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Ultrastructure and probable function of urstigma (Claparède organ) in mites of the families Trombiculidae and Microtrombidiidae (Acariformes: Parasitengona)

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Abstract

Urstigma (Claparède organ) in larvae of *Platytrombidium fasciatum* (C.L. Koch, 1836) and *Camerotrombidium pexatum* (C.L. Koch, 1837) (Acariformes: Microtrombidiidae) as well as of *Hirsutiella zachvatkini* (Schluger, 1948) and *Leptotrombidium orientale* (Schluger, 1948) (Acariformes: Trombiculidae) was investigated by scanning and transmission electron microscopy. Urstigma in mites of both families is represented by small multicellular organ generally located between coxae I and II and provided externally by a complex cuticular armature and a hemispherical protected cover (cup, lid). The organ is built up of light cells with few organelles except for mitochondria and microtubules. The cells form deep reciprocal folds on their inner lateral sides and demonstrate a somewhat apical activity supposedly of both endocytotic and exocytotic nature. However, neither robust pleats (strong placations) of the apical plasma membrane, nor basal infoldings of the cells were observed in the urstigma. A cuticular plate devoid of conspicuous pores covers the surface of the urstigma and leaves a rather narrow subcuticular space. The supposed initial function of this organ in Acariformes for the transport of ions and fluids is found to be significantly reduced in these families according to morphological evidence. In trombiculid larvae, in comparison with microtrombidiid ones, the urstigma shows further reduction of its morphological components as well as of probable functional properties. Intercellular processes providing functional activity of urstigmae and their comparative anatomy are also discussed.

Keywords : morphology, fine structure, larvae, Parasitengona.

Introduction

The urstigma (Claparède organ) is a highly specialized larval organ found in most Acariformes, which is considered to play an important role in the process

of regulation of water and salt balance in hypo-osmotic media (*see* ALBERTI, 1979; BAKER, 1985; FASHING, 1988; GOLDSCHMIDT *et al.*, 1999). According to this function, urstigmae appear to closely correspond to the specific chloride cells of freshwater insects (KOMNICK, 1977). Generally located in a number of one pair between coxae I and II, larval urstigmae are thought substituted in active postlarval instars by most prominent structures called "genital papillae" or "acetabula" located not only on genital valves (GRANDJEAN, 1948; ALBERTI, 1976; VERCAMMEN-GRANDJEAN, 1976; WITALINSKI *et al.*, 1990; *etc.*), but also on coxae and even immediately on the ventral body wall in some water mites (*see* BENFATTI & GERECKE, 1999; GOLDSCMIDT *et al.*, 1999). Nevertheless, the general distribution of those organs among postembryonic instars in Acariformes is thought to obey to the "Oudemans-Grandjean rule" (JOHNSTON & WACKER, 1967) with some essential exceptions (GRANDJEAN, 1946; KRANTZ, 1977; ANDRÉ, 1991). However, the urstigmae in mites of the suborder Actinedida, in particular from the cohort Parasitengona, remain poorly investigated morphologically, and this does not allow us to clarify its functional and phylogenetic tendencies in the higher trombidiform mites with certainty. Correspondingly, urstigmae of trombiculid and trombidiid larvae have not been studied previously in detail, and as far as is known there are no observations using transmission electron microscopy until now.

On the basis of the above-mentioned considerations, the main purpose of this study is to provide a detailed ultrastructural examination of urstigmae of the representatives of the families Trombiculidae - *Hirsutiella zachvatkini* (Schluger, 1948) and *Leptotrombidium orientale* (Schluger, 1948), and Microtrombidiidae - *Platytrombidium fasciatum* (C.L. Koch, 1836) and *Camerotrombidium pexatum* (C.L. Koch, 1837) and to evaluate their probable functional peculiarities.

Materials and methods

Trombiculid larvae used in this study were obtained from a laboratory culture that had been maintained for more than twenty years in the Laboratory of Parasitology, Zoological Institute Russian Academy of Sciences (*see* SHATROV, 1993, 1996). Adults of microtrombidiid mites were collected from the soil surface in Leningrad district during spring-summer period of 1996. Mites presumably of the same species were initially placed into small plastic jars with soil particles as a substrate. Approximately two weeks later mites had laid eggs, from which active unfed larvae hatched during another two weeks and were taken for fixation. Identification of the mite species was made by Dr. J. Makol from the Agricultural University of Wroclaw (Poland).

