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Ultrastructure of coxal glands in the unfed microtrombidiid larvae, *Platytrombidium fasciatum* (C. L. Koch, 1836) and *Camerotrombidium pexatum* (C. L. Koch, 1837) (Acariformes: Microtrombidiidae)

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Abstract

The anatomy and ultrastructure of the coxal glands of larvae of the microtrombidiid mites *Platytrombidium fasciatum* (C. L. Koch, 1836) and *Camerotrombidium pexatum* (C. L. Koch, 1837) were investigated using transmission electron microscopy. The coxal glands are paired organs generally situated between the brain and the frontal lobes of the midgut, running along the axis of the body. Based on the cellular organisation, the coxal glands may generally be divided into two different tubular portions – a proximal tubule and a distal tubule. The proximal tubule coils around the distal tubule and is provided with long microvilli of the apical plasma membrane of the cells. The distal tubule possesses in its middle zone basal infoldings of the basal plasma membrane, which contain elongated mitochondria, and terminates in a cuticular ectodermal excretory duct. As in the majority of other Parasitengona, the coxal glands of microtrombidiid larvae are devoid of a proximal sacculus. The cells of the tubules connect with each other via septate desmosomes and reveal a particular secretory activity through functioning of Golgi bodies. The cells of the proximal and the distal tubules are tightly adjoined to each other and to the cells of the midgut epithelium without a delimiting basal lamina between their cells. The organisation of the coxal gland highly corresponds to that of transportation epithelia with an additional secretory function. The coxal glands in the microtrombidiid larvae, as supposedly in other Parasitengona, probably play a major role in the ion/water balance of the mite organism and presumably mostly function in preserving water, preventing desiccation of the mites.

Keywords: morphology, electron microscopy, osmoregulation, excretion, Parasitengona

Zusammenfassung

Ultrastruktur der Coxaldrüsen bei ungefütterten Milbenlarven von *Platytrombidium fasciatum* (C. L. Koch, 1836) und *Camerotrombidium pexatum* (C. L. Koch, 1837) (Acariformes: Microtrombidiidae) – Anatomie und Ultrastruktur der Coxaldrüsen der Larven der microtrombidiiden Milben *Platytrombidium fasciatum* (C. L. Koch, 1836) und *Camerotrombidium pexatum* (C. L. Koch, 1837) wurden mit dem Transmissions-

Elektronenmikroskop untersucht. Die Coxaldrüsen sind paarige Organe, die zwischen dem Gehirn und den vorderen Bereichen des Mitteldarmes entlang der Körperachse liegen. Die Coxaldrüsen können in Übereinstimmung mit der zellulären Organisation grundsätzlich in zwei unterschiedliche Tubusabschnitte – einen proximalen und einen distalen Tubulus – geteilt sein. Der proximale Tubulus windet sich um den distalen Tubulus und hat lange Mikrovilli auf der apikalen Plasmamembran der Zellen. Der distale Tubulus wird begrenzt durch einen kutikularen ectodermalen Exkretionsgang und sitzt im mittleren Bereich basal umhüllt von der basalen Plasmamembran, die Mitochondrien enthält. Wie auch bei anderen Parasitengona, sind die Coxaldrüsen der microtrombidiiden Larven ohne proximalen Sacculus. Die Zellen der Tubuli verbinden sich untereinander mittels »gap junctions« und »septiren Desmosomes«, und außerdem offenbart eine detaillierte sekretorische Aktivität die Funktion des Golgi-Apparates. Die Zellen des proximalen und distalen Tubulus berühren sich miteinander und auch mit den Zellen des Mitteldarmepithels ohne eine abgrenzende basale Schicht zwischen ihren Zellen. Die Organisation der Coxaldrüse entspricht stark der Organisation von Transportepithelien mit zusätzlicher sekretorischer Funktion. Die Coxaldrüsen bei den microtrombidiiden Larven, wie angeblich bei anderen Parasitengona, spielen eine Hauptrolle in der Aufrechterhaltung des Ionen-/Wassergleichgewichts des Milbenorganismus und haben vermutlich eine wichtige Funktion für die Bindung des Wassers im Organismus zur Verhinderung der Austrocknung der Milben.

1. Introduction

Coxal (tubular) glands in Arachnida, and in particularly in the Acari, are supposed to function mainly in the ion/water regulation of the mite organism. These paired glands are known to be of mesodermal origin (Beklemishev 1964, Evans 1992) and each of them is generally composed of a proximal sacculus (supposed remnant of the coelom) and of a convoluted tubule or labyrinth (coelomoduct) (Evans 1992). The cells of the latter are provided with basal plasma membrane infoldings with many adjacent mitochondria (mitochondrial pump) and with a microvillar border on the apical cell surface (Groepler 1969, Alberti & Storch 1974, 1977, Alberti 1979, Alberti & Crooker 1985, El Shoura & Roshdy 1985, Evans 1992, Alberti et al. 1997, Alberti & Coons 1999). The sacculus is supposedly a site of ultrafiltration of the haemolymph into the organ (Groepler 1969, Hecker et al. 1969, Alberti & Coons 1999), whereas the organisation of the tubule suggests active reabsorption of ions and water from the lumen of the gland, highly corresponding to the structure of transportation epithelia (Diamond & Tormey 1966, Berridge & Oschman 1969, Berridge 1970). The gland terminates with a cuticular (ectodermal) excretory duct.

Despite extensive literature available for the light-optical composition and structure of the coxal glands in acariform mites (see Alberti & Coons 1999), little is known about electron-microscopic organisation of the glands in many taxa, especially their larvae. Investigation of fine morphology may to some extent clarify the structural bases of the proposed transportation processes of ion/water across the gland epithelium. The latter, on the other hand, may lead to a better understanding of the ecophysiological condition and needs of the animals.

Among the higher actinedid mites from the cohort Parasitengona, a group characterised by a complex life cycle and larval parasitism on vertebrate and invertebrate hosts, water mites (Croneberg 1878, Michael 1895, Thon 1905, Schmidt 1935, Bader 1938, Mitchell 1955,

ALBERTI & COONS 1999), calyptostomatids (VISTORIN-THEIS 1978), trombidiids (MOSS 1962, ALBERTI & COONS 1999) and trombiculids (BROWN 1952, MITCHELL 1964, SHATROV 1995, 2000) have been variously studied in respect to their morphology, including coxal glands, mainly, however, only by light-optical methods. As is shown in these studies, the coxal glands in this branch of the Acari, as well as in other Actinotrichida, have lost their individuality in the course of evolution joining by their duct with ducts of the prosomal salivary glands, thus probably taking part in the formation of the salivary secretion (MITCHELL 1970). Larvae of the family Trombiculidae, parasitising vertebrate animals and thus of medical importance, were studied previously by both light-optical (JONES 1950, VOIGT 1971, SCHRAMLOVÁ 1978), and electron-microscopic methods (SHATROV 1995, 2000). Conversely, coxal glands of the larvae of the closely related group, Trombidiidae sensu lato, parasitising arthropods have not been studied until now.

Based on these considerations, the main purpose of this study is to provide detailed electron-microscopic observations and to clarify some physiological functions of the coxal glands in unfed larvae of *Platytrombidium fasciatum* (C. L. Koch, 1836) and *Camerotrombidium pexatum* (C. L. Koch, 1837) (Acariformes: Microtrombidiidae). Adult mites of these species are proposed to be studied subsequently.

