

ULTRASTRUCTURE OF COXAL GLANDS IN THE ADULT
MICROTROMBIDIID MITE
PLATYTROMBIDIUM FASCIATUM (C.L. KOCH, 1836)
(ACARIFORMES: MICROTROMBIDIIDAE)

BY ANDREW B. SHATROV¹

(Accepted November 2006)

MORPHOLOGY,
ULTRASTRUCTURE,
OSMOREGULATION,
COXAL GLANDS,
ACARIFORMES,
MICROTROMBIDIIDAE,
PLATYTROMBIDIUM FASCIATUM

SUMMARY: Morphology and ultrastructure of coxal glands of the adult microtrombidiid mite *Platytrombidium fasciatum* (C.L. Koch, 1836) (Acariformes: Microtrombidiidae) were studied by means of transmission electron microscopy and on semi-thin toluidine blue stained sections. The paired tubular coxal glands run along the axis of the body and occupy ventral and medial position. The cuticular excretory ducts of the coxal glands and the posterior alveolar salivary glands are joined together immediately after leaving the glands thus forming a common salivary duct (podecephalic canal) of each side of the body. Electron-microscopically, the coxal glands are found composed of two different kinds of tubes, which may be termed as a distal tube, giving rise to the excretory duct, and a proximal tube succeeding distal one and forming a basal (posterior) part of the organ. The distal tube goes backward up to the caudal end of the gland, where it makes several large loops directing forth and back, and then transforms into the proximal tube. The latter chaotically coils around the distal tube in anterior direction and finally terminates blindly at a distance of approximately 1/3 from the anterior termination of the gland. The cells of the tubes arrange around the central lumen as a rosette and are tightly adjoined each other leaving no conspicuous extracellular space between the adjacent cells of both the same and the opposite tubes. The cells of the proximal and the distal tubes are both provided with basal infolds (labyrinth) with mitochondria. The apical cell surface of the proximal tube bears long, tightly packed microvilli, whereas the apical plasma membrane of the distal tube remains flat and is armed with only scarce short protrusions. Lateral cell borders inside the gland are folded, and the adjacent cells are connected via septate desmosomes. Irregularly outlined nuclei of the both types of tubes are organized identically with rather small heterochromatin particles and a large nucleolus. Small Golgi bodies produce few small vesicles. No clear evidences of pinocytotic and exocytotic activity as well as vesicular transport across the glandular walls were observed. Nevertheless, the gland structure corresponds well to the organization of the transportation epithelia, and the coxal glands obviously take part in water excretion and ion/water regulation of the mite organism.

1. Zoological Institute Russian Academy of Sciences, 199034, St.-Petersburg, Russia, Tel.: + 7(812)7140151, Fax: + 7(812)7140444, e-mail: chigger@mail.ru