For transmission electron microscopy (TEM), active larvae of both trombiculid and microtrombidiid mites were initially fixed in 2.5% glutaraldehyde in 0.1 M phosphate buffer (pH 7.2-7.4) for 2-4 h. After immersion in the fixative fluid animals were either carefully pierced with tiny insect pins for better penetration of fixative solutions or were left intact. Mites

were then washed in several changes of 0.2 M phosphate buffer, postfixed in 2% osmium tetroxid in phosphate buffer containing 8.56% sucrose for 1-6 h to overnight, dehydrated in alcohol and acetone series, and finally embedded in an araldite mixture. Serial ultrathin sections both in transverse (as a rule) and in longitudinal planes were made on a LKB-III ultramicrotome, and after staining with uranyl acetate and lead citrate, were examined with Tesla BS-500 and LEO-900 transmission electron microscope at 60-90 kV. For preliminary and general observations, semi-thin sections were stained with toluidine blue and investigated under an Amplival light optical microscope.

For scanning electron microscopy (SEM), larvae after alcohol fixation and alcohol and acetone treatment were dried at the critical point of carbonic acid in a Hitachi HCP-2 vacuum evaporator, covered with a platinum layer in an Eiko-5 apparatus and examined with a Hitachi S-570 electron microscope at 20 kV.

List of Abbreviations: AC – additional cell; AV – additional valve; BL – basal lamina; CB – cell borders; CC – cuticular cap; CGl – coxal gland; CPl – cuticle of prelarva; CS – cuticular stalk; CU – cuticle of urstigma; CV – clear vesicles; CxI – coxa I; DV – dense vesicles; FCC – frontal cuticular cap; G – Golgi body; H – haemocyte; HC – hemispherical caver; LgI – leg I; M – mitochondria; MI – membrane invaginations; Mt – microtubules; N – nucleus; Nu – nucleolus; Pr – polyribosomes; SGl – salivary gland; Ur – urstigma; V – vacuole.

Results

Microtrombidiidae

In *P. fasciatum* and *C. pexatum* the urstigmae are organized identically.

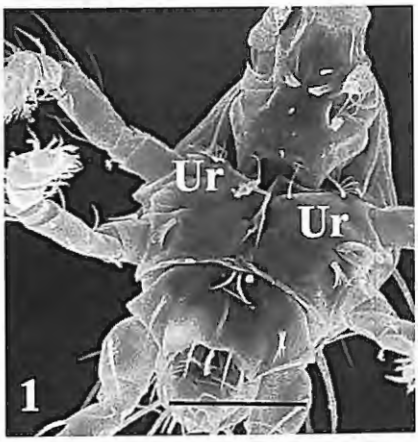
From the external SEM examination, the urstigmae are located on the ventral body wall just between coxae I and II, approximately in the middle level of the body in unfed larvae (Fig. 1). A protected cuticular cap with the flat surface rather resembling an eyelid covers the urstigma from the front side (Fig. 2). The backside of the organ is frequently protected by a smaller back lid. The remaining middle part of the urstigma exposed freely is represented by an own cuticle of the organ in the form of a hemispherical cuticular cover bearing tiny pits of pore foramens (Figs 2, 6, 7). That is all what may be seen from the outside. One specimen of *P. fasciatum* captured during moulting from quiescent prelarva to active larva, has demonstrated a dissimilarity of the external organization of the urstigma armature between the prelarva and the active larva (Fig. 3) (*see* SHATROV, 1998).

TEM examinations reveal that the urstigma is a relatively large multicellular organ, which protrudes into the body cavity in the form of a flat-walled irregular sac being enveloped by a basal lamina (Figs 4, 5). It appears that the proper urstigma is hidden, besides frontal and back cuticular caps, by a complex system of the inner additional valves or flaps (Figs 5, 6), which flank the urstigma on the sides in a transverse plan (Fig. 6). The immediate

hemispherical cuticular cover of the proper urstigma is provided with external pore foramens and with curved and hardly identified pore canals in it (Figs 6-8) and is mostly concealed under the protecting cuticular lids. In the zone where the organ protrudes into the body there is observed a more or less developed beam waist (constriction), which is nearly inconspicuous at the middle line of the urstigma (Fig. 4) and, on the contrary, more prominent on its periphery (Fig. 5).

The urstigma is mostly composed of light cells with clear cytoplasm forming a body of the organ, and also of flat additional cells surrounding the upper sides of the organ beneath the lateral valves (Figs 4, 6) and located irregularly on the surface of the organ in its deeper part (Fig. 11) being encompassed by a united delimiting basal lamina. The cells have a general orientation from the basal lamina to the upper side of the urstigma and possess rather irregular outlines forming deep mutual folds on their inner lateral borders (Figs 6, 7, 9, 11). Cells are connected via hardly identified septate desmosomes located irregularly. A basal plasma membrane remains flat and does not form conspicuous infoldings (Fig. 12), although the neighboring cell borders may show folds nearly from the immediate cell bases (Fig. 11). The cells are provided with a relatively large number of mitochondria scattered freely throughout the cytoplasm with somewhat concentration to the middle parts of the cells (Fig. 4, 10) or to the cell apexes near the periphery of the urstigma (Fig. 9). Mitochondria are sometimes long and curved with a dense matrix and tightly packed cristae. Nuclei 2.7-3.6 ìm in diameter with irregular outlines and decondensed chromatin occupy predominantly middle and basal parts of the cells (Figs 5, 11, 12). The round to oval nucleolus is located eccentrically. The cells also contain free ribosomes and polysomes, hardly identified Golgi bodies built up of few and rather narrow cisterns and finally a small number of dense vesicles of moderate size frequently situated in the vicinity of the Golgi zones (Figs 10-12). A various number of clear vesicles and vacuoles of quite different sizes are also present in the cytoplasm for the most part both in the apical and in the marginal zones of the cells (Figs 8, 9, 10). Microtubules oriented predominantly along the cell axis are found rarely (Figs 7, 8). Conspicuous elements of endoplasmic reticulum were not identified with certainty in the cells of urstigmae of microtrombidiid larvae.

Figs 1-6. Ultrastructure of urstigmae of *Camerotrombidium pexatum* (1, 5) and *Platytrombidium fasciatum* (2-4, 6) larvae (Microtrombidiidae). 1-3 – SEM, 4-6 – TEM. 1 – General view of the ventral body side showing location of the urstigmae. Scale bar – 85 μm; 2 – Left urstigma from medial aspect. Scale bar – 10 μm; 3 – Moulting specimen from lateral aspect showing differences in the urstigmae organization in prelarva and larva stages. Scale bar – 25 μm; 4- General view of the right urstigma. Scale bar – 3 μm; 5 - Oblique section through the right urstigma near its periphery. Scale bar – 3 μm; 6 – Lateral side of the apical portion of the left urstigma showing a cuticular cap and additional valve. Scale bar - 1 μm.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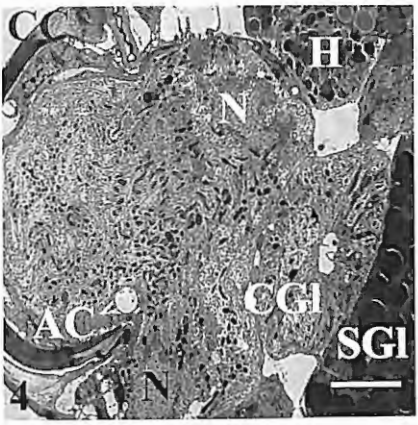
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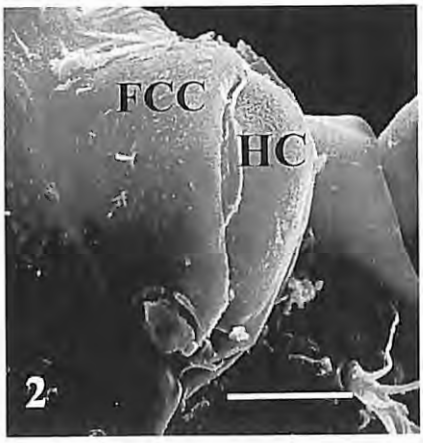
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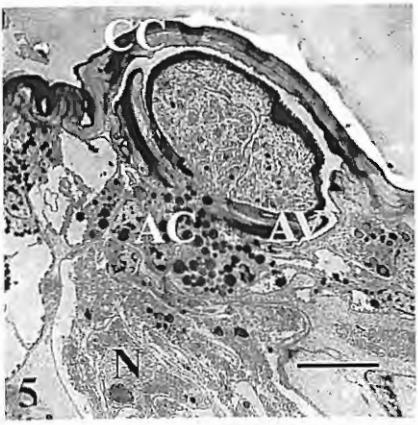
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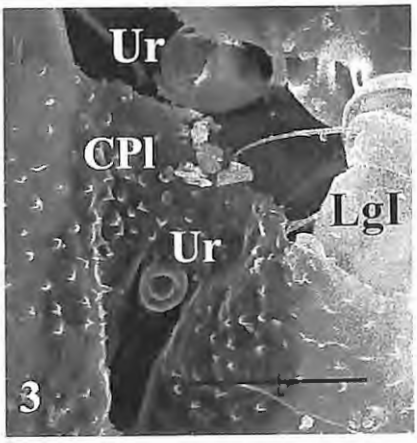
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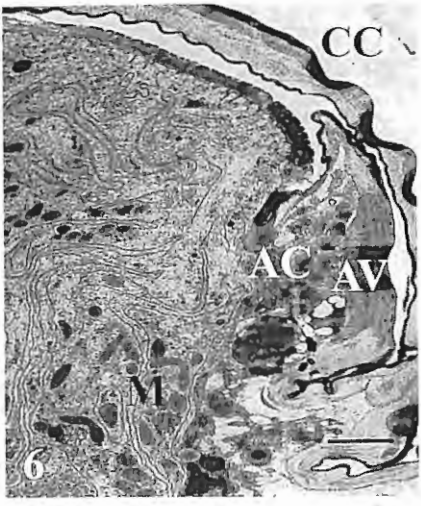
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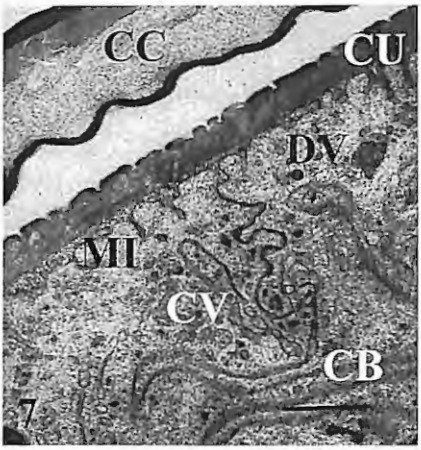
The most interesting feature of the cell organization is an activity of their apical and lateral plasma membranes. The apical plasma membrane in the center of the urstigma, which appears concealed under the cuticular cap and covered with its own cuticle provided with curved and hardly identified pore canals, forms narrow invaginations, from the tips of which small clear vesicles are seen to pinch off in a relatively large number (Figs 7, 8). The latter may obviously fuse with each other and supposedly with the lateral cell borders, thus transporting particular substances, presumably ions and water, from the outside into the intercellular milieu and further into the haemocoelic space of the organism. However, the precise origination and fate of these small clear vesicles, especially in deeper parts of the cells, remains of problematical question and may originate from different sources. In particular, the opposite lateral cell membranes on their whole length constantly demonstrate periodical distensions (widening) of the intercellular space, containing a substrate of low to moderate density (Fig. 8), and even the figures of blebbing of the plasma membrane with resulting vesicles and, sometimes, large vacuoles immersing into the cytoplasm (Figs 7, 10, 12). These vesicles may probably fuse with dense vesicles of the Golgi origin to form vesicles of middle size and of moderate to high electron density. The latter are sometimes observed to come to the apical rim of the cytoplasm (Fig. 8) and supposedly fuse with the apical cell membrane thus, conversely, secreting particular substances from the cell into the narrow subcuticular space. It is obviously seen that the process of formation and secretion of these vesicles proceed via the opposite direction to the above-mentioned process of the vesicles uptake from the outside and their distribution through the cytoplasm.

Additional cells situated on the periphery of urstigmae are not involved in the transporting activity highly characteristic for cells of the organ. These are flat cells with an elongate nucleus (Figs 4, 11) and contain some number of lipid and lipoprotein inclusions (Figs 5, 6), mitochondria and microtubules. It is of interest that on the periphery of the organ these additional cells delimit the cells of the urstigma and cuticle of the protecting cuticular lids (Fig. 9).