2. Materials and Methods

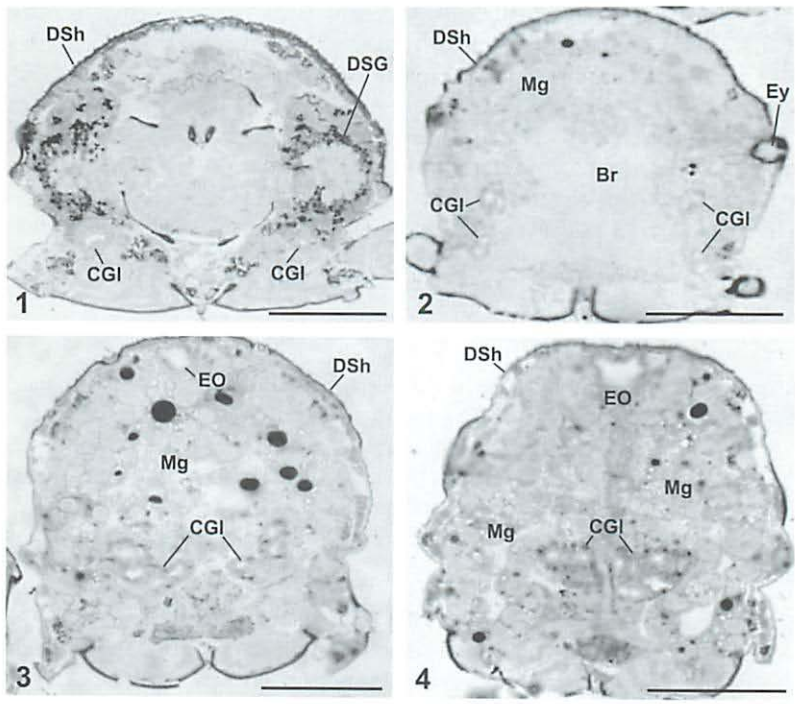
Larvae used in this study were obtained from adult mites collected from the soil surface in the Leningrad province during the spring-summer period of the years 1996 – 2000. Mites were initially placed into small plastic jars with soil particles as a substrate. Approximately two weeks later mites had laid eggs, from which active unfed larvae hatched in the course of the following two weeks and were taken for fixation.

For transmission electron microscopy (TEM), active larvae of both species were initially fixed in 2.5 % glutaraldehyde in 0.1 M phosphate buffer (pH 7.2 – 7.4) for 2 – 4 h. After immersion into the fixative fluid, mites 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 tetroxide 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 ultra-thin sections both in transverse and in longitudinal (sagittal) planes were made on an LKB-III ultramicrotome and, after staining with uranyl acetate and lead citrate, examined with Tesla BS-500 and LEO-900 transmission electron microscopes at 60 – 90 kV. For preliminary and general observations, semi-thin sections were stained with toluidine blue and investigated and photographed under Amplival and Leica DMLS-2 light optical microscopes.

3. Results

3.1. General observations

In unfed microtrombidiid larvae, one pair of coxal glands occupies a lateral and ventral position in the mite body, generally situated between the midgut and the brain (synganglion) and running along the axis of the body. In light-optical sections they are hardly distinguishable having a tubular form anteriorly beneath the dorsal salivary glands and irregular outlines more to the posterior – on the sides and behind the brain and beneath the



Figs 1 – 4 Sequential transverse sections through the anterior portion of the body of the unfed microtrombidiid larva *Camerotrombidium pexatum* on the level of:

1: Anterior parts of the dorsal salivary glands;

2: Middle portion of the brain;

3: Posterior termination of the brain;

4: Behind the brain, showing general position of the coxal glands. Semi-thin toluidine blue stained sections. Scale bars – 50 μm.

List of Abbreviations: AZ – anterior zone; Br – brain; BI – basal infolds; BL – basal lamina; Cu – cuticle; CGl – coxal gland; DL – duct lumen; DSh – dorsal shield; DSG – dorsal salivary gland; DT – distal tubule; DV – dense vesicle(s); Ey – eye; EC – ectoderm cell; ED – excretory duct; EO – excretory organ; G – Golgi body; JC – junction complex (septate desmosome); HS – haemocoelic space; ITr – initial trunk; L – lipid inclusion; Lu – lumen; Ly – lysosome; M – mitochondria; Mg – midgut; MgL – midgut lumen; Mt – microtubules; Mv – microvilli; MZ – middle zone; N – nucleus; Nu – nucleolus; PT – proximal tubule; PZ – posterior zone; R – ribosome; RER – rough endoplasmic reticulum; SD – septate desmosome; Tr – trachea; TTr – terminal trunk; VSG – ventral salivary gland

gut (Figs 1 – 4). Behind the brain, the paired glands may come into contact with each other being, however, separated by delimiting basal laminas (see below). Despite the enlargement of the glandular mass in the posterior portion, the glands obviously lack a proximal sacculus as in the majority of other Parasitengona, including larvae (Bader 1938, Brown 1952, Mitchell 1955, Voigt 1971, Schramlová 1978, Alberti et al. 1997, Alberti & Coons 1999). Thus, the glands are totally composed of the tubular components. The glands are

weakly stained in the anterior portions and stronger in the posterior ones being, however, devoid of granulation throughout their length (Figs 1 – 4). The overall length of the gland is around 80 – 90 μm in both species (the total length of the larvae is 200 – 220 μm), the width in the distal (anterior) tubular portion is 12 – 15 μm, whereas the proximal (posterior) irregularly outlined portion may achieve 30 μm. The excretory cuticular duct, after leaving the gland, turns upwards and soon joins the duct of the dorsal gland. The common salivary duct (podocephalic canal) joins the duct of the ventral gland and finally opens into the postero-lateral area of the subcheliceral cavity on each side of the body (Fig. 5).

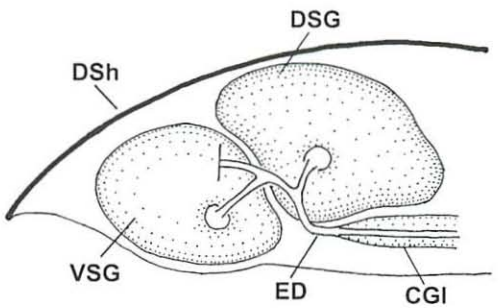


Fig. 5 Schematic drawings of microtrombidiid mite larvae displaying: relative position of the salivary and coxal glands and their ducts on longitudinal (sagittal) plane; cutting line indicates an opening of the common salivary duct into the subcheliceral space (organs of only one side of the body are demonstrated). For abbreviations see page 58.

Based on cellular organisation at the electron-microscopic level, the coxal glands in microtrombidiid larvae may generally be divided into two main different tubular portions – a proximal tubule and a distal tubule, continuing into an ectodermal cuticular duct (Fig. 6). Following from the excretory duct in the posterior direction, the distal tubule runs straight backwards up to the posterior end of the gland, then turns straight forward going nearly up to the anterior end of the gland where it is transformed into the proximal tubule. The latter turns again backwards and coils around the distal tubule during its entire course first in the posterior and then in the anterior direction, and finally ends blindly not far from the anterior termination of the distal tubule (Fig. 6). Thus, the entire gland is composed of the two tightly adjoined

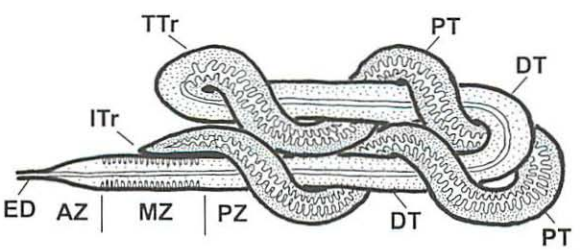


Fig. 6 Schematic drawings of microtrombidiid mite larvae displaying: approximate positional relationship of the gland tubules and trunks on longitudinal (sagittal) section. For abbreviations see page 58.

distal and proximal tubules and shows two trunks or branches during its course, which may be conveniently termed as the initial trunk, running from the origination of the duct backward, and the terminal trunk, going from the caudal turn of the gland in anterior direction. In the anterior portion of the gland, compressed between the brain and the antero-lateral gut lobes, the gland trunks are placed one above the other, i.e. the initial trunk occupies a ventral position, whereas the terminal trunk is located more dorsally lying above the initial trunk. In the posterior portion of the gland, behind the brain, the gland trunks become horizontally arranged with the initial trunk taking a medial position. Whereas the initial trunk of the gland, especially in its anterior portion, consists of sharply outlined proximal and distal tubules (Figs 7, 8), the remaining gland is composed of freely convoluted and coiled tubules (Figs 3, 4, 9). At the caudal termination of the glands, where several bends of the tubules are present together, a particular enlargement of the glandular mass may be observed. However, no sacculus at the termination of the proximal tubule was identified.