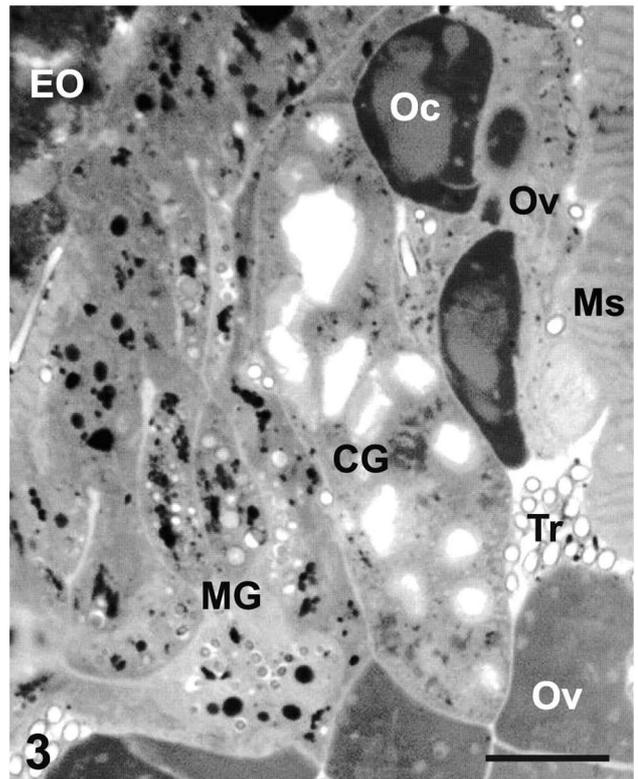
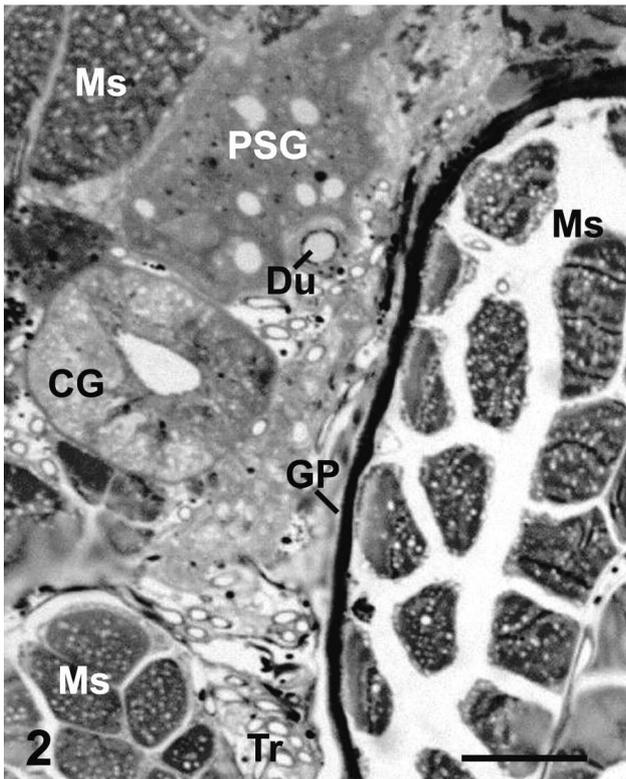
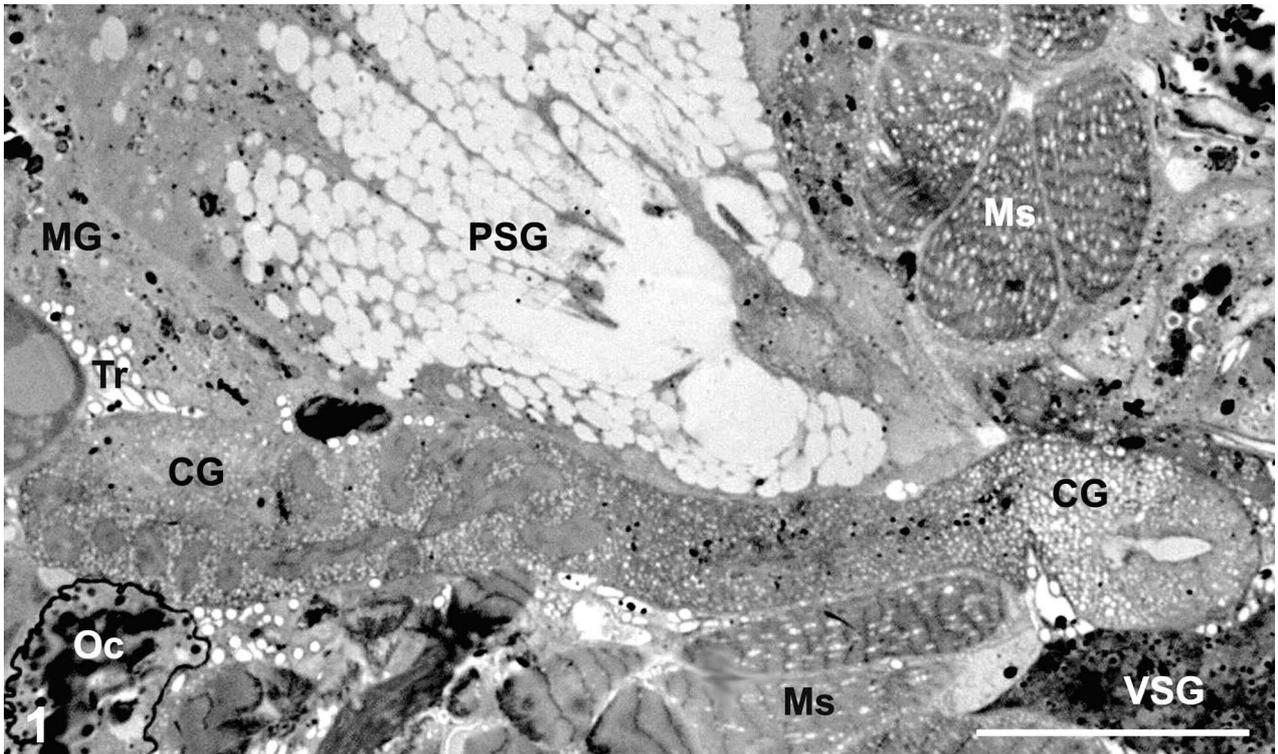
RÉSUMÉ: La morphologie et l'ultrastructure des glandes coxales de l'adulte de *Platytrombidium fasciatum* (C. L. Koch, 1836) (Acariformes: Microtrombidiidae) ont été étudiées en microscopie électronique à transmission et en coupes demi-minces colorées au bleu de toluidine. Les glandes paires tubulaires coxales courent le long de l'axe du corps et sont en position ventrale et médiane. Les canaux excréteurs cuticulaires des glandes coxales et des glandes salivaires alvéolaires postérieures sont réunis immédiatement dès la sortie des glandes pour former un canal salivaire commun (canal podocéphalique) des deux côtés du corps. En électro-microscopie les glandes coxales sont formées de deux types de tubes : le tube distal donne le début de canal extérieur et le tube proximal poursuit le tube distal en formant une partie basale de l'organe. Le tube distal se dirige vers l'arrière jusqu'à l'extrémité de la glande où il forme plusieurs cercles dirigés vers l'arrière et vers l'avant, puis se transforme en tube proximal. Ce dernier dessine une courbe chaotique autour et en avant du tube distal pour s'achever en aveugle à une distance de 1/3 avant le bord antérieur de la glande. Les cellules des tubes sont disposées en rosette autour de la cavité centrale et sont jointives ne permettant pas de voir une portion d'espace extracellulaire du même tube ou des autres tubes. Les cellules du tube proximal et distal sont munies de plis basaux de la membrane plasmique (labyrinthe basal) comprenant des mitochondries. La surface apicale des cellules du tube proximal forme de longues microvillosités bien compactes tandis que la membrane apicale plasmique des cellules du tube distal reste plane avec quelques courtes excroissances. Les bords latéraux des cellules sont plissés, les cellules elles-mêmes sont connectées à l'aide de desmosomes septaux. Les noyaux de forme irrégulière des deux types de tube sont identiques et contiennent de petites particules d'hétérochromatine et un grand noyau. Des vésicules de Golgi de petite dimension constituent de petites bulles peu nombreuses. Les processus de la pinocytose et de l'exocytose aussi bien que le transport vésiculaire à travers la paroi de la glande n'ont pas été remarqués. La structure de la glande correspond bien aux épithéliums de transport et la glande coxale elle-même prend part probablement à l'excrétion d'eau et aux processus de la régulation de la concentration ionique.

INTRODUCTION

The excretory coelomoducts of Chelicerata, or coxal glands, generally known under a common term nephridia, are of a mesodermal origin and typically open by an ectodermal excretory duct between leg's bases (coxae) on the ventral body region (BEKLEMISHEV, 1964; ALBERTI *et al.*, 1997; ALBERTI & COONS, 1999). The coxal glands, mostly organized in a number of one pair, are generally composed of a proximal coelomatic sacculus and of a convoluted tubule (labyrinth). Before entering the excretory duct, the tubule may form a particular distal ampul or sac (bladder). A fundamental character of all Actinotrichida, however, is that the coxal glands are connected with prosomal alveolar salivary glands (podocephalic sys-

tem) by their excretory ducts (ALBERTI & STORCH, 1977; ALBERTI *et al.*, 1997; ALBERTI & COONS, 1999) to form a common salivary duct (podocaphalic canal) on each side of the body. In the cohort Parasitengona, to which the family Microtrombidiidae belongs, the proximal sacculus is found to be reduced that is considered as one of the synapomorphic characters of this cohort (WITTE, 1991).

Based on the morphological data available, in particular ultrastructural investigations, the coxal glands are assumed to function in osmoregulation and maintenance of ion/water balance in the arthropod organism (see FAWSEK, 1891; THOR, 1904; BUXTON, 1913; RASMONT, 1959; GROEPLER, 1969; HECKER *et al.*, 1969; WOODRING, 1973; ALBERTI & STORCH, 1973, 1974, 1977; ALBERTI, 1979; ALBERTI & CROOKER,



FIGS. 1-3. Semi-thin toluidine blue stained sections indicating localization of the coxal glands in adult mites *Pl. fasciatum*. 1. — Longitudinal section through coxal gland and posterior alveolar salivary gland. Scale bar. 50 μ m. 2. — Transverse section through anterior tubular portion of coxal gland situated laterad to the lateral wall of the gnathocoxal plate. Note excretory duct (Du) of posterior salivary gland. Scale bar — 20 μ m. 3. — Transverse section through posterior vertically stretched portion of coxal gland situated between midgut and ovary with oocytes. Note widened lumens of the coxal gland tubes. Scale bar — 20 μ m.

1985; ELSHOURA & ROSHDY, 1985; EVANS, 1992; ALBERTI *et al.*, 1997; ALBERTI & COONS, 1999; SHATROV, 2000; FILIMONOVA, 2004; etc.). The proximal sacculus, frequently built up of podocytes, is the site of ultrafiltration of solutions and fluids from the haemolymph into the organ and formation of the primary urine, whereas the labyrinth, the cells of which are provided with apical microvilli and basal plasma membrane infoldings containing mitochondria (mitochondrial pump), acts in selective transport of ions and solutions across the tubular wall, thus functioning in osmoregulation.