Figs 7-12. TEM ultrastructure of urstigmae of *Platytrombidium fasciatum* (7, 9-12) and *Camerotrombidium pexatum* (8) larvae (Microtrombidiidae). 7 – Apical surface of urstigma provided with a proper cuticle, and cuticular cap covering them from above. Note microtubules in the right side of the figure. Scale bar – 0.5 μm; 8 – Detail of the apical zone of urstigma with a proper cuticle and cuticular cap tightly opposed, showing vesicular activity in the apical cytoplasm. Scale bar – 0.5 μm; 9 – Part of the apical portion of urstigma close to its periphery provided with additional cell delimiting cells of the urstigma and cuticle of the cuticular cup. Scale bar – 1 μm; 10 – Detail of the deeper part of urstigma showing clear vacuoles and vesicles as well as dense vesicles and mitochondria within the cytoplasm crossed by cell borders. Scale bar – 0.5 μm; 11 – Basal portion of urstigma with clear nucleus showing additional cell encompassed by the delimiting basal lamina. Scale bar – 1 μm; 12 – Basal portion of urstigma with nucleus and nucleolus together with small Golgi bodies and dense vesicles. Scale bar – 1 μm.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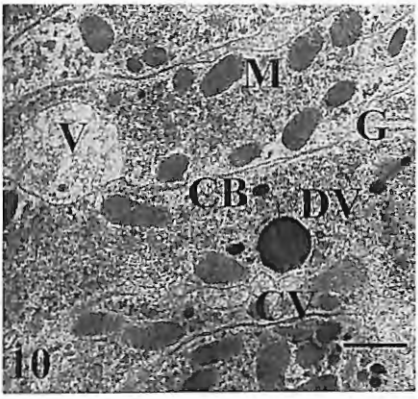
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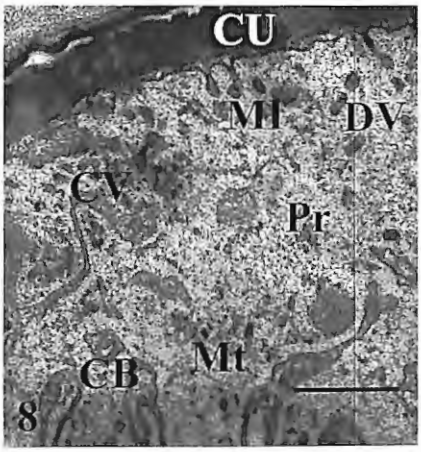
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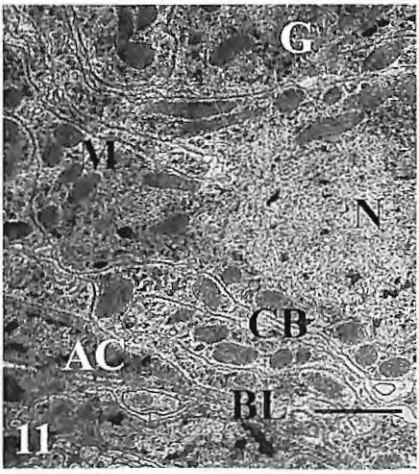
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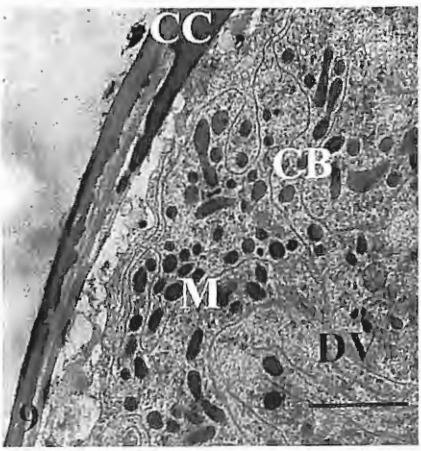
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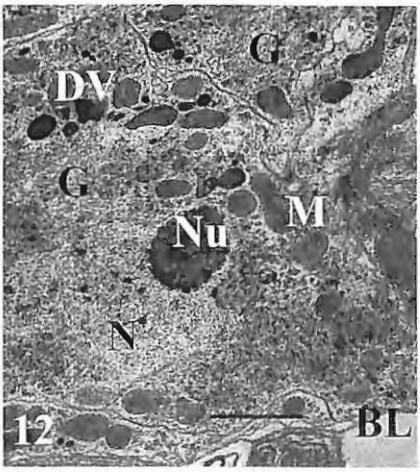
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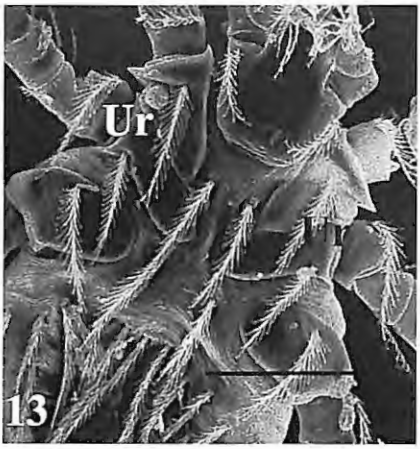
Trombiculidae

Despite the fact that the urstigmae in the representatives of this family are found to be rather more conspicuous organs than in microtrombidiids, judging from their external examination, their internal organization as well as their probable functions appears to be significantly reduced. In comparison with microtrombidiid larvae, the urstigmae in trombiculids occupy a more frontal position and are located not between the coxae, but in the indentations of coxa I at its postero-lateral angle (Fig. 13).

A hemispherical cuticular cap with a flat surface extending from the front side covers the entire urstigma (Figs 14, 15), so that the organ looks like a mushroom, under the cap of which a short cuticular stalk is seen disposed (Fig. 14). In the whole, cuticular components of the urstigmae, in comparison with the microtrombidiid ones, are strongly developed in their thickness and massiveness, being composed of the same parts found in the microtrombidiid urstigma, like additional lateral valves, etc. (Fig. 15). It is important to note, however, that in trombiculid larvae, in contrast to microtrombidiid ones, the proper cuticle of the urstigma is restricted to a rather small area, very massive and composed of a dense flocculent material provided with irregular cavities (Figs 15, 16). No pore foramens were identified on the apical surface of this cuticle. Beneath the cuticle there may be sometimes observed a dense granular substance, a presumable result of the process of cell secretion (Figs 16, 18).

Conversely, the internal cell components of the organ are seen reduced in volume, number and possible functional activity, although the cells reveal nearly just the same organization as described above. The cells are poorly provided with organelles apart from groups of mitochondria, separate microtubules, free ribosomes and some vesicles and dense granules (Fig. 15). Golgi bodies and endoplasmic reticulum were not clearly identified in the cells of the urstigmae of trombiculid larvae. Whereas the basal cell membrane as well as basal delimiting lamina remains predominantly flat, inner cell borders are significantly folded, frequently leaving a conspicuous intercellular space (Fig. 17). Occasionally, the figures of blebbing of the plasma membrane into the cell are observed along the lateral cell margins, resulting in clear vesicles lying within the cytoplasm in the vicinity of the lateral cell borders. In the apical cytoplasm, there may be found a number of vesicles of a moderate to high electron density, which appear to secrete their contents into a narrow

Figs 13-18. Ultrastructure of urstigmae of *Leptotrombidium orientale* (13-16) and *Hirsutiella zachvatkini* (17,18) larvae (Trombiculidae). 13-14 – SEM, 15-18 – TEM. 13 – General view of the ventral body side. Scale bar – 60 μm; 14 – Right urostigma of the same specimen located in the posterior invagination of coxa I. Scale bar – 7.5 μm; 15 – General view of urostigma in its medial zone showing a massive cuticular armature. Scale bar – 1 μm; 16 – Apical portion of urstigma of the same specimen provided with dense vesicles and microtubules without conspicuous subcuticular space. Scale bar – 0.5 μm; 17 – Oblique section of a peripheral part of urstigma showing curved cell borders and dense granules in the basal portion of urstigma. Scale bar – 1 μm; 18 – Vesicular activity in the middle-apical zone of urstigma. Scale bar – 0.5 μm.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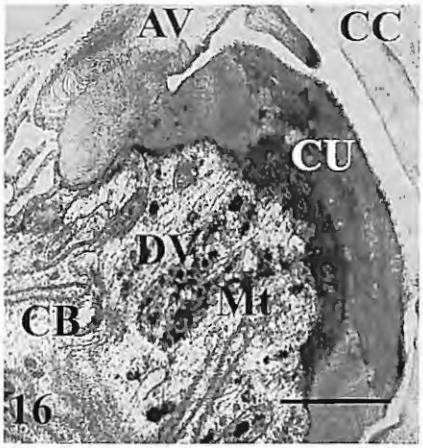
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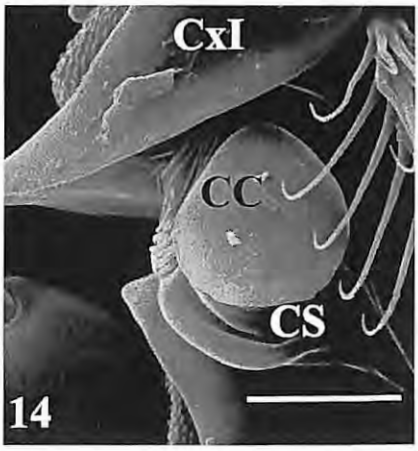
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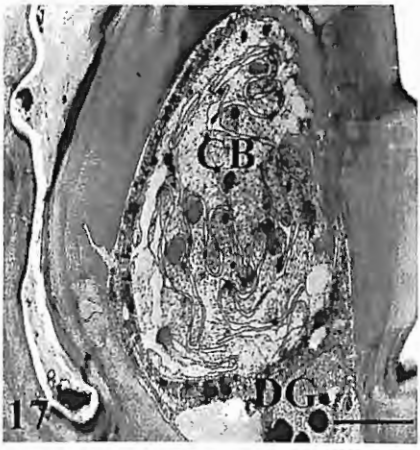
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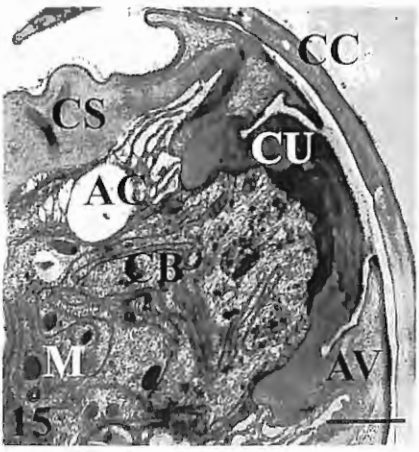
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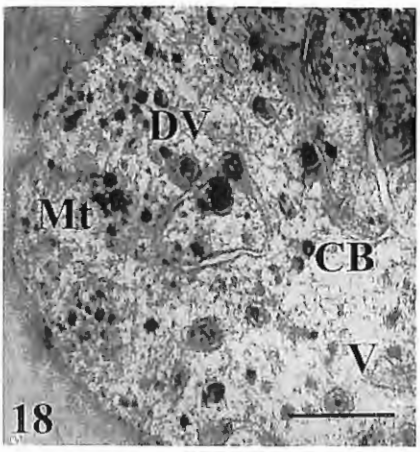
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subcuticular space that supposedly may lead to an increase of the cuticular volume (Figs 16, 18). On the other hand, in the middle parts of the cells, dense vesicles may secrete particular substances into a more or less wide intercellular space where they appear to accumulate forming relatively large dense aggregates (Figs 17, 18). Neither apical membrane invaginations, nor absorptions of clear vesicles, as seen in the microtrombidiid urstigmae, are found in trombiculid larvae. Instead, microtubules as agents of intracellular transport may be seen coming to the apical plasma membrane (Figs 15, 16) supposedly assisting in secretion activity. In rare cases, some vesicular activity may be also revealed at the basal cell surface, indicating a weak transport process. Occasionally, associations of dense granules may be also seen both in the basal (Fig. 17) and in the apical cell portions. Their role in the cell functioning still remains unclear.

The additional cells are also present in the trombiculid urstigmae, but mainly in the reduced forms. For the most part, they flank the apical sides of the urstigma, lying just beneath a thick cuticle of the stalk (Fig. 15) and contain lipid inclusions. In *L. orientale*, they are found to form long slim extensions of their apical surfaces invading a narrow space situated within the bases of the additional valves (Fig. 15).

Discussion

Although the urstigmae or Claparède organs are mentioned and even studied in many works carried out at the light optical microscope level (*see* GRANDJEAN, 1946, 1948, 1955; VERCAMMEN-GRANDJEAN, 1976; KRANTZ, 1977; *etc.*), very little information is available until now on the internal fine morphology of the different representatives of such a huge taxon (ALBERTI, 1979; FASHING, 1988; ALBERTI & COONS, 1999). Very often, the Claparède organs are considered together with the so-called "genital papillae" of active post-embryonic instars (*see* ALBERTI, 1977), which are generally thought to be homologous structures and function in osmoregulation (FASHING, 1988) in animals inhabiting hypo-osmotic media (GOLDSCHMIDT *et. al.*, 1999). This assumption is made on the basis both of the histochemical evidence (ALBERTI, 1977, 1979) and of the close resemblance of the cells of urstigmae to the chloride cells of some aquatic insects (KOMNICK, 1977), in which they function as effective ion-absorbing sites. Recently, other structures presumably concerned with ion and water balance, called axillary organs, ring organs or acetabula-like structures have been described both in Acaridida (FASHING & MARCUSON, 1997, WITALINSKI *et al.*, 2002) and in Actinedida (GOLDSCMIDT *et al.*, 1999) that have essentially verified the "Oudemans-Grandjean rule" (JOHNSTON & WACKER, 1967, ANDRÉ, 1991). The cells of all those organs are highly characterized by a great concentration of mitochondria ("mitochondrial pump") closely associated with tight infoldings of the basal plasma membrane and pleats of the apical ones (KOMNICK, 1977; GOLDSCHMIDT *et al.*, 1999) that are considered to be the general and most evident structural feature for transporting epithelia.

From the cytological point of view, vesicular transport, which is obviously recognized in trombiculid and especially in microtrombidiid larvae, implies a particular compensation mechanism for restoring of the apical plasma membrane. Due to scarcity of intracellular synthetic compartments producing membrane components, the main role for compensation of the apical membrane after uptake of some vesicles may have been transferred to the lateral cell membranes, which truly demonstrate a particular activity in formation of vesicles and vacuoles. It is clear, however, that such mechanism in any way may not be considered as having a great intensity. At the same time, cells are not provided with a developed apparatus for intracellular digestion and, therefore, cannot actively treat the materials absorbed via pinocytosis. Small Golgi bodies obviously take part not in producing lysosomes, but some granules for export from the cells.

Despite a very scarce information concerning variety of those organs in acariform mites, in particular from the suborder Actinedida, the present investigation clearly indicates that in the higher terrestrial trombidiform mites from the cohort Parasitengona, namely in Trombiculidae and Microtrombidiidae, in contrast to other actinedids so far studied, there is observed an obvious reduction of some important morphological characteristics and, consequently, proposed functional properties. Indeed, mitochondria are not abundant and are not arranged in a regular fashion, and the cell membrane does not show conspicuous basal infoldings and apical pleats. It is more likely that in the Claparède organs of these groups, a possible transport of ions and water seems to take place not immediately through the membrane with the help of a "mitochondrial pump", but due to vesicles carrying substances from the apical surface of the cells into the intercellular space and further into the body cavity, or vice versa. It is a question, however, whether this way of molecular transport is more ancient or, conversely, more derived than membrane transport, or not? And, correspondingly, do the urstigmae of the Parasitengona share plesiomorphic features or, contrary, apomorphic ones? In any case, an absence of apical microvilli, basal infoldings as well as conspicuous pore canals within the proper cuticle of the urstigmae, which join external media with the apical membrane, may indicate a significant reduction of some essential functions of these organs and, as a consequence, a significant decrease of the transport activity. The latter is especially characteristic for trombiculid larvae with reduced internal components of the urstigma. What may serve as a true apomorphic feature presumably for the branch Trombiculoidea-Trombidioidea, are the additional cells, which have not been described previously with certainty. This question, however, needs to be investigated in more detail.

Thus, as clearly seen from this consideration, in the higher trombidiform mites, there is expected a progressive significant reduction of the functional activity of the larval Claparede organs that is apparently seen from the comparison of microtrombidiid mites with the highly specialized group such as trombiculids. From a phylogenetic stand point, the latter group together with some smaller families forms the superfamily Trombiculoidea

(WELBOURN, 1991) and, in contrast to Microtrombidiidae constituting another superfamily – (i.e.Trombidioidea), is thought to be a more derived taxon.

A great variety in the external manifestation of the Claparède organs in Acariformes (GRANDJEAN, 1946, 1948, 1955; VERCAMMEN-GRANDJEAN, 1976; BAKER, 1985; FASHING, 1988) need to be verified on the electron microscope level and also by other sophisticated methods that could clarify not only a specificity of the fine intracellular transporting processes but, probably, a phylogenetic relationships of mites within the Acariformes. In particular, the extremely long and articulated Claparède organs found in representatives of Caeculidae (GRANDJEAN, 1946; VERCAMMEN-GRANDJEAN, 1976) need to be explained from both the functional and ultrastructural point of view. Although the urstigmae are generally considered utilized for the uptake of water in the terrestrial Acariformes (ALBERTI, 1977, 1979), a significant reduction of the external manifestation of the organ in some trombidiids (VERCAMMEN-GRANDJEAN, 1976; SHATROV, unpublished data) has to be explained ecologically. In particular, trombiculid larvae live a very short time before they have found an appropriate vertebrate host and for the most part they inhabit moist conditions in soil and, after infestation of hosts, they frequently seek the concealed and humid locations in their ears, waists, etc. This situation may be referred to as the main evolutionary reason for the reduction of the urstigmae. Trombidiid larvae, conversely, run fast on the surface of various substrates seeking an arthropod host, which, clearly, does not provide an appropriate humid condition during the parasitic life of the larvae. Such habits, however, favorable for maintenance of osmoregulatory functions, do not seem to abolish a general tendency to reduction of urstigmae and their functions in the higher terrestrial trombidiform mites. It is interesting to note, that in prelarvae urstigmae have a different form (see Fig. 3) than in larvae, and their external organization, in contrast to the larval stage, appear to be very similar in representatives of both these families (*see* SHATROV, 1998).

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