The proximal and the distal tubules are composed of cells arranged around the central lumen as a rosette. Cells of the neighbouring proximal and distal tubules are very tightly adjoined to each other without a delimiting basal lamina (Figs 7, 8, 9, 11). In their anterior portions, the initial and the terminal trunks of the gland are always enveloped by an own basal lamina allowing different portions of the gland to be delimited (Figs 7, 8). In the posterior portions of the gland, a delimiting basal lamina between the glandular cells and other tissue such as the midgut epithelium may be absent (Figs 9, 10). No special muscle or connective-tissue envelopes were found surrounding the coxal glands of unfed larvae (Figs 7, 8, 9).

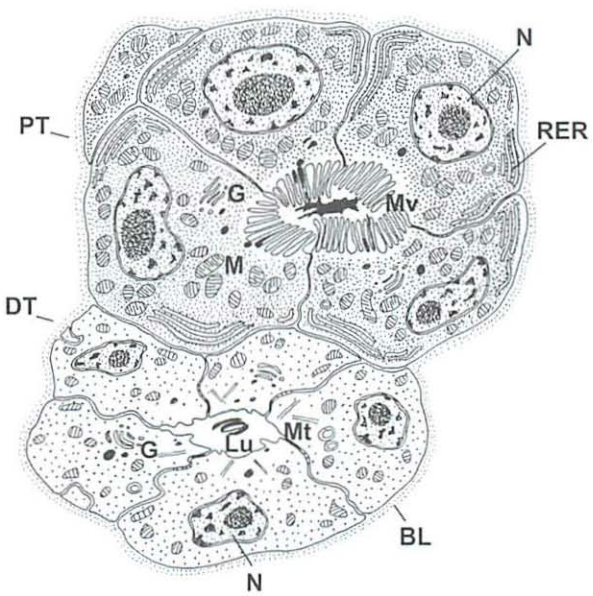
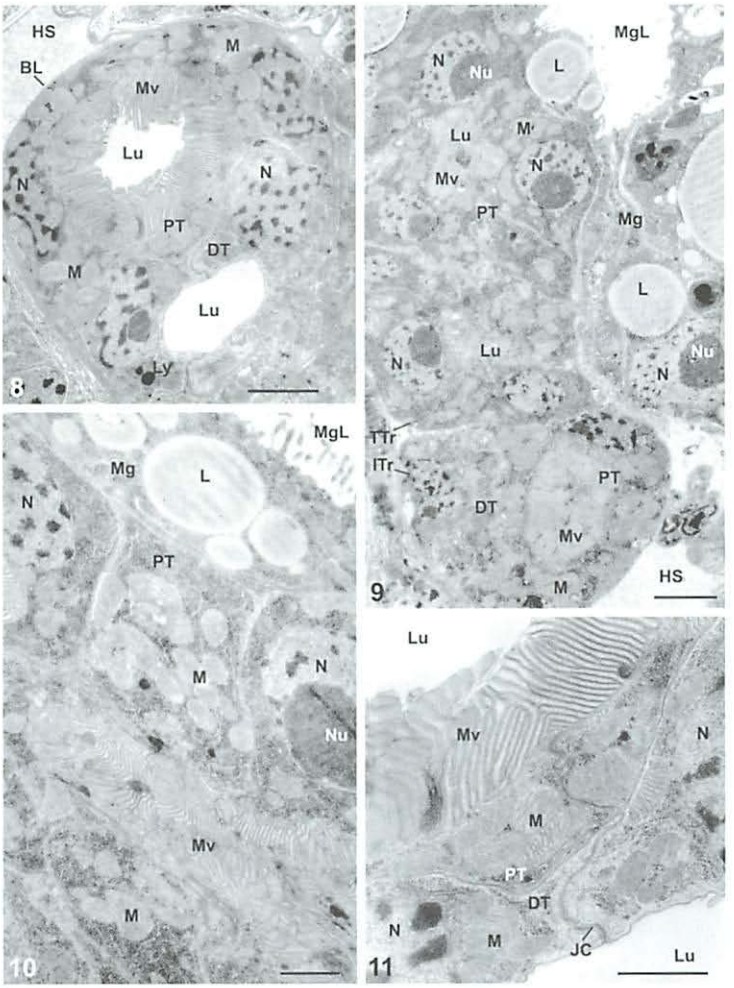


Fig. 7 Coxal gland of microtrombidiid mite larvae. Schematic drawing of transverse section through the initial trunk in its anterior third composed of the proximal and distal tubules and encircled with the basal lamina (see detail description in text). For abbreviations see page 58.



Figs 8 – 11 TEM micrographs of the coxal gland and its proximal tubule

8: *Camerotrombidium pexatum*, transverse section of the initial trunk composed of the proximal tubule provided with apical microvilli and of the distal tubule devoid of conspicuous basal infolds, which are tightly adjoined each other. Note the basal lamina encompassing the trunk. Scale bar – 2 μm.

9: *Platytrombidium fasciatum*, transverse section through the coxal gland consisting of the terminal (dorsal) and initial (ventral) trunks compressed between the midgut (on the right side) and the brain (on the left side – not visible here). Scale bar – 2 μm.

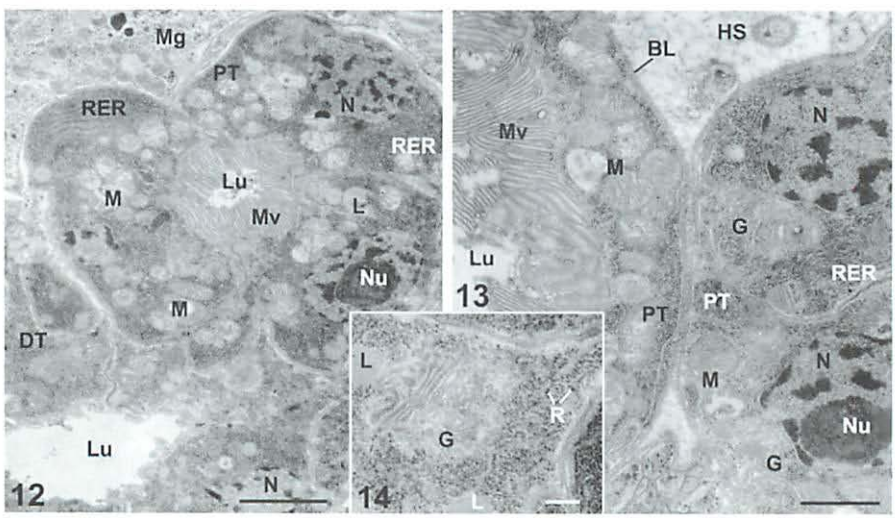
10: *Pl. fasciatum*, longitudinal section through the midgut wall and the proximal tubule in its middle portion showing tight contact between the midgut and the glandular epithelia and a collapsed gland lumen marked by tightly packed microvilli. Scale bar – 1 μm.

11: *C. pexatum*, contact zone between the proximal and the distal tubules with the wide lumens, at the posterior portion of the gland. Scale bar – 1 μm. For abbreviations see page 58.

3.2. Proximal tubule

The proximal tubule, due to its rather convoluted character, especially in the posterior regions, possesses quite irregular outlines with a general diameter varying from 5 to 10 μm or larger. Sometimes, the tubule gives the impression of being a chaotic pile of cells, especially in areas on the periphery of the gland, where the central lumen is not visible (Fig. 9). In general, in a transverse section of a particular tubule, from 3 to 7 cells may be identified grouped around the central lumen (Fig. 12). The gland borders on the dorsal salivary gland and the brain, from which it is separated by a delimiting basal lamina. At the same time, the proximal tubule also borders on the midgut wall in an extensive area that is deeply inserted into the midgut epithelium (Figs 9, 10). There is no basal lamina between the glandular and the midgut cells throughout their entire border, so that the cells of the different tissue immediately contact each other without any delimiting structures or spaces (Fig. 10). In the most posterior portions of the proximal tubule, the basal lamina underneath the glandular epithelium is again present, delimiting the paired glands (Fig. 13).

The proximal tubule is composed of oval, prismatic or irregularly shaped cells with a relatively dense cytoplasm frequently provided with numerous free ribosomes and long curved cisterns of rough endoplasmic reticulum (RER) (Figs 12, 13). The cells are clearly outlined due to flat margins with a narrow strip of the clear cytoplasm underneath the lateral plasma membrane (Fig. 14). The apical cytoplasm is typically free of organelles and appears



Figs 12 – 14 TEM micrographs of the proximal tubule of *Camerotrombidium pexatum* larvae

12: Transverse section through the proximal and the distal tubules tightly associated with each other at the posterior portion of the gland surrounded by cells of the midgut. Scale bar – 2 μm.

13: Contact zone of the paired coxal glands, their proximal tubules, in the area behind the brain. Scale bar – 1 μm.

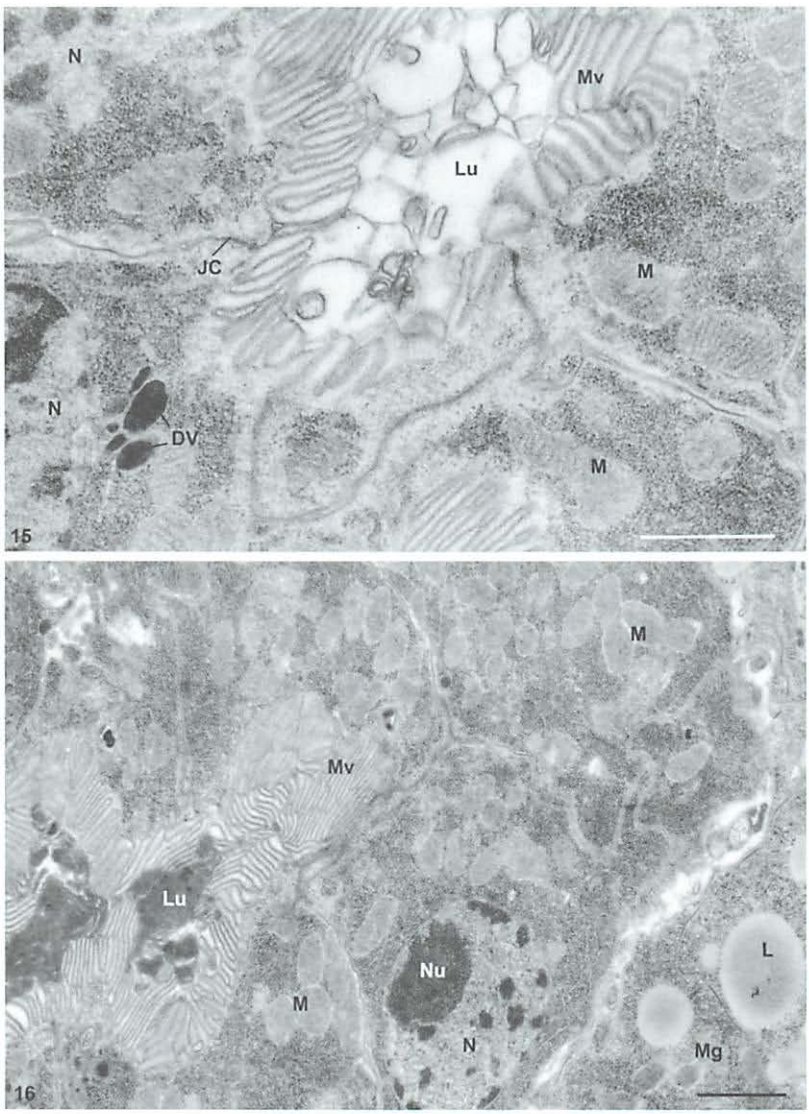
14: Golgi body in the cell of the proximal tubule; note lipid inclusion and the cell borders indicated by the clear zone beneath the lateral cell membrane. Scale bar – 0.2 μm. For abbreviations see page 58.

electron-lucent. The nuclei may be flattened against the basal or lateral plasma membrane especially in the anterior portions of the gland, where the tubule is narrower (Fig. 8). Conversely, in the posterior portions of the gland, where the gland mass is expanded, the nuclei are large, up to 2.5 – 3 μm in diameter, containing a large, round, eccentrically located nucleolus and relatively small heterochromatin particles scattered within the clear nucleoplasm (Figs 12, 13). Somewhat swelled mitochondria are large oval and electron-lucent, and provided with loosely packed cristae (Figs 12, 13). Mitochondria are relatively numerous and scattered in groups freely throughout the cytoplasm except the apical cell zone. Golgi bodies consisting of few narrow electron-dense cisterns accompanied by a group of small vesicles at the distal pole are typically located near the perinuclear zone and situated in the area that is mainly free of ribosomes (Figs 13, 14). The Golgi bodies appear to produce relatively small and scarce electron-dense vesicles, which are apparently transported towards the apical plasma membrane and obviously discharge their contents into the lumen between the microvilli (Figs 15, 16). As a result, the central lumen of the tubule, especially in the posterior portions of the gland, is frequently filled by an amorphous electron-dense mass (secretion) (Fig. 16). Nevertheless, the lumen in the anterior portions of the tubule is always empty. Scarce electron-dense secondary lysosomes as well as residual bodies and lipid inclusions may also sometimes be seen in the cells of the proximal tubule. In contrast to trombiculid larvae (Shatrov 1995) and some water mites (Alberti & Coons 1999), the cells of the proximal tubules of the coxal glands of unfed microtrombidiid larvae do not contain a noticeable amount of glycogen particles.

The most significant characteristic of the cells of the proximal tubule are long, tightly packed electron-lucent microvilli of the apical plasma membrane facing the lumen of the tubule (Figs 7, 8, 11, 15, 16). The lumen may be inconspicuous (collapsed) (Fig. 9, 10), or voluminous (Fig. 8) irrespective of the position of the tubule. Very often, however, large areas of the gland may be occupied by these microvilli, thus indicating the potential presence of the central lumen (Fig. 10). In contrast to trombiculid mite larvae (Shatrov 1995, 2000), these microvilli do not contain a central core of microfilaments or fibres. The basal plasma membrane remains flat throughout the proximal tubule and does not form conspicuous invaginations into the cytoplasm (Figs 8, 10, 12, 13). The intercellular space between adjacent cells is quite narrow and may rarely show small local dilations (Figs 14, 15). The cells connect each other via long septate desmosomes at the apical cell borders with an intercellular cleft of about 10 – 13 nm. These desmosomes, typical for invertebrate epithelia (Hudspeth & Revel 1971, Satir & Gilula 1973, Lane 1982), possess hardly identified septae, which are predominantly masked by an electron-dense extracellular matrix, especially in the upper portions of the junctions (Figs 11, 15). These septate junctions are frequently accompanied by a flocculent electron-dense material of still unknown origin that is more clearly seen in the distal tubule.