In the cohort Parasitengona, comprising several superfamilies of terrestrial (soil) and water mites with parasitic larvae and free-living deutonymphs and adult mites, the coxal glands, mostly known as tubular glands, are investigated in a variable extent, mainly anatomically on the light-optical level in both adult mites (CRONEBERG, 1878; MICHAEL, 1895; THON, 1905; SCHMIDT, 1935; BADER, 1938; BROWN, 1952; MITCHELL, 1955, 1964; VISTORIN-THEIS, 1978; SHATROV, 1995, 2000) and the larvae (JOHNS, 1950; VOIGT, 1971; SCHRAMLOVÁ, 1978; SHATROV, 2000, 2006.). Only few species of the Parasitengona are studied electron-microscopically (SHATROV, 2000; ALBERTI & STORCH, 1977; ALBERTI & COONS, 1999). Generally, in the Parasitengona, feeding by liquid food using extra-oral (extra-intestinal) digestion (COHEN, 1995, 1998), both the alveolar salivary and the tubular (coxal) glands are found well developed and achieve very large size in the body volume, playing an important role in the mite physiology.

Recently, ultrastructure of coxal glands in the unfed microtrombidiid larvae *Platytrombidium fasciatum* (C.L. Koch, 1836) and *Camerotrombidium pexatum* (C.L. Koch, 1837) were examined in detail (SHATROV, 2006). It is shown that the coxal glands are composed of the two main 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, whereas basal infolds are practically absent. Conversely, the distal tubule possesses in its middle zone the basal infoldings containing elongated mitochondria. As in the majority of other Parasitengona, the coxal glands of microtrombidiid larvae are devoid of a proximal sacculus. It is assumed

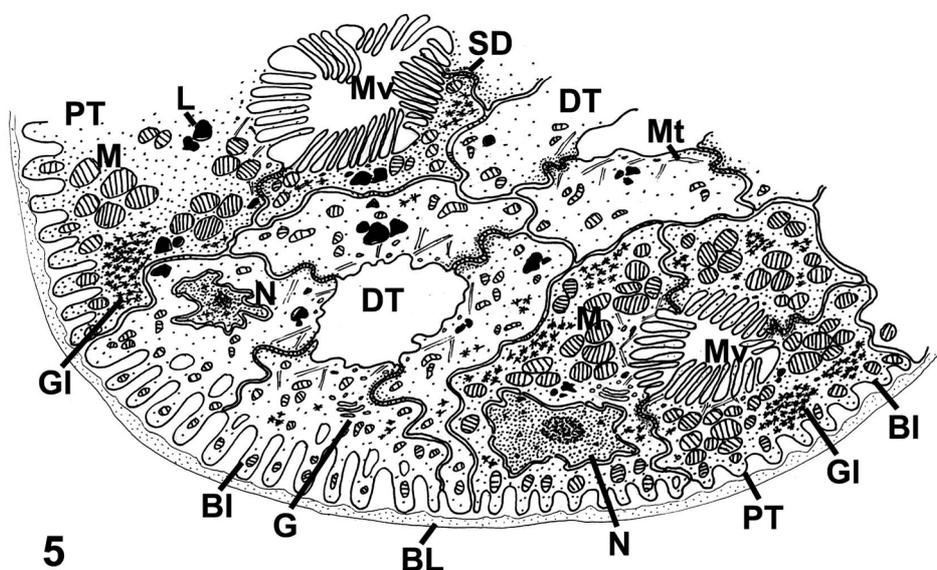
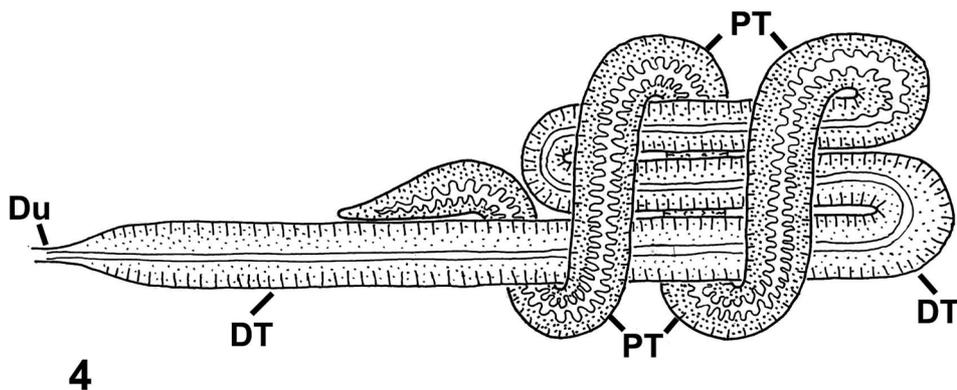
that the coxal glands in larvae mostly function in preserving water, preventing desiccation of the mites.

The main purpose of this study is to provide a detail electron-microscopical description of the coxal glands in the adult mite, *Platytrombidium fasciatum* (C.L. Koch, 1836) and to compare the organization of the coxal glands in unfed larvae and fed adult mites of the same microtrombidiid species living in boreal ecophysiological conditions. The ultrastructural examination of the organ taking part in important function of ion and water regulation may clarify some physiological needs of the animal as well as some evolutionary tendencies in this branch of the Acari.

MATERIAL AND METHODS

Mites used in this study were collected from the soil surface in Leningrad district during spring-summer of 1996. Mites presumably of the same species were initially placed into small plastic jars with soil particles as a substrate and then, one week after capture, some of these mites were taken for fixation. Remaining mites were mounted on slides and identified by Dr. J. MAKOL from the Agricultural University of Wrocław (Poland) as *Platytrombidium fasciatum* (C.L. Koch, 1836), which are the most widespread species in this region. All investigated mites were found to be females.

For transmission electron microscopy (TEM), adult 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 into the fixative fluid, animals were carefully pierced with tiny insect pins for a better penetration of the fixatives. Mites were then washed in several changes of 0.2 M phosphate buffer, post-fixed in 2% osmium tetroxide in phosphate buffer containing 8.56% sucrose for 1-6 h to overnight, dehydrated in ethanol and acetone series, and finally embedded in an araldite mixture. Serial ultra-thin sections both in transverse and 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 microscopes at 60-90 kV. For preliminary and general observations, semi-thin sections



Figs. 4-5. 4. — Schematic drawing indicating approximate anatomical organization of coxal gland in adult mites *Pl. fasciatum*. 5. — Schematic drawing showing part of transverse ultra thin section through the gland composing of several proximal and distal tubes.

were stained with toluidine blue and investigated under Amplival and Leica DMLS-2 light optical microscopes.

List of abbreviations: BI – basal infolds, BL – basal lamina, CG – coxal gland, Cut – cuticle, DT – distal tube, Du – excretory duct, DV – dense vesicle, EO – excretory organ, G – Golgi body, Gl – glycogen, GP – gnathocoxal plate, L – lysosome, Lu – lumen, M – mitochondria, MG – midgut, Ms – muscles, Mt – microtubules, Mv – microvilli, N – nucleus, Nu – nucleolus, Oc – oocyte, Ov – ovary, PSG – posterior salivary gland, PT – proximal tube, R – ribosomes, RB – residual body, SD – septate desmosome, Tr – trachea, VSG – ventral salivary gland

RESULTS

General and light-optical observations.

In adult microtrombidiid mite *P. fasciatum*, one pair of coxal glands, having a tubular form, are stretched along the axis of the body in a ventral and medial position, just lateral to the brain, from the level of gonads (ovaries) up to the gnathosoma (FIG. 1). The overall length of the gland is around 230-250 μm . In their course from back to forth, the coxal glands variously border free haemolymph (haemocoelic space), ovaries, midgut, coxal muscles, brain

and posterior and ventral alveolar salivary glands, contacting at the same time with various number of tracheae (FIGS. 1-3). Anterior third of the coxal glands is situated just beneath and in close contact to the posterior alveolar salivary glands (FIGS. 1, 2). The cuticular excretory ducts of these glands are joined together immediately after leaving the glands thus forming a common salivary duct (podecephalic canal) of each side of the body. Anterior portion of the coxal gland is regularly tubular with widened or collapsed lumen (central canal) and has a diameter of around 30-40 μm (FIG. 2). Posterior portion of the gland, where its tubes apparently form folds and loops, possesses irregular shape in transverse sections being frequently flattened in a horizontal, oblique or vertical plan with a maximum diameter of around 45-50 μm and even sometimes up to 140 μm (FIG. 3). At this place, highly resembling glomerule, numerous lumens of the sectioned tubes may be greatly widened (FIG. 3) or, on the contrary, collapsed in different specimen studied. In light-optical sections, the coxal glands are weakly stained and show no obvious particular granulation (FIGS. 1-3). Neither proximal sacculus nor distal sac (bladder) was identified with certainty in the coxal glands of adult microtrombidid mites.

Electron-microscopical observations.

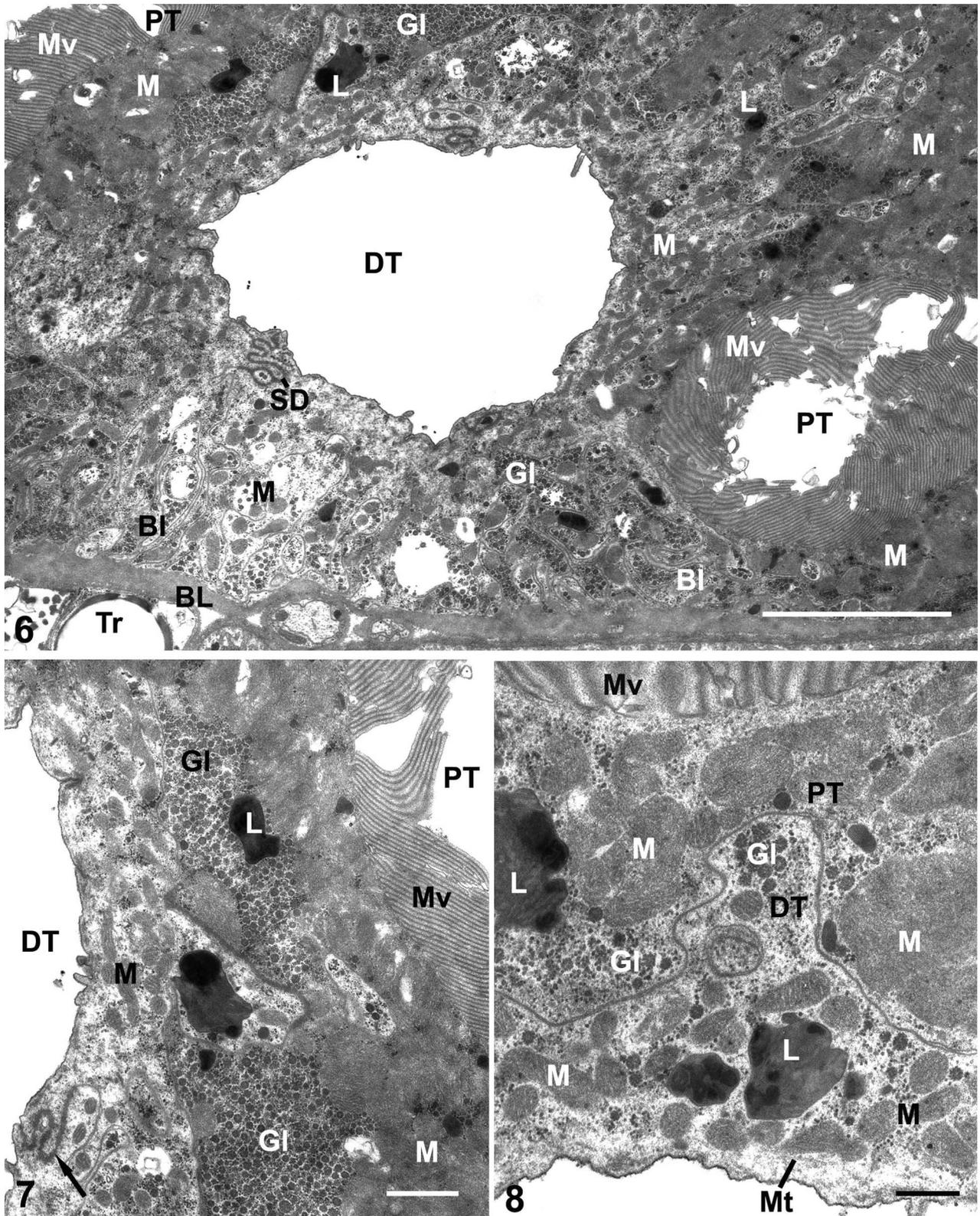
Electron-microscopically, the coxal glands are found composed of two different kinds of tubes, which may be termed as a distal tube, giving rise to the excretory duct, and a proximal tube succeeding distal one and forming a basal (posterior) part of the organ (FIG. 4). The exact course of the tubes is hardly distinguishable because the tubes and their loops are tightly interweaving, especially in the posterior portion of the gland. Nevertheless, some evidences indicate that the distal tube runs, from the origination of the duct, first straight backward and then variously bends in its course up to the caudal end of the gland, where it apparently may make several large loops directing forth and back, and at last transforms into the proximal tube. The latter chaotically coils around the distal tube in a general anterior direction and finally terminates blindly at a distance of approximately 1/3 from the anterior termination of the gland (FIGS. 1, 4).

The cells of the tubes arrange around the central lumen as an irregular rosette (FIGS. 5, 6). The adjacent distal and proximal tubes are rather irregularly shaped in transverse sections and tightly adjoined each other without a delimiting basal lamina between them (FIGS. 6-8). The cells of the opposite tubes typically leave very narrow extracellular space and have greatly folded cell borders (FIGS. 7, 8). The cells contact each other via septate junctions with an electron-dense matrix and hardly distinguishable septae (FIG. 5). Cell margins inside the gland never form a structure like basal infolds (labyrinth) and is not provided with conspicuous amount of mitochondria associated with the cell membrane (FIG. 8). In transverse sections, the coxal glands look like a very extensive chaotic agglomeration of tubes marking by their lumens (FIGS. 5, 6), in which the proximal tubes are found dominated. The entire gland in its whole course is surrounded by a thick, electron-light, finely granulated delimiting basal lamina 0.15 to 0.24 μm in width (FIGS. 5, 6, 9, and 13).

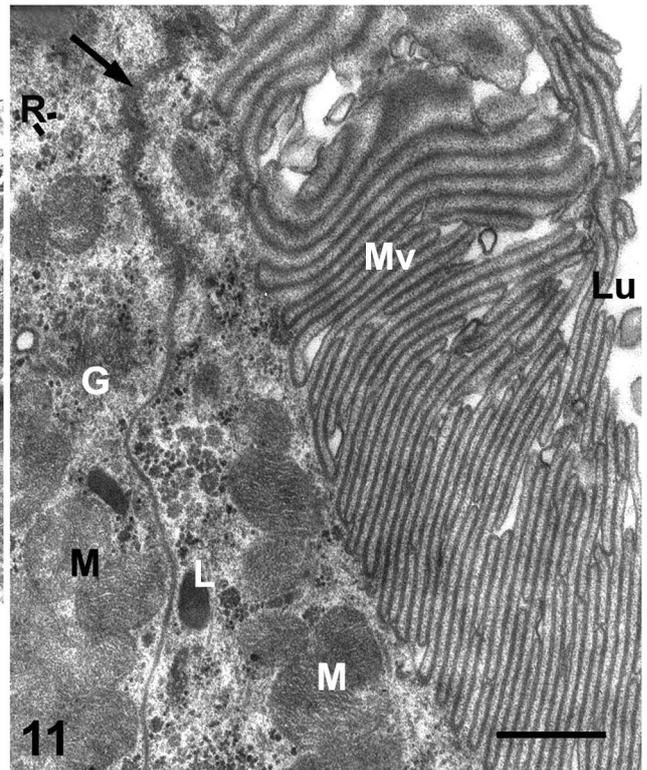
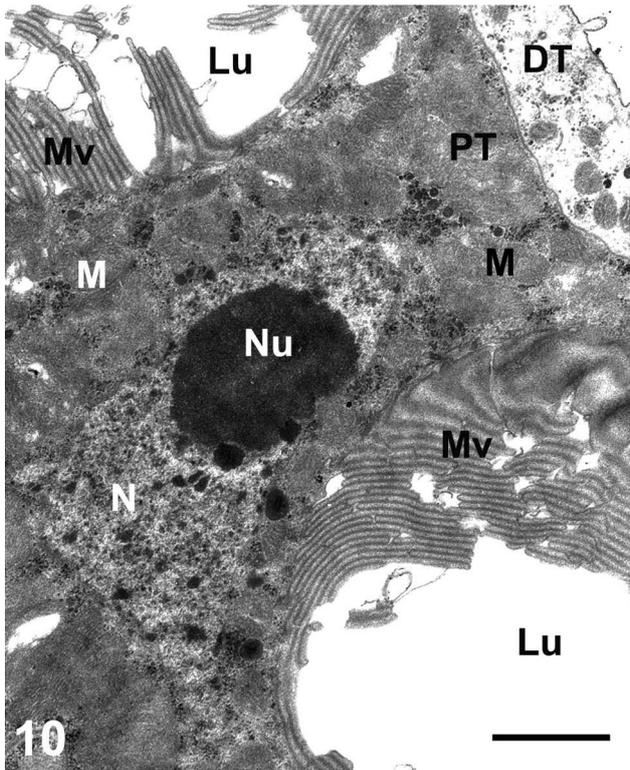
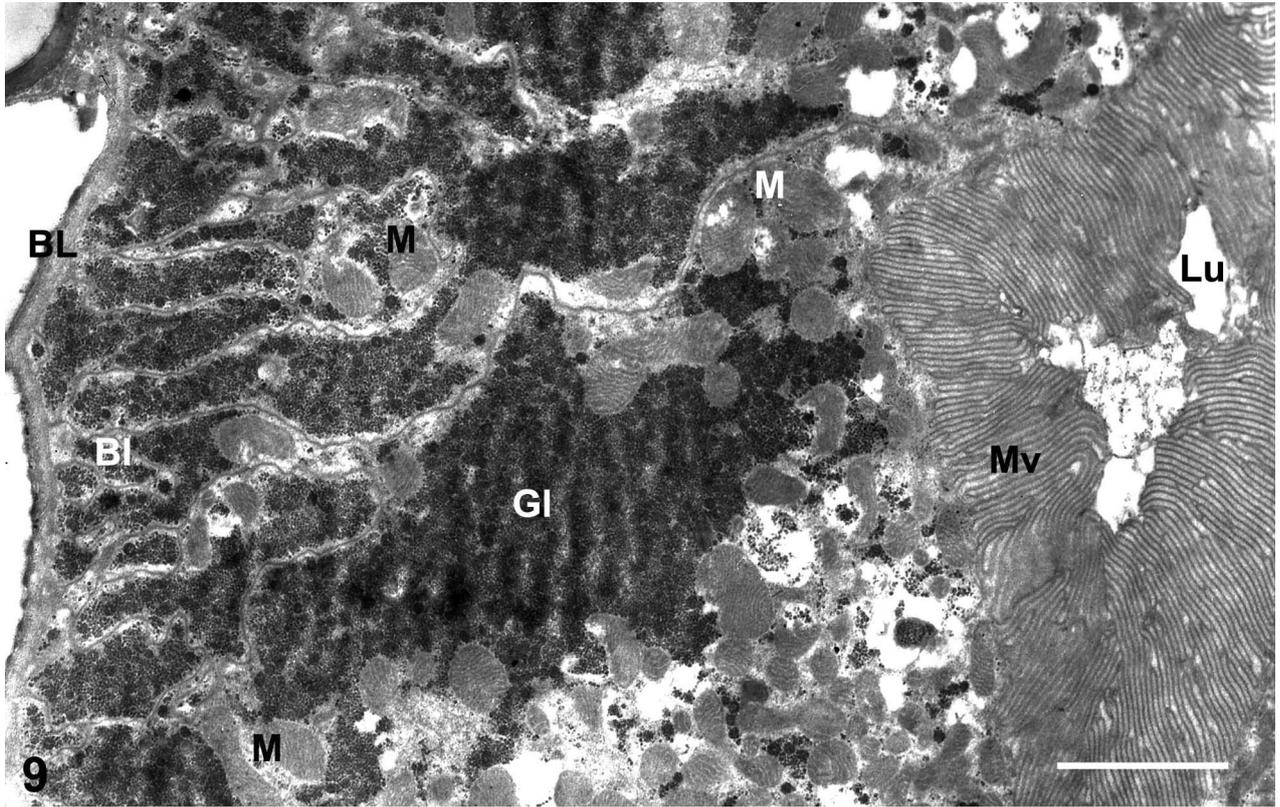
Each of the proximal and the distal tubes are found organized identically through their whole course despite the length of the gland and coils of the tubes.

The most characteristic feature of the proximal tube is long, up to 2.7 μm , uniform and tightly packed microvilli on the apical cell surface bordering the lumen (FIGS. 5, 6, 7, 9, and 11). The latter may be wide (FIG. 6) or, contrary, nearly totally collapsed (FIG. 9). Occasionally, only the presence of the large masses of microvilli indicates the place of the obscured lumen of the proximal tube. Typically, the microvilli are straightly erected, curved, or may be arranged at certain angle to the cell surface even to lie horizontally (FIGS. 7, 11). The tips of microvilli may be also sometimes curved at various angles. The microvilli contain only the cytoplasmic matrix without a particular core of fibrils or filaments (FIG. 11).

The tube walls vary greatly in width from 0.15 to 10.3 μm irrespectively of the tube location – inside the gland or at the border of it. The cells looking outside the gland and bordering by the basal lamina are provided with basal plasma membrane infolds variously expressed but always present (FIG. 5, 9). These infoldings contain various number of large, oval to elongated, mitochondria (from 0.7x0.3 to 1.5x0.8 μm) with a matrix of moderate electron



FIGS. 6-8. Ultrastructure of coxal gland in adult mites *Pl. fasciatum* and interrelations of its tubes. Transverse ultra thin sections. 6. — General view of part of coxal gland showing one distal and two proximal tubes tightly adjoined each other. Scale bar — 4 μ m. 7. — Part of the opposite proximal and distal tubes with thin walls and folded contact between them. Note glycogen particles in the cell of the proximal tube. Arrow indicate cell junction (septate desmosome) between cells of the distal tube. Scale bar — 1 μ m. 8. — Part of the flattened cells of the opposite proximal and distal tubes inside the gland. Note the difference between the organization of mitochondria in the proximal and distal tubes. Scale bar — 0.5 μ m.



FIGS. 9-11. Organization of the proximal tube in the coxal gland of adult mites *Pl. fasciatum*. 9. — Part of the wall of the tube looking outside the gland and underlined by the basal lamina. The cells show basal infolds and are filled with glycogen. The central lumen is nearly obscured. Scale bar — 2 μm . 10. — Part of the two proximal tubes inside the gland with nucleus of one of them bordering the distal tube. Note that the cell borders of the proximal tube are practically indistinguishable. Scale bar — 1 μm . 11. — Apical portions of the cells of the proximal tube contacting each other via special cell junction (septate desmosome) (arrow) and bearing long microvilli protruding into the lumen. Scale bar — 0.5 μm .

density and tightly stacked cristae arranged obliquely (FIG. 9). Dense groups of such mitochondria, which may occupy a large area, are frequently observed in the middle cell zone between the basal infolds and the apical cell surface (FIGS. 5, 7, 8, and 10). Nevertheless, the mitochondria are never found in close association with the apical microvilli.

The nuclei, 5-7 μm in a maximum diameter, typically possess very irregular outlines and rather small heterochromatin particles scattered throughout the electron-clear, finely granulated nucleoplasm (FIGS. 5, 10). A large nucleolus, 1.7x1.3 μm , is located eccentrically. The nuclei are situated in the middle portion of the cells and slightly flattened along the basal lamina. The cells of the proximal tube contain, in contrast to larvae (SHATROV, 2006), various and frequently large amount of glycogen, which tends to locate in the basal cell portions, although, also occurs throughout the cell volume (FIGS. 5, 7, 9).

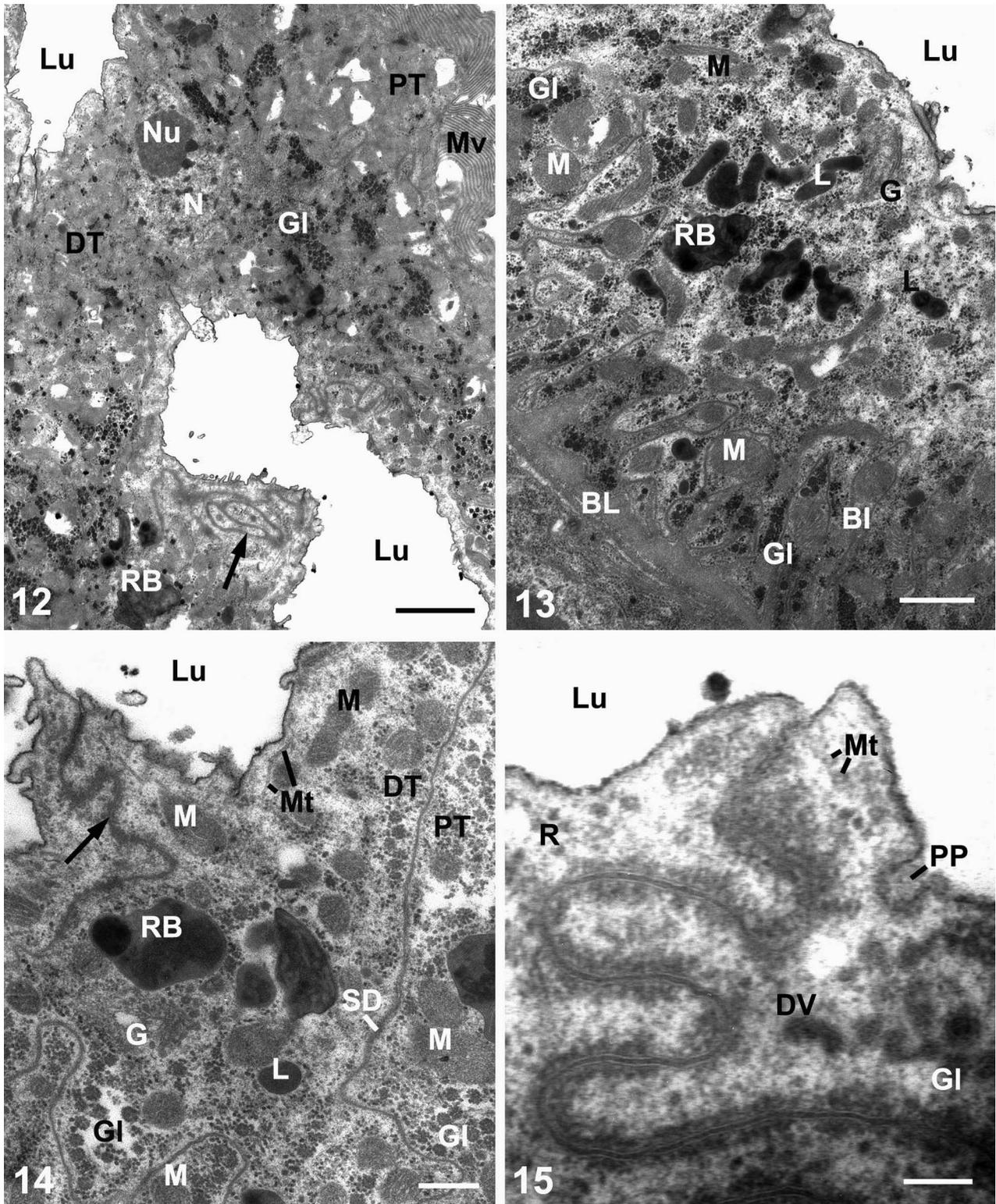
The cells of the proximal tube contain small Golgi bodies mostly situated in the apical cell zones (FIGS. 5, 11). The Golgi bodies consist of several narrow cisterns accompanied by some amount of small, electron-clear vesicles, around 0.04 μm in diameter. Besides that, some number of electron-dense vesicles as well as lysosome-like electron-dense bodies may be also found scattered throughout the cell cytoplasm and especially in the zone just beneath the cell surface (FIGS. 5, 8, 11). Some of these vesicles may seemingly fuse with the apical plasma membrane between the microvilli and discharge their contents into the lumen of the tube. Apical cell cytoplasm also contains scarce microtubules running in different directions (FIG. 5). Electron-dense secondary lysosomes (residual bodies), which are large, up to 2.2x0.9 μm , irregularly shaped and sometimes heterogeneous in their contents, may also be sometimes present in the cells of the proximal tube (FIGS. 8). The ground cytoplasm of the cells is of a moderate electron density with the organelles rather tightly packed within the cell volume.

Lateral cell borders in the walls of both the proximal and the distal tubes may be folded and are frequently lost among organelles leaving a very narrow extracellular space (FIGS. 7, 9). Adjacent cells contact each other via septate junctions (desmosomes), with an electron-dense matrix and a cleft between mem-

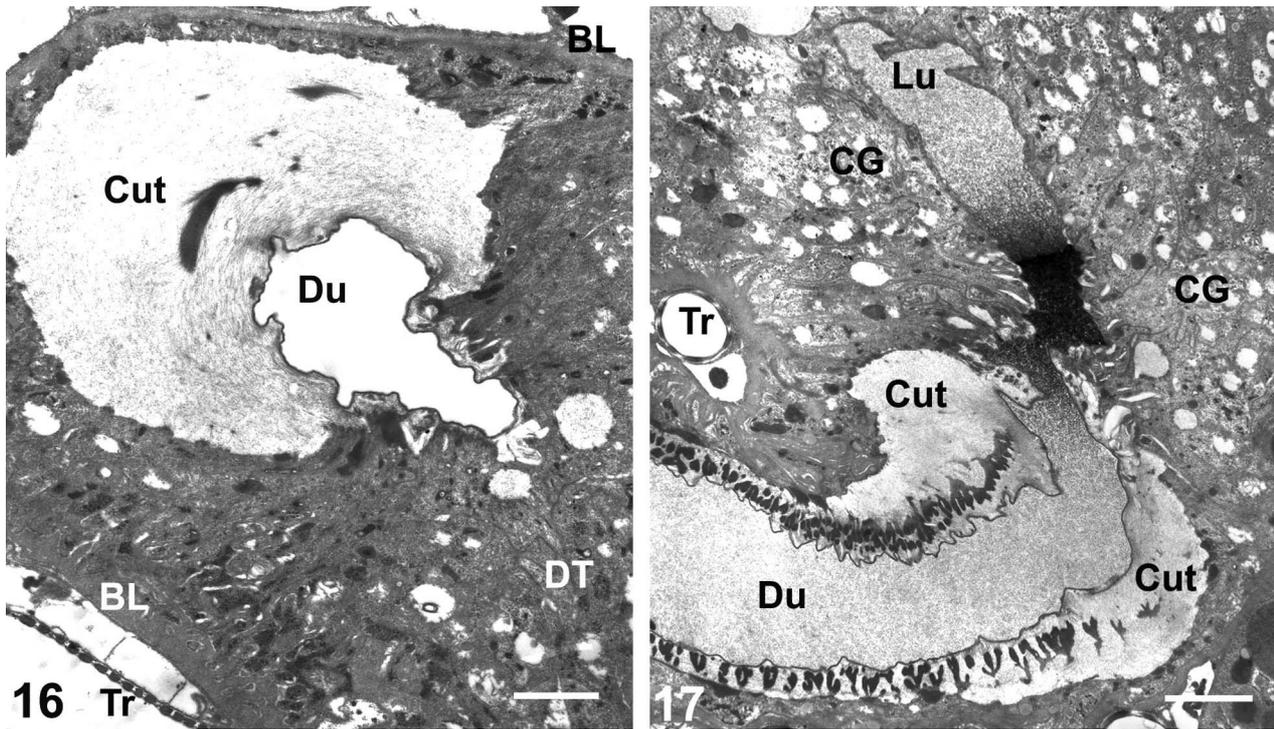
branes from 0.014 to 0.03 μm . The cell junctions attract particular flocculent cytoplasmic material flanking the contacts in the apical cell zones (FIGS. 5, 7, 11).

The cells of the distal tube, varying in height from 0.9 to 8.4 μm , possess the cytoplasm lighter than that in the proximal tube with relatively smaller amount of organelles (FIGS. 5, 6, 7, and 10). In contrast to the proximal tube, the apical cell surface of the distal tube does not form conspicuous microvilli and remaining flat, slightly folded, or bears extremely scarce, short, irregular microvilli (FIGS. 5, 6, 7, and 12). In the posterior portions of the gland, the cell surface of the distal tube may be occasionally armed with longer single or grouped together microvilli, apparently indicating the zone of transformation the proximal tube into the distal one (FIG. 12). Conversely, the basal plasma membrane, looking outside the gland and bordered by the basal lamina, as in the proximal tube, forms basal infoldings (labyrinth) provided with mitochondria (FIGS. 5, 13). The mitochondria, elongated to oval in their shape, are somewhat smaller (from 0.15 to 0.9x0.2 μm), electron-denser and occur in lesser amount than in the proximal tube (FIGS. 7, 8). In the cells of the distal tube, the mitochondria never form conspicuous associations, and from the basal to the apical cell portion the number and the sizes of the mitochondria somewhat decrease (FIG. 13). Organizations of the nuclei (around 5x2.2 μm in diameter), Golgi bodies as well as the cell contacts are practically identical to those found in the proximal tube (FIGS. 12, 14, 15). Nevertheless, the glycogen rosettes are not common inclusions in the cells of the distal tube and may be found in a significantly lesser number than in the proximal tube (FIG. 7). Conversely, the number of the secondary lysosomes (residual bodies) may be somewhat greater, and in certain places they may be associated in particular groups in the middle cell zone mostly in the posterior portions of the gland (FIGS. 13, 14).

The apical clear cytoplasm of the cells of the distal tubes is penetrated with microtubules running in different direction, which may occasionally form particular agglomerations in a form of a loose network in certain places just beneath the apical plasma membrane (FIGS. 5, 14, 15). The latter remains inactive



FIGS. 12-15. Organization of the distal tube in the coxal gland of adult mites *Pl. fasciatum*. 12. — Distal tubes inside the gland with nucleus and widened lumens flanking by the proximal tube. Arrow shows a greatly folded cell contact between the cells of the distal tube. Scale bar — 2 μ m. 13. — The external wall of distal tube underlined by the basal lamina showing basal infolds and residual bodies (secondary lysosomes) in its cells. Note Golgi body in the apical cell zone. Scale bar — 1 μ m. 14. — Apical portions of the cells containing some amount of glycogen particles, Golgi body, residual bodies as well as microtubules just beneath the apical plasma membrane. Note the close contact between the cells of the distal and proximal tubes via septate desmosome. Arrow indicates cell junction between the cells of the distal tube. Scale bar — 0.5 μ m. 15. — Folded septate desmosome between the cells of the distal tube. Note pinocytotic pit of the apical plasma membrane, dense vesicles and transverse sectioned microtubules occupied the very apical cell zone. Scale bar — 0.1 μ m.



FIGS. 16-17. Excretory duct of the coxal gland of adult mites *Pl. fasciatum*. 16. — The base of the excretory duct beginning just immediate from the distal tube and providing with a thick cuticle. Scale bar — 2 μ m. 17. — The joining of the excretory duct of the coxal gland, containing the electron-dense substrate in its lumen, with the duct of the posterior salivary gland (on the left-hand side). Scale bar — 3 μ m.

and extremely rarely reveals single vesicles resembling pinocytotic ones (FIG. 15). As a whole, cells of both the proximal and the distal tubes show no indication of either vesicular or extracellular transport across their walls. No any particular muscle or connective tissue envelope was observed encircled the coxal glands.

Before origination of the excretory duct, the cells of the distal tube typically gradually lose most of the organelles and become lighter. However, immediately at the site of the duct origination, the cytoplasm of the cells becomes denser and the cells become flattened. In this short zone, the mesoderm cells of the gland, having yet the basal infolds, are apparently replaced by the ectoderm cells starting formation the cuticle of the excretory duct (FIG. 16). Nevertheless, no special transition zone, or end-piece, between the distal tube and the duct, due to any particular cytological characteristics, may be identified with certainty. In different specimen studied, the distal end of the distal tube may be either totally collapsed or,

contrary, somewhat widened that, increases, correspondingly, the diameter of the tube. It is characteristically that in the latter case, the posterior portion of the gland has the tubes predominantly collapsed, and in the case when the distal tube collapsed, the proximal gland portion has the tubes mostly widened. This may indicate the pumping the fluids along the gland to the excretory duct that is expectedly realized due to the haemolymph pressure upon the gland. The lumen of the glandular tubes remains free of contents and is mostly electronic empty, except one case when a flocculent electron-dense substance of unknown origin was observed at the site of the duct formation and fusion with the duct of the posterior salivary gland (FIG. 17).

DISCUSSION

As seen from this investigation, ultrastructural organization of the coxal glands in the adults of microtrombidiid mite *P. fasciatum* generally corres-

ponds to that found in representatives of other Parasitengona (ALBERTI & STORCH, 1977; ALBERTI & COONS, 1999; SHATROV, 2000). The gland is conspicuously divided into the proximal and the distal tubules and lacks the proximal sacculus. The tubes form various loops and run in close mutual apposition without a delimiting basal lamina between the cells of different tubular portions. Cells of the proximal tube show a voluminous microvillous brushborder, and the both tubes possess basal infoldings provided with mitochondria. Both the proximal and the distal tube are uniformly organized throughout their whole length despite various bends and coils, and the distal bladder is obviously absent.

Anatomically, our data on *P. fasciatum* somewhat disagree with those showing previously for the trombicid mite *Allothrombium lerouxi* Moss, 1962, in which the tubular (coxal) glands are found composed of two tubes of unknown composition running back and forth and provided with a distal elongated sac (bladder) serving supposedly as a saliva reservoir (Moss, 1962).

Comparison of the coxal glands in adult mites and in larvae of *P. fasciatum* (SHATROV, 2006) shows several fundamental differences both in a gland composition and in the organization of the tubular cells in these developmental stages. In larvae, two separate individual trunks, running back and forth, each composed of the interweaving proximal and distal tubules and enveloped by an own basal lamina, are expressed. The proximal tubule of the larvae, in contrast to adult mites, is devoid of the basal labyrinth in its cells. The distal tubule, divided into free different zones, reveals basal infolds situated only in its middle zone. Thus, the basal plasma membrane of the coxal gland cells in larvae mostly remains flat except for a comparatively short portion of the distal tubule. Conversely, the apical plasma membrane reveals similar organization in both larvae and adults showing characteristic long microvilli in the proximal tubule and scarce short microvilli in the distal one. The secretory activity of the gland cells in larvae, mediated by the functioning of the Golgi bodies and the presence of vesicles, is seen higher than in adults, and the lumen of the proximal tubule may be filled with an electron-dense matrix. The basal lamina underlying the glandular epithelium in larvae, like in some other Parasitengona

(ALBERTI & STORCH, 1977), may be absent between the proximal tubule and the midgut epithelium, situated around and in close apposition with the basal (posterior) portions of the gland. These places demonstrate an intimate contact between these two organs and imply an obvious possibility of the direct transport of ions and substances of low molecular weight across the basal cell membranes from the midgut to the coxal gland. Conversely, in adult mites, the thick basal lamina is present throughout the entire borders of the coxal gland, particular in its posterior portion, bordering various tissues. As a whole, a proximal “glomerule” in adults with interlacement of tubes is comparatively much larger than in larvae, and the tubular lumens may be extremely wide.

Organization of the coxal glands in the representatives of the related family Trombiculidae (SHATROV, 2000), which larvae parasitize vertebrates, shows a great similarity with those found in microtrombicidiids with the exception of some details. In particular, the cytoplasm density of the tube cells is inverted, i.e. the cells of the proximal tubule of trombiculids possess the cytoplasm lighter than the cells of the distal tubule. An intercellular space of a moderate width, in contrast to microtrombicidiid mites, is found expressed in trombiculids beneath the long septate desmosomes connecting the adjacent tubular cells. The number of ribosomes, mitochondria as well as lysosomes and residual bodies are found to increase during the course of ontogenesis in the cells of the coxal glands of trombiculid mites (SHATROV, 2000). As in microtrombicidiids, the cells of the proximal tubes of trombiculid mites accumulate large masses of glycogen. Besides that, the cells also contain the very large irregularly outlined heterogonous inclusions supposedly of the secondary lysosome nature. The latter were not found in the cells of microtrombicidiid mites. These inclusions resemble the residual bodies accumulating in the pyramidal cells of the type I alveoli during the feeding of ixodid tick *Amblyomma americanum* (BARKER *et al.*, 1984). In trombiculids, these inclusions are never secreted into the lumen of the gland and remain to be storage in the cells during the whole life of the mite. This indicates the increasing of the particular irreversible metabolic processes with the age of trombiculid mites. The latter situation, on

the contrary, