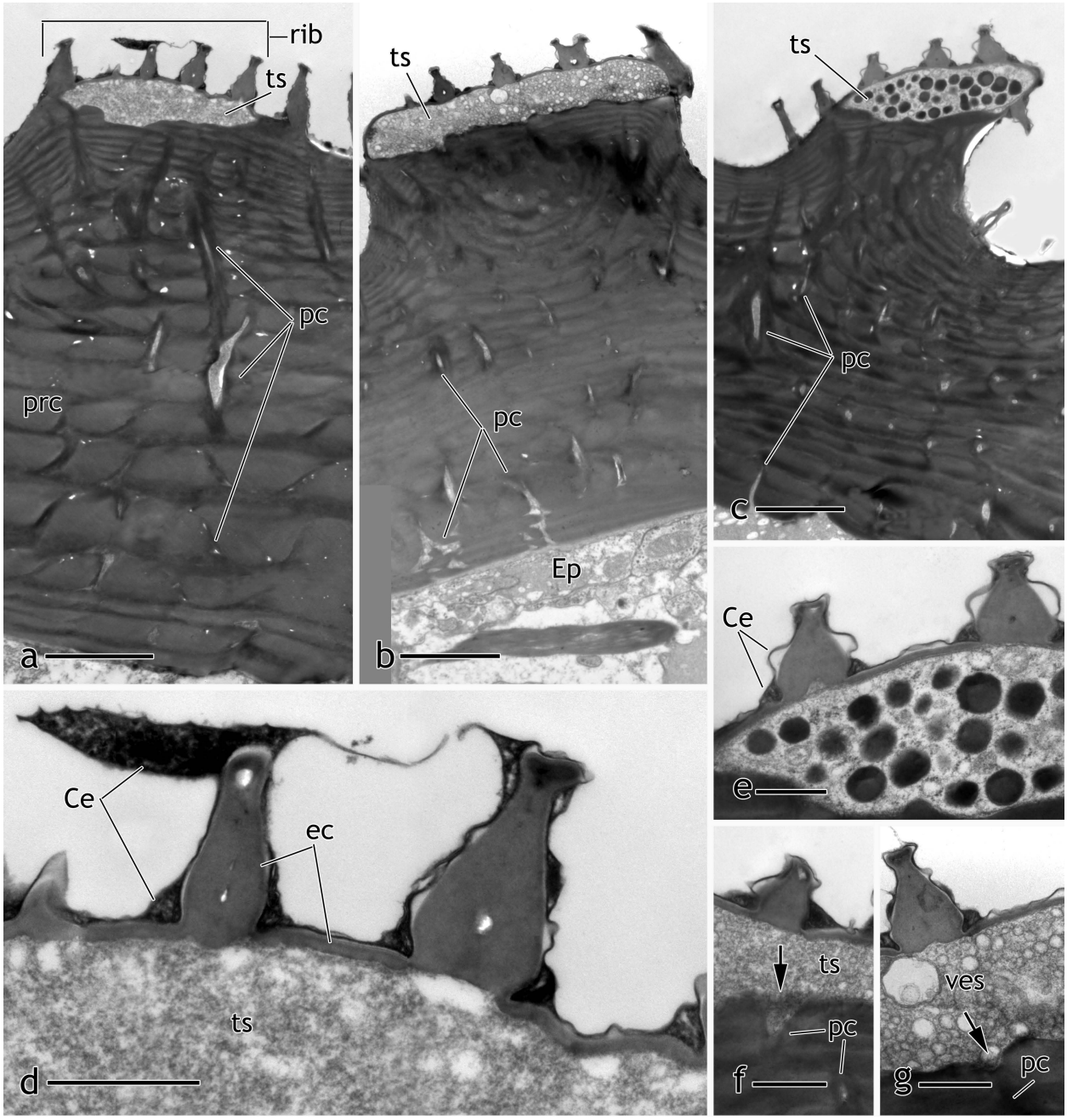


FIGURE 5: Some aspects illustrating the cuticle of the ribs of the cuticular network. a – Overview showing the thick procuticle and an obliquely cut rib. Note that the lumen in the tunnel system underneath a rib is filled with a material similar to that in the reservoir space of the pustule. Scale bar: 2 μm; b – This rib contains a material showing many vesicles. Scale bar: 2 μm; c – This rib contains many electron-dense granules. Scale bar: 2 μm; d – Detail of Figure 5a showing that the distal cover of the tunnel system is made from epicuticle. The very thin inner epicuticle shows no indentations. Note cerotegument. Scale bar: 0.5 μm; e – Detail of Figure 5c showing distinct dense granules in the tunnel system. Scale bar: 0.5 μm; f – The pore canal traversing the procuticle opens (arrow) into the tunnel system of the ribs. Scale bar: 0.5 μm; g – Detail of Figure 5b showing distinct and intact vesicles in the space underneath the rib. Arrow points to end of tangentially sectioned pore canal. Scale bar: 0.5 μm.
Abbr.: Ce, cerotegument; ec, inner epicuticle; Ep, epidermis; pc, pore canal; prc, procuticle; rib, rib; ts, tunnel system; ves, vesicle.

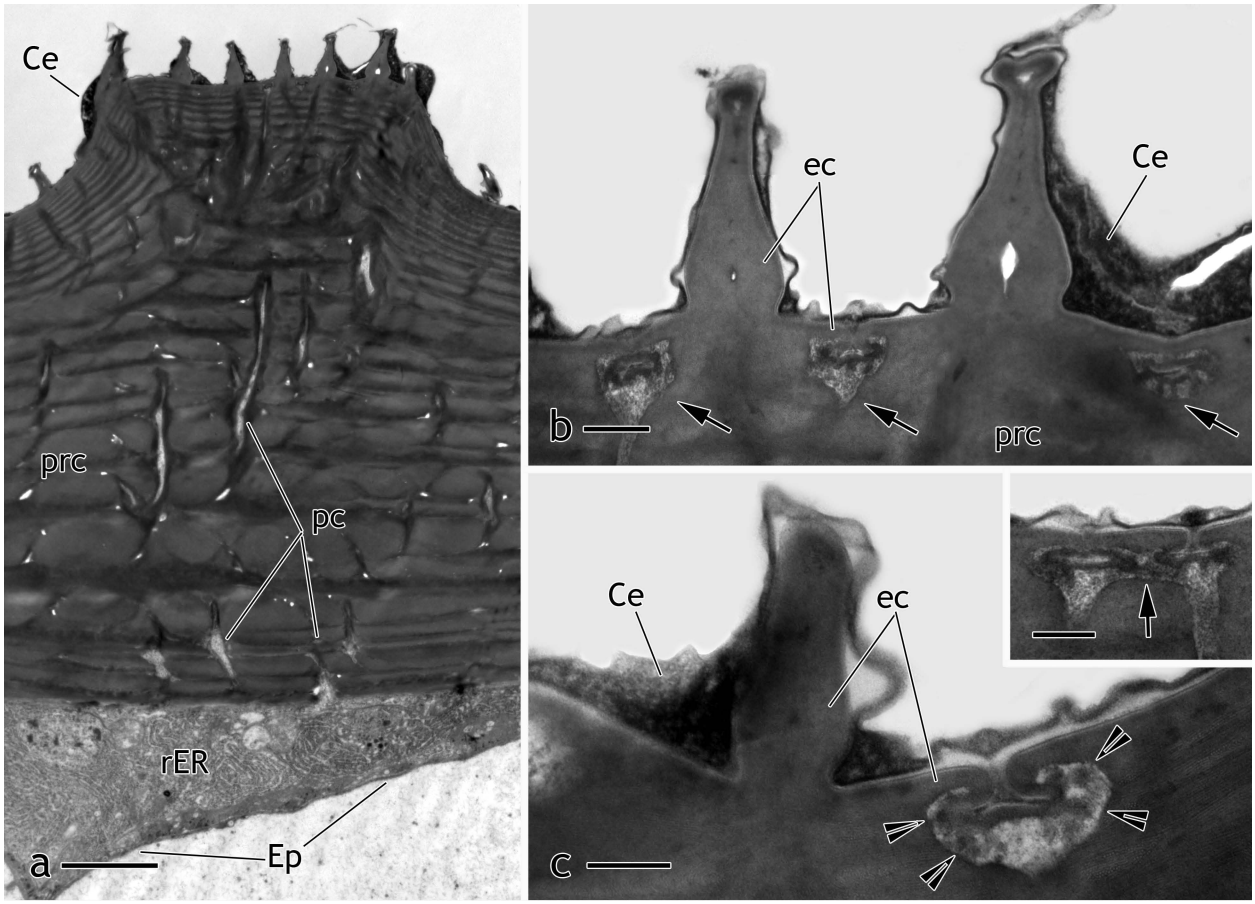


FIGURE 6: Structure of "normal" cuticle, *i.e.*, of cuticle not bearing ribs. a – Overview. Note numerous pore canals and prominent rough endoplasmic reticulum in epidermis. Scale bar: 2 μm. b – Detail showing the distal terminations of three pore canals (arrows). Note varying thickness of epicuticle being rather thick when building the tiny processes (platelets) and very thin when approaching the indentations over the pore canals. Scale bar: 1 μm. c – Epicuticular indentation above the termination of a pore canal in higher magnification. Arrowheads indicate clusters of dense material (see also Figure 6b). Scale bar: 0.2 μm. Inset – The terminal parts of neighbouring pore canals may connect (arrow). Scale bar: 0.2 μm.
Abbr.: Ce, cerotegument; ec, inner epicuticle; Ep, epidermis; pc, pore canal; prc, procuticle; rER, rough endoplasmic reticulum.

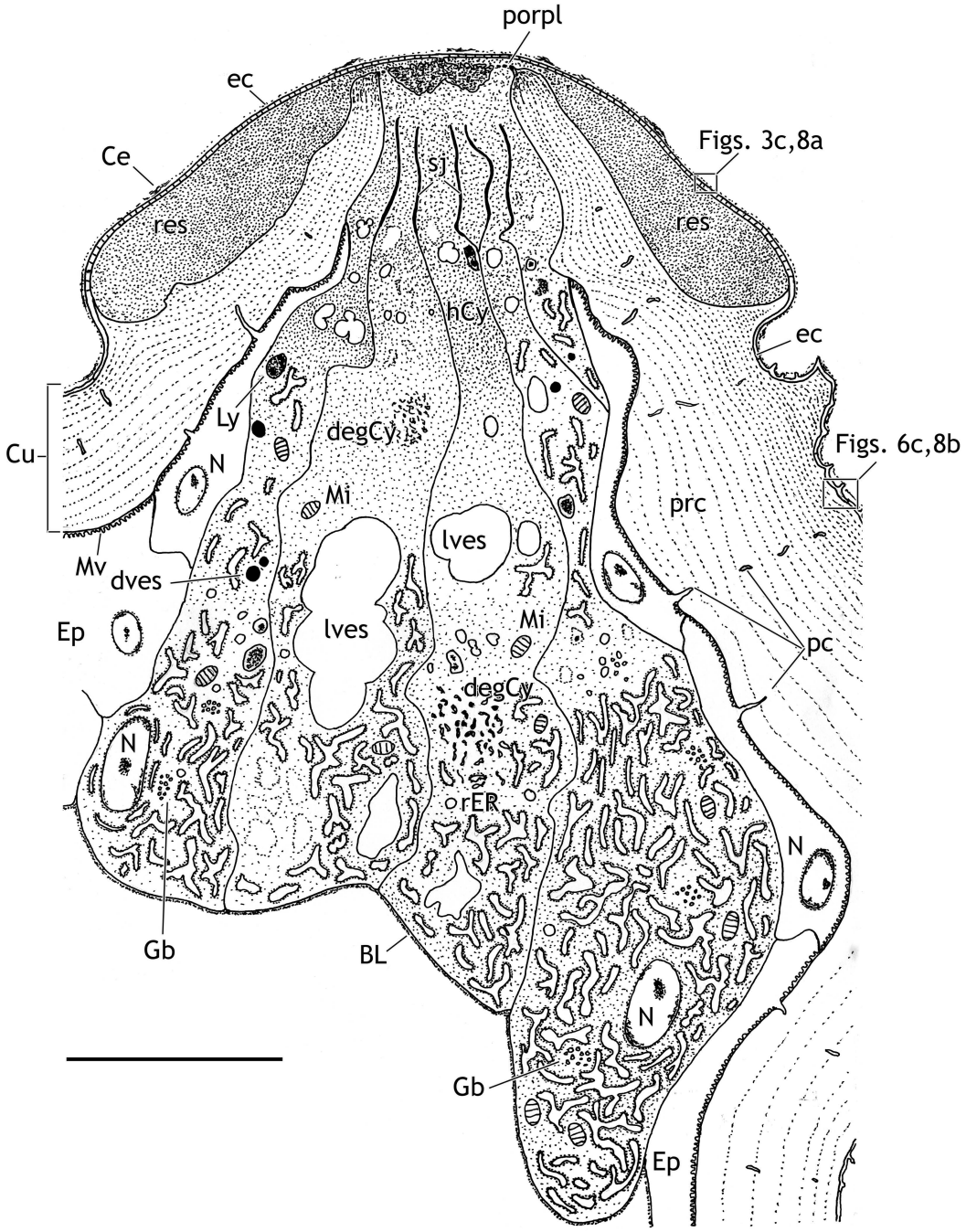


FIGURE 7: Schematic drawing of a section through a pustule of *Labidostoma luteum* (compare Figure 2a,d) showing the cuticular and cellular components. "Normal" epidermal cells are only indicated. Note many indentations in the epicuticle covering the reservoir space. Squared areas are shown in higher magnification in Figures 3, 6, 8. Scale bar: 10 μm.
Abbr.: BL, basal lamina; Ce, cerotegument; Cu, cuticle; degCy, degenerating cytoplasm; dves, electron-dense vesicle; ec, inner epicuticle; Ep, epidermis; Gb, Golgi body; hCy, area of homogenous cytoplasm; lves, electron-lucent vesicle; Ly, lysosome; Mi, mitochondrium; Mv, microvilli (of "normal" epidermal cells); N, nucleus; pc, pore canal; porpl, porose plate of procuticle; prc, procuticle; rER, rough endoplasmic reticulum; res, reservoir space; sj, septate junction.

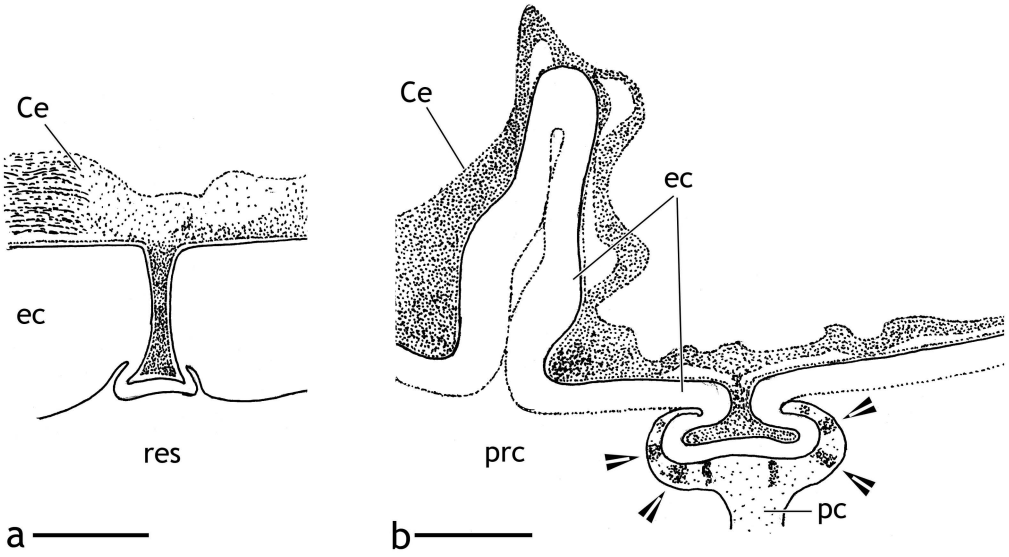


FIGURE 8: Schematic drawings of epicuticular indentations from cuticular regions indicated in Figure 7. a – From pustule. Note relatively long indentation of the, in this peripheral region thickened, inner epicuticle. The indentation reduces the thickness of the inner epicuticle just above the termination of the pore canal considerably. Scale bar: 0.2 μm; b – From "normal" cuticle. Note relatively thin inner epicuticle, which becomes even thinner towards its indentation. The thin epicuticular layer above the termination of the pore canal has almost the same thickness as that at the base of an indentation of the pustule. Note clusters of dense material (arrowheads). Scale bar: 0.2 μm.
Abbr.: Ce, cerotegument; ec, inner epicuticle; pc, pore canal; prc, procuticle; res, reservoir space of pustule.

tions, which do not reach the procuticle, however (Figure 2c,d).

As mentioned already, the cuticle of the mite is nicely sculptured. Over wide areas of the idiosoma a network of ribs is present. These ribs and the spaces they surround are finely structured by small platelets (Figure 1a-d). Ribs and platelets are made of epicuticle (Figures 5 and 8b). The ribs contain a space between the epicuticle and the underlying, multilayered procuticle, which is filled with a material similar to that found in the space of the pustule (Figure 5a,d). Remarkably, the space under the ribs may also include distinct granules (Figure 5c,e) and intact vesicles (Figure 5b,g). In the region between the ribs, pore canals run through the procuticle and terminate under the epicuticle with a wider portion which embraces small, peculiar indentations of the inner epicuticle (Figures 6 and 8b). Thus, as in the epicuticle of the pustule, a thin layer of inner epicuticle separates the lumen of the pore canal from that of the indentation. Clusters of dense material form bridges between the epicuticular indentation and the procuticle (Figures 6b-c and 8b). Terminations of neighbouring pore canals may be connected (Figure 6c-Inset). Since the inner epicuticle in these areas is slightly thinner than that of the pustules, the epicuticular indentations are also shorter. Under the ribs, the pore canals open into the mentioned space (Figure 5f,g). In contrast to the surrounding cuticle, the tiny indentations of the inner epicuticle appear to be absent or are extremely rare on the ribs (Figure 5d-g).

DISCUSSION

It is evident that the pustule of *Labidostoma luteum* represents a glandular structure. However, this gland shows a number of peculiarities. Most remarkable is the external, cuticular protuberance with its space between procuticle and epicuticle. This space is regarded here as a reservoir in which

secretions delivered from the underlying cells are stored. The procuticle does not only show a reduction in thickness in the area of the pustule, but is also provided with few but wide penetrations regarded as enlarged pore canals. The next peculiarity is that there is no open connection to the external medium through which the secretion could be delivered. Finally, the mode of producing the secretion is much peculiar in so far as the rough ER and Golgi bodies are involved but then, the apical cytoplasm seems to be gradually dissolved and delivered through the wide pore canals and porose plates into the reservoir space.

The absence of a real open connection of the gland towards the external medium is comparable to the secretory porose organs found in many oribatid mites (Alberti and Norton 1997). In these organs and in the pustules, the secretion has to move through the thin inner epicuticle. In many actinotrichid mites, the inner epicuticle forms small indentations above the terminations of the pore canals penetrating the procuticle (but never the epicuticle) (Alberti *et al.* 1981; Alberti and Coons 1999; Alberti *et al.* 2001). This is also the case in *Labidostoma luteum* in areas of the "normal" cuticle, but also in the pustules. This structural peculiarity makes the epicuticular layer above the pore canals very thin and thus the distance which the secretion has to pass through very short. This evidently facilitates diffusion, which thus likely is the mode of getting the secretions outside. However, tiny channels in the inner epicuticle above the pore canals may improve this mode of excavation (see also Alberti and Norton 1997).

Glands which have an orifice which really penetrates the cuticle are rare in prostigmatid mites. To the author's knowledge they only occur in freshwater mites, which possess several rather large dermal glands in the idiosoma that serve in part as defense structures against predators (e.g., fish), others are related to reproductive behaviour (e.g., Vitzthum 1940/43; Alberti and Coons 1999; Proctor and Garga 2004; Shatrov 2008; Kirstein and Martin 2010; Smit and Alberti 2010). Many Oribatida and Acaridida (= Astigmata, Astigmatina) also possess a pair of quite large glands called opisthonotal glands (also lateral opisthosomal, abdominal or oil glands) with a real orifice, which serve interspecific communication and/or defense (Kuwahara 1991, 2010; Raspotnig 2010, Heethoff *et al.* 2011) and are regarded as a synapomorphy uniting these taxa besides other characters (Sarcoptiformes; OConnor 1984, 2009; Norton 1998; Sakata and Norton 2001; Raspotnig 2006; Norton and Behan-Pelletier 2009). The large glands of all these groups differ structurally and with regard to their position in the mite's body. They occur as singular structures within their wider systematic relationships. Thus, it seems evident that the glands, *i.e.* the pustules of Labidostomatidae (Prostigmata, Labidostomatina), the dermal glands of Hydrachnidia (Prostigmata, Parasitengona) and the opisthonotal glands of Oribatida and Acaridida (Sarcoptiformes) have evolved independently within Actinotrichida (= Acariformes) representing autapomorphies of the taxa possessing them.

A peculiar structure until recently of unknown function, which is of much interest in the context of this paper, are the lateral protuberances called, e.g., "verrues dorsales" (Grandjean 1947) or "urnulae" (Southcott 1961) of balaustiine mites (Prostigmata, Parasitengona, Erythraeidae). Like the pustules of Labidostomatidae, they are located behind the pair of lateral eyes and are present in one or two pairs on deutonymphs and adults (Southcott 1961; Lindquist 2001). These organs have been shown by Yoder *et al.* (2006, 2010) to represent glandular structures that secrete a defensive allomone and an alarm pheromone. A potential role of the urnulae in osmoregulation has also been considered (Maḳol *et al.* 2012). According to the images provided by the authors (e.g., Grandjean 1959; Yoder *et al.* 2006; Maḳol 2010; Maḳol *et al.* 2012) it is not evident whether a real opening is present or not. In contrast to Labidostomatidae, urnulae are absent in the larval balaustiines (Grandjean 1957; Maḳol 2010; Maḳol *et al.* 2012). Again these structures occur quite isolated within Erythraeidae representing an autapomorphy of Balaustiinae. In any case, the rather similar position of urnulae and pustules may be of functional significance.

In contrast to Actinotrichida, dermal glands are

frequent in all Anactinotrichida (= Parasitiformes) and differ structurally from those of Actinotrichida but are similar throughout Anactinotrichida. This similarity is most obvious with regard to the evacuation canals and orifices all provided with a peculiar cuticular structure called "calyx" that is always lacking in actinotrichid mites (e.g., Fain 1966; Athias-Henriot 1969; Alberti and Coons 1999; Coons and Alberti 1999; Alberti 2006). At this moment, another cuticular feature should be emphasized which refers to the small indentations of the inner epicuticle above the terminations of the pore canals. These indentations have been found in representatives of all actinotrichid main groups (e.g., "Endeostigmata", Prostigmata, Oribatida, Acaridida) but never in Anactinotrichida (Alberti *et al.* 1981; Alberti and Coons 1999; Alberti 2006). Along with other characteristics, this stresses the fundamental separation of both main groups and in fact, it becomes more and more evident, that Acari is not a monophyletic taxon (e.g., Alberti 2006; Dunlop and Alberti 2008; Dabert *et al.* 2010; Pepato *et al.* 2010; Dunlop *et al.* 2012).

Turning back to Labidostomatidae, it seems worthy to comment on the peculiar cuticle. This is much and intricately sculptured placing these orange-red coloured mites among the most beautiful creatures of the soil mesofauna. The fine sculpture together with the cerotegument likely prevents the cuticle of getting in direct contact with water when the soil is flooded, e.g., during heavy rainfalls, providing some kind of plastron as is assumed also for other soil arthropods (e.g., Alberti *et al.* 1981; Messner *et al.* 1992). But *Labidostoma luteum* (and likely other species of Labidostomatidae) offers a further peculiarity: the projecting network of ribs. As shown here these ribs are provided with a space between epicuticle and procuticle similar to the reservoir space of the pustule. Likely, the spaces in the ribs are communicating (Alberti *et al.* 1981) providing a network of tunnels filled with secretion and covering most of the body.

A model illustrating a possible evolutionary start point of such a modification of the cuticle forming wide spaces between pro- and epicuticle may be represented by the observed connections between the terminations of neighbouring pore canals. A similar terminal connection between neighbouring pore canals forming a wider confluent space underneath the epicuticle was observed in certain Oribatida (Alberti and Norton 1997).

Since other sources are not recognizable, it seems most likely that the secretions filling the tunnels of the network are produced by the epidermal cells and reach the tunnel system through the pore canals. Like in the pustules, the pore canals after traversing the procuticle open into the space between procuticle and epicuticle. As we found occasionally intact vesicles in the tunnel system, it seems evident that cellular components contribute to the contents of the tunnels as is the case of the reservoir space of the pustules.

In contrast to other components, which reach the surface of the body via the "normal" pore canals to form the cerotegument, the components filling the tunnel system are retained here like the secretion of the pustules. Thus, the pustule seems to represent a specialized and isolated region of the tunnel system. However, it differs not only by size and shape but also by the presence of indentations in the inner epicuticle. These are quite frequent in the pustule and the "normal" cuticle, but rare or even absent in the ribs.

Remarkably, Grandjean (1942a) already regarded the pustules as a structure that has evolved from the "normal" pores (*i.e.*, the pore canals): "Les pustules sont donc des pores perfectionnés."

Of course, one would like to know the function of these structures. Only speculations are possible at the moment. It may be that the tunnel system or ribs may contain a secretion which has defensive properties being, e.g., poisonous or untasty for potential predators. Thus it may represent a kind of permanent chemical coat of chain mail which will be effective when a predator bites the mite. On the contrary, the secretion of the pustule may continuously deliver substances through the many epicuticular indentations, thus contributing to the cerotegument (which is continuous with the contents in the indentations) with a component serving interspecific communication and/or creating an adverse atmosphere around the mite preventing at-

tacks by a potential predator. Thus a function of the pustules comparable to those of the urnulae of balaustiine mites (see above) seems imaginable.To substantiate these speculations the chemistry of the secretions and the behaviour against potential predators need to be studied.

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