3.3. Distal tubule

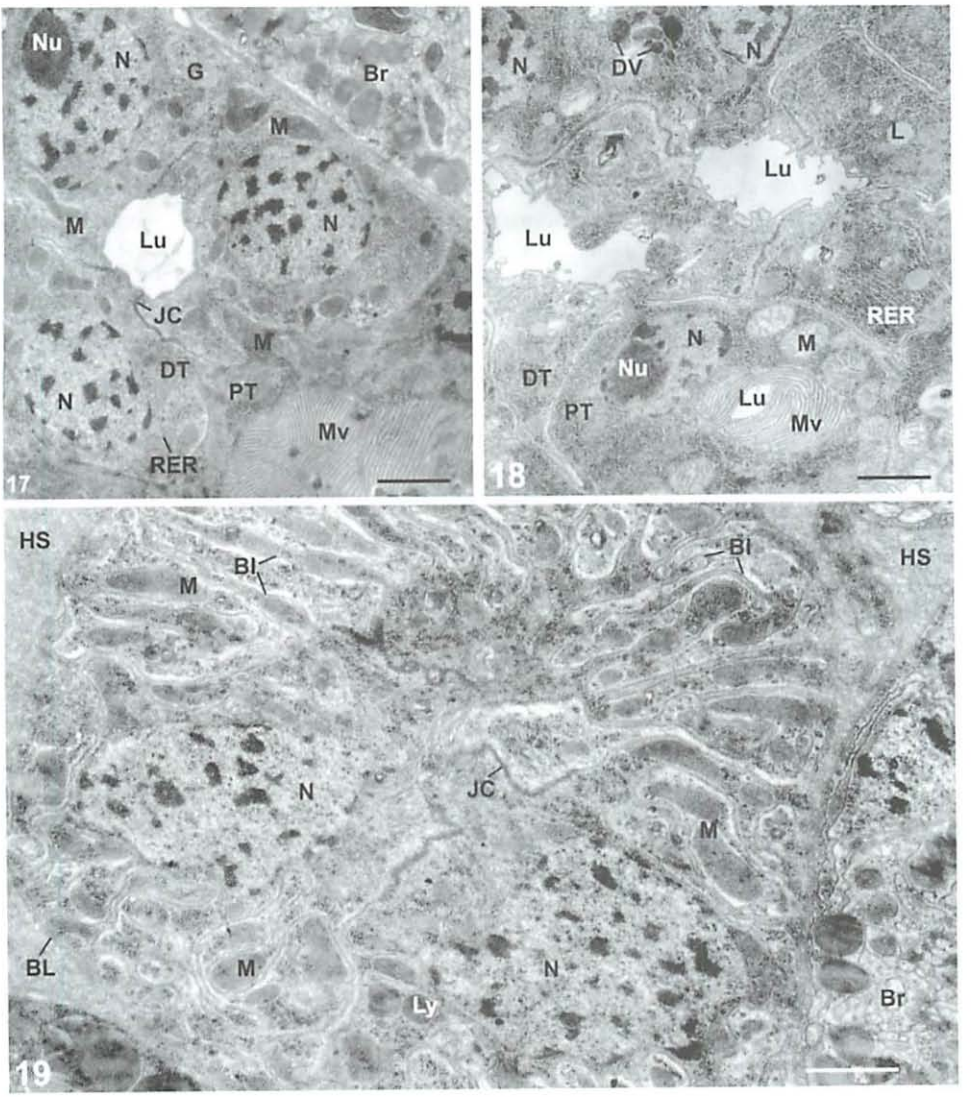
The distal tubule is characterised by a more regular arrangement of the cells around the central lumen, which may be wide (Figs 8, 17), or, rarely, totally closed (Fig. 19). The lumen is predominantly empty, or may contain electron-dense bodies partly resembling residual bodies (Figs 7, 22). In transverse sections, the outlines of the distal tubule are irregular in the posterior portions of the gland (Fig. 17) and become round in the anterior ones (Figs 20, 21, 25). Correspondingly, the diameter of the tubule varies from 7 to 15 μm.



Figs 15 – 16 TEM micrographs of the proximal tubule of the coxal gland of microtrombidiid mite larvae

15: *Camerotrombidium pexatum*, longitudinal section through the tubule; note dense vesicles indicating probable secretory activity and tightly packed microvilli on the apical cell surface. Scale bar – 1 μm.

16: *Platytrombidium fasciatum*, transverse section through the tubule containing a dense matrix in the lumen and surrounded by the midgut epithelium. Scale bar – 1 μm. For abbreviations see page 58.



Figs 17 – 19 TEM micrographs of the distal tubule

17: *Platytrombidium fasciatum*, transverse section of the posterior zone of the tubule tightly adjoined the proximal tubule bordering with the brain. Scale bar – 1 μm.

18: *Camerotrombidium pexatum*, posterior bend of the tubule indicating the margin between the initial and the terminal trunk, transverse section. Scale bar – 1 μm.

19: *Pl. fasciatum*, transverse section through the middle zone of the distal tubule with the collapsed lumen and provided with basal infolds containing mitochondria. Scale bar – 1 μm. For abbreviations see page 58.

The cells of the distal tubule are more electron-lucent than those of the proximal tubule and typically lack prominent RER elements and vast amounts of free ribosomes (Figs 7, 19, 20, 21). The nuclei are also somewhat smaller, 2 – 2.5 μm in diameter, and are characterised by a more irregular shape and a relatively small nucleolus. Nevertheless, the organisation of the Golgi bodies accompanied by few dense vesicles is nearly the same as in the cells of the proximal tubule (Fig. 23). Certain amounts of secondary lysosomes and lipid inclusions are also present in the cells of the distal tubule (Figs 21, 22). In contrast to the proximal tubules, the apical cell membrane does not form long microvilli but only scarce short irregular processes of the apical cytoplasm extending into the lumen (Figs 7, 22). Rarely, long microvilli may be occasionally seen bordering the lumen of the distal tubule only in the posterior portions of the gland (Fig. 18). The cytoplasm of the apical cell zone, as in the proximal tubules, is mainly electron-lucent and typically contains only few organelles (Figs 21 – 23). In the most posterior portion of the gland, the caudal bend of the distal tubule, indicating the margin between the initial and the terminal trunks of the gland, occurs (Fig. 18).

Based on the general organisation of the cells of the tubule and especially the character of the basal cell membrane and distribution of the mitochondria, the distal tubule may be divided into three distinctly recognisable portions – a posterior zone, a middle zone and an anterior zone, the margins of which are not sharp. The cells of the posterior zone are more electron-dense and irregularly outlined and contain round mitochondria scattered freely throughout the cytoplasm (Figs 7, 17). The basal plasma membrane is flat and does not form conspicuous invaginations into the cytoplasm. This zone occupies the entire length of the terminal trunk and the greater part of the initial trunk.

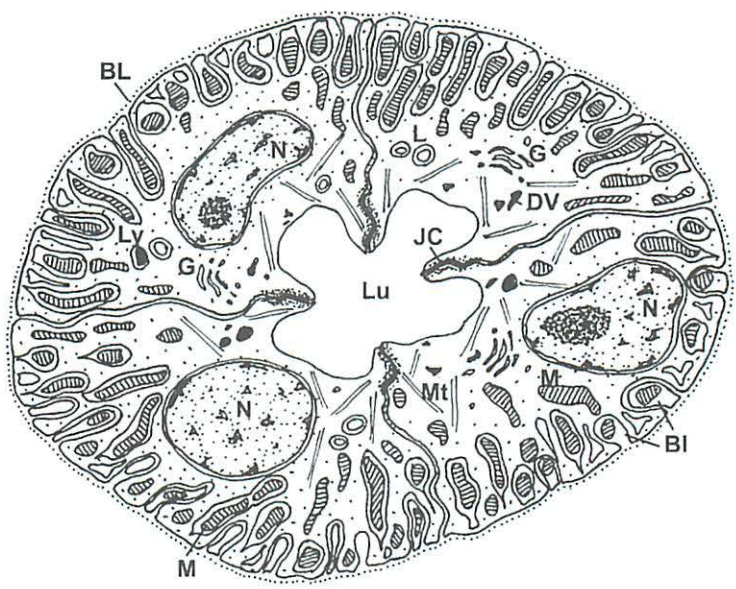
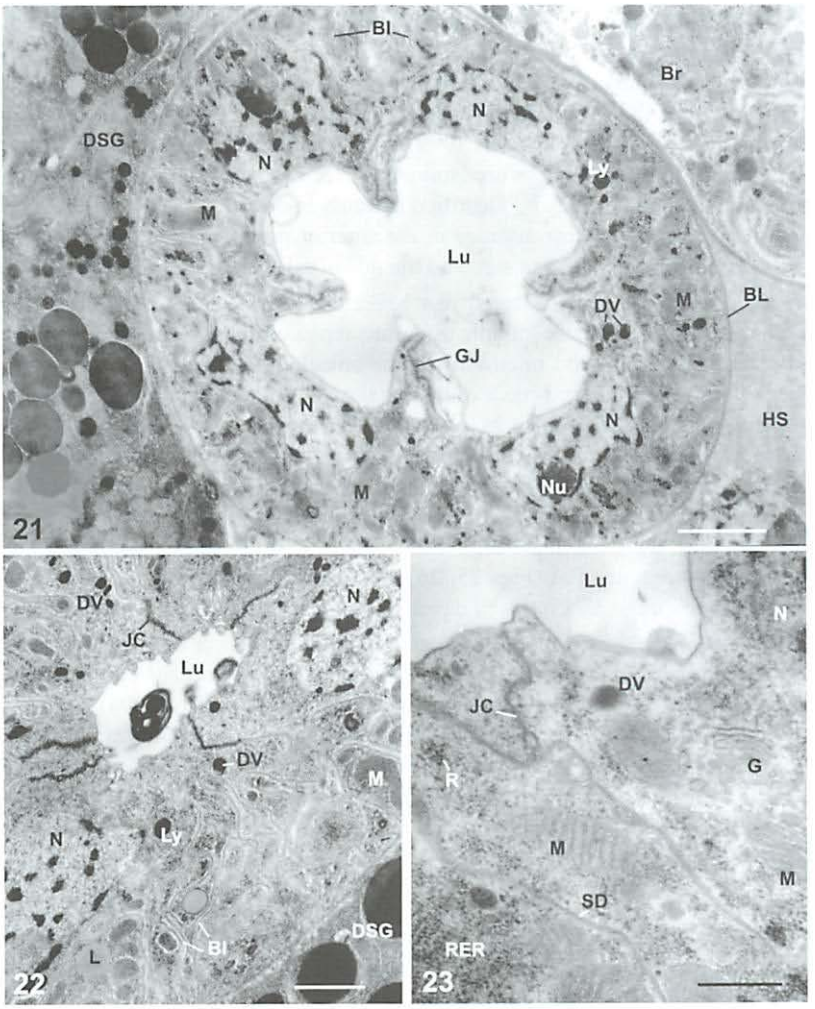


Fig. 20 Schematic drawing of transverse section of the distal tubule in its middle zone with the basal labyrinth (see explanation in text). For abbreviations see page 58.

The cells of the middle zone are more regularly prismatic and are characterised by prominent basal infoldings of the basal plasma membrane (basal labyrinth) occupying $^1/_2$ to $^3/_4$ of the cell height (Figs 19 – 22, 24). The cytoplasmic compartments of the labyrinth contain



Figs 21 – 23 TEM micrographs of the distal tubule of the coxal gland

21: *Camerotrombidium pexatum*, transverse section of the round tubule in its middle zone with the wide and empty lumen into which the contact cell zones are extended. Scale bar – 2 µm.

22: *Platytrombidium fasciatum*, transverse section of the middle zone of the tubule with a dense particle in the lumen and a dense flocculent material indicating the apical cell contacts. Scale bar – 1 µm.

23: *C. pexatum*, apical cell portions in the middle zone of the tubule with Golgi body and dense vesicle. Scale bar – 0.5 µm. For abbreviations see page 58.

elongated mitochondria. The mitochondria may be long and curved, achieving 1.5 μm in length, with a more electron-dense matrix than that of the mitochondria of the proximal tubule and with obliquely stacked cristae (Figs 19, 24). Corresponding to such a cellular organisation, the irregularly shaped nuclei predominantly occupy an apical position above the labyrinth (Figs 20, 21), or, contrarily, are immersed into the latter (Fig. 19). Numerous microtubules running in different directions are observed in the apical cytoplasm as in the subsequent, anterior zone of the tubule (Fig. 24). In the most anterior portion of this zone, the regions of the intercellular connections project apically into the lumen (Figs 20, 21) as in some acaridid mites (ALBERTI & COONS 1999). In this portion, the cells form a regular rosette around the central lumen, which is predominantly free of contents and devoid of microvilli (Fig. 25). Three to five cells may be identified in transverse sections of the tubule. The middle zone occupies a relatively short distance in the anterior portion of the initial trunk situated between the brain from the median side and the dorsal salivary gland from the lateral side.

Finally, in the anterior zone, located just beneath the anterior termination of the dorsal salivary glands, the cells of the middle zone are replaced by electron-lucent cells mostly lacking the basal labyrinth and microvilli on the apical cell surface (Fig. 25). This zone is probably a homologue of the end-piece of the coxal glands of the other mites studied (ALBERTI & COONS 1999). The central lumen in this zone is wide, round and free of contents. Due to the absence of the basal infolds, the nuclei become rounder and contain electron-lucent nucleoplasm with scarce chromatin particles. The anterior zone of the distal tubule is characteristically not accompanied by the proximal tubule, which terminates more posteriorly (Fig. 6). In this area, the gland lies freely within the haemocoel, being enveloped by the basal lamina that always remains flat (Figs 25, 26). Among the larvae studied, the terminal zone may be variously expressed, being well developed or nearly absent.

The distal tubule ends with more dense and compact ectoderm cells, which produce the cuticle of the excretory duct (Fig. 26). This process is realised nearly by the same manner described previously for the ducts of the salivary glands (SHATROV 2004). Apparently, no terminal bladder (sac) of the coxal glands, as shown in some water mites (MICHAEL 1895, SCHMIDT 1935, BADER 1938, ALBERTI & COONS 1999), is found in unfed microtrombidiid larvae.

4. Discussion

A general description and comparative analysis of the coxal glands in the Arachnida was made by BUXTON (1913) and afterwards the organisation of the coxal glands in different arachnid groups was to some extent clarified using electron-microscopic methods (RASMONT 1959, GROEPLER 1969, HECKER et al. 1969, ALBERTI 1979, EL SHOURA & ROSHDY 1985). The morphology of the coxal glands of the studied animals indicates that their main function is focused on osmoregulation, showing at the same time particular variations according to the ecophysiological conditions, under which the given animal lives. Since in the course of ontogenesis and moulting processes the entire gland is not renewed and does not undergo significant changes except for the cuticular excretory duct (SHATROV 2000), the coxal gland is apparently to be of a mesodermal origin as in other arachnids studied (BEKLEMISHEV 1964).

As shown in this study, the anatomy of the coxal glands in the unfed microtrombidiid larvae generally agrees with that described for other actinedid mites (ALBERTI & STORCH 1977,

ALBERTI & COONS 1999). Such an organisation of the tubular portion of the coxal glands consisting of proximal and distal tubules may be also recognised in the other mites studied (ALBERTI & COONS 1999), characterised by different cell types in different tubular portions. In adults of the trombidiid mite *Allothrombium lerouxi* Moss, 1962, the tubular (coxal) glands are also composed of two tubes running backward and forward, and moreover have a distal elongated sac serving supposedly as a saliva reservoir (MOSS 1962). The posterior bend of the gland and the presence of two different particular trunks or tubes were, however, not clearly indicated in trombiculid mites, neither in adults (BROWN 1952, MITCHELL 1964) nor in larvae (VOIGT 1971, SCHRAMLOVÁ 1978, SHATROV 1995). No distal sacculus was found in mites of this group. In water mites, which show a large variety in their biology and morphology, the coxal glands appear to have corresponding morphological variations (CRONEBERG 1878, MITCHELL 1955), possessing tubes that run backwards and forwards (BADER 1938) as well as a distal bladder(s) (MICHAEL 1895). In the erythraeid mites, the tubular glands are shown bent several times but lacking a distal sacculus (THOR 1904). Conversely, the coxal glands of calyptostomatids consist of a sacculus and a tubule (VISTORIN-THEIS 1978). In other acariform mites besides Parasitengona, the coxal glands are typically composed of a tube curving several times in different directions and of a proximal sacculus that is shown in Actinedida (MICHAEL 1896, ALBERTI 1973, ALBERTI & STORCH 1974, 1977, ALBERTI & COONS 1999) and Oribatida (WOODRING & COOK 1962, WOODRING 1973, ALBERTI & STORCH 1977, ALBERTI et al. 1997, ALBERTI & COONS 1999). However, a simple tubule with only one caudal bend and without a proximal sacculus is found in the Tetranychidae (BLAUVELT 1945, MILLS 1973, ALBERTI & STORCH 1974, MOTHES & SEITZ 1980, 1981, ALBERTI & CROOKER 1985). In the Myobiidae, a rather thin curled tubule of the gland is found terminating in a dilated distal sac serving, supposedly, for reabsorption of fluids (FILIMONOVA 2004). This apparently excludes the homology of the distal sac in myobiids and the bladder in certain water mites. Conversely, in the Acaridida, where Malpighian tubules are originally present, the so-called supracoxal glands are found to be rather modified and even reduced (PRASSE 1967, RHODE & OEMICK 1967, BRODY et al. 1976, WHARTON & FURUMIZO 1977, ALBERTI & COONS 1999).

Concerning the ultrastructural organisation of the coxal glands, the main problem is to correlate observed morphological characteristics of the given gland and its proposed functions realised in the particular ecophysiological conditions under which the mite lives.

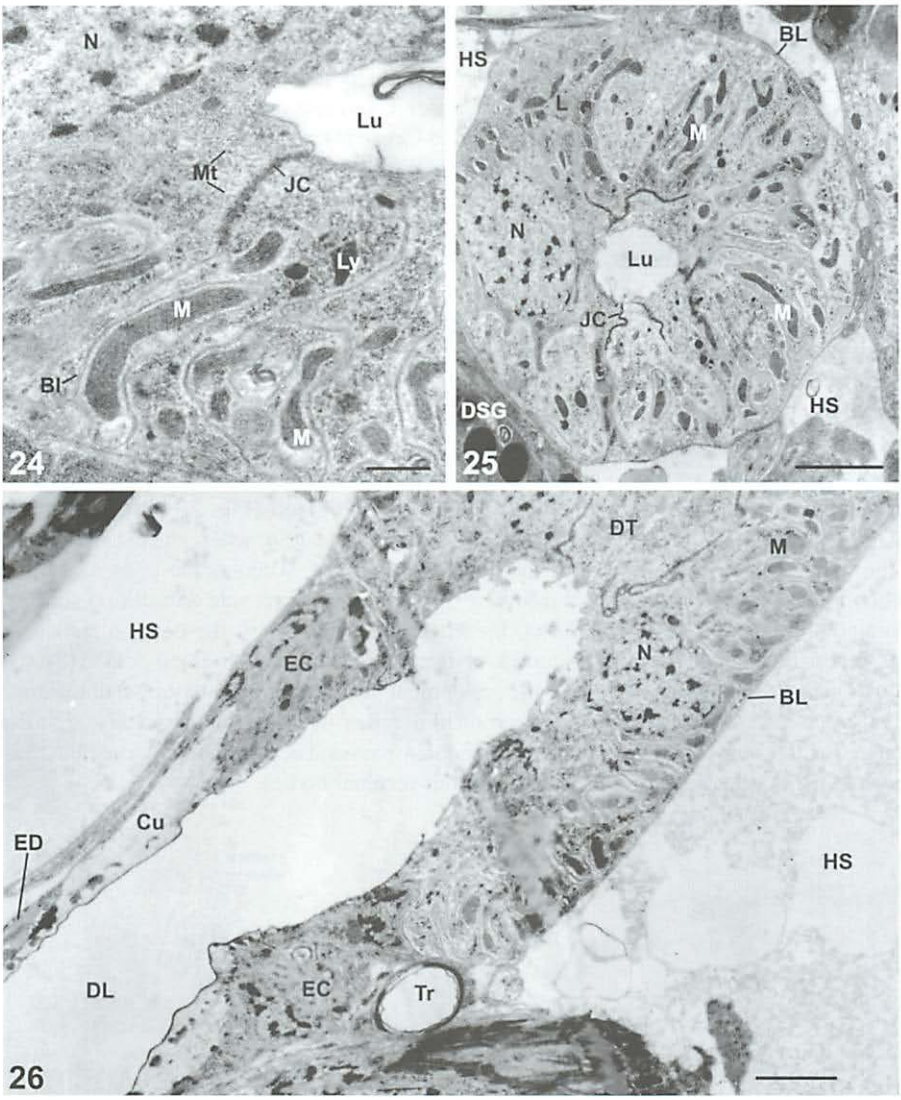
Regarding mites, it is generally accepted that the sacculus, if present, is specialised for filtration or ultrafiltration of the haemolymph fluid into the lumen of the organ, whereas the convoluted tubule (labyrinth) with its microvillar border and high mitochondrial density (mitochondrial pump) serves, conversely, for the active reabsorption of ions and water from the lumen back into the haemolymph (EVANS 1992). Admission of ultrafiltration across the wall of the coxal gland in its proximal portion (sacculus) as a mechanism for urine formation inevitably implies a significant blood (haemocoel) pressure in the body cavity. On the other hand, the simple filtration of solutes (diffusion) along an osmotic gradient may also take place across the wall of the sacculus without substantial haemocoelic pressure (BERRIDGE & OSCHMAN 1969). Another mechanism of filtration of the solution from the haemolymph into the filtrating chamber of the coxal glands is described in ticks, where muscles act to dilate the chamber's volume thus providing haemolymph pressure (LEES 1946). Subsequent reabsorption of ions takes place during movement of the fluids along the tubules of the gland.

Concerning the Parasitengona, as well as other Actinedida, the most important question is

the occurrence of the coxal glands as a part of the prosomal gland complex. Functionally, this evolutionary acquisition in the higher trombidiform mites might correlate with the closing of the midgut and transformation of the hindgut into a specialised excretory organ (MITCHELL 1970, EVANS 1992). The reduction of an immediate joint of the midgut and the hindgut (excretory organ) in the higher trombidiform mites like the Parasitengona leads, first, to loss of the Malpighian tubules in representatives of this group with a transfer of the excretory function to the excretory organ, and, second, to the need of removing the excess water ingested during feeding outside of the gut. Such a morphological adaptation apparently results in the formation of prominent coxal glands functioning mostly in osmoregulation. In those groups where the junction of the midgut and the hindgut is not totally reduced, like tetranychids, a prominent filtrating sacculus is not present (BLAUVELT 1946, ALBERTI & CROOKER 1985), even if these mites take up large amounts of water (MCENROE 1961a, b). In this case, the elimination of water takes place via the gut, whereas the transpiration (loss of water) is supposedly realised through the walls of the tracheal trunks (MCENROE 1961a). Thus, the hindgut in tetranychids apparently functions in reabsorption of water that is a characteristic feature of the coxal glands of more derived groups (MCENROE 1963). On the other hand, in those groups, like the Acaridida, in which other organs (Malpighian tubules) function in reabsorption of water, the coxal glands may be modified or even lost (WOODRING 1973, WHARTON et al. 1979, ALBERTI & COONS 1999). Indeed, in representatives of the Acaridida, which have passed to feeding on hard substrates, like keratin etc., the need to remove the excess water significantly decreases, leading to a restriction of both filtration and reabsorption and so to deviation and minimalisation of morphological expression of the coxal (supracoxal) glands (BRODY et al. 1976). The terminal sac in myobiids (FILIMONOVA 2004), supposedly functioning in reabsorption, probably indicates the need for additional conservation of water in the organism. Another unusual source of water is a particular secretion (containing potassium chloride) of some acaridides, which absorbs water from the air during movement down the podocephalic canal (WHARTON & FURUMIZO 1977). Entering the buccal cavity, such a secretion becomes enriched with water and is ingested back into the gut.

It is evident from this general consideration that the more liquid substances the mite ingests during feeding, the larger the proximal filtrating portion of the coxal gland evolves, mostly functioning in the removal the excess water from the organism. In this consideration, the absence of a sacculus in parasitengones, which ingest large masses of liquid food during feeding due to extra-oral (extra-intestinal) digestion (MITCHELL 1970), looks somewhat strange. Moreover, the joining of the coxal glands with the salivary glands may be functionally explained only by two basically controversial reasons: firstly, by feeding on food without a large amount of water and, secondly, by the need for concentration and reservation of water in the organism (BERRIDGE 1970). If the former is not evident, the latter is extremely important for mites, which cannot live in a dry atmosphere and actively lose water by means of transpiration, which is especially relevant for trombiculids (SHATROV 2000) and for nearly all other mites with a soft cuticle. Consequently, the function of water conservation apparently predominates over the function of removing excess water in mites of this group.

From the cytological point of view, the presence of the long microvilli in the apical cell surface of the proximal tubule apparently suggests the probability of the transport of fluids from the lumen into the haemolymph (DIAMOND & TORMEY 1966, BERRIDGE & OSCHMAN 1969, BERRIDGE 1970, WALL et al. 1970 etc.), i.e. reabsorption of solutes and water (Fig. 27).



Figs 24 – 26 TEM micrographs of the distal tubule of the coxal gland of *Platytrombidium fasciatum* mite larvae

24: Part of the wall of the middle zone provided with the basal labyrinth and apical surface lacking microvilli. Scale bar – 0.5 μm.

25: An area of transformation of the middle zone with dark cells into the anterior zone composed of the electron-lucent cells without the basal infolds; transverse section. Scale bar – 2 μm.

26: Longitudinal section of the terminal portion, at the base of the excretory duct composed of electron-dense ectoderm cells; note the absence of envelope of muscle or connective tissue around the coxal gland. Scale bar – 2 μm. For abbreviations see page 58.

At the same time, the absence of mitochondria situated close to the microvilli as well as the total absence of intercellular spaces and basal infoldings in the cells of the proximal tubules seem to indicate low transport intensity in the unfed larvae poorly provided with free haemolymph. Indeed, to reabsorb the excess water it is necessary, first of all, to absorb fluids into the lumen. The lumen of the tubule in unfed larvae is not wide or can even be collapsed. On the other hand, ultrafiltration of fluids across the epithelium from the haemolymph to the lumen in the proximal tubule can also doubtfully be very high, because unfed larvae recently hatched from eggs apparently cannot create the necessary haemolymph pressure. However, filtration of particular substances across the glandular epithelium from the haemolymph into the organ along an osmotic gradient cannot be totally excluded (Fig. 27). Presence of large number of mitochondria in the cells of the proximal tubules may indicate active transport of solutes as well. Otherwise, it is hard to imagine why such a long proximal tubule has developed. It is most likely, however, that it is a pre-adaptation functioning in due course in large adult mites.

Conversely, the distal tubule, due to the presence of basal infoldings and the apparent mitochondrial pump, appear to be able to selectively absorb and filter some amounts of ions and water from the haemolymph into the lumen of the gland (Fig. 27). Nearly the same situation is observed in trombiculid larvae (SHATROV 1995, 2000), where the proximal portion of the gland is rich in microvilli in the apical cell surface, whereas the cells of the distal portion are provided with the basal infoldings. It is interesting to note that during feeding of trombiculid larvae on vertebrate hosts, the intercellular spaces in the coxal glands do not conspicuously dilate, whereas the lumen of the internal channel become wider (SHATROV 2000). During the subsequent course of development through active and quiescent instars, the organisation of the coxal glands of trombiculid mites does not undergo any significant changes, except somewhat increasing the glandular mass and accumulating waste materials in the cytoplasm in the form of large heterogeneous residual bodies.

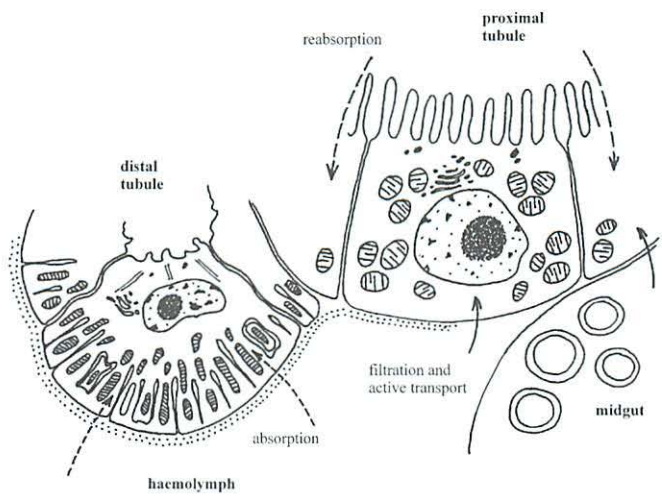


Fig. 27 Schema illustrating the transportation processes through the walls of the coxal gland tubules

The most remarkable feature of the coxal glands arrangement in microtrombidiid larvae is the very tight association of the glandular cells and the midgut epithelium, being devoid of a delimiting basal lamina throughout the cell margins. Specialised junctions as well as basal cytoplasmic extensions between the cells of the coxal glands and the midgut epithelium, which supposedly might play a role in the transport of fluids and ions (see ALBERTI & COONS 1999), were not clearly observed in the species studied. Nevertheless, such a very tight association suggests a rather intimate relationship between these two organs and possible removal of excess water from the gut immediately through the epithelium of the coxal glands (Fig. 27). It is most likely, however, that the organisation of both the midgut and the coxal gland epithelia in the unfed larvae are not definitively formed and have to undergo further development during the process of the larval feeding and subsequent transformation into long-living deutonymphs and adult mites.

Excretion does not evidently take place in the tubular glands of microtrombidiid larvae, although it is shown for some acariform mites, in particular oribatids (WOODRING 1973, ALBERTI & COONS 1999). As is well known, in the evolution of the Parasitengona, a total functional separation has taken place between the coxal glands, which take part in the water balance of the organism, and the excretory organ, which functions in the excretion of nitrogenous residues. The observed secretion in both proximal and distal tubules cannot be adequately explained from the functional point of view and needs further elucidation, in particular, in comparison with feeding larvae and postlarval instars. It cannot be excluded, however, that the coxal glands, being part of the salivary gland complex, also produce some particular secretion that plays a role in composing the saliva and its action within the host/prey tissues (MITCHELL 1970).

Based on the organisation of the coxal glands in microtrombidiid larvae, it may be concluded that these organs, as supposedly in the other Parasitengona, play a role mostly in water retention in the mite organism additionally to the behavioural reactions preventing desiccation of the living mites.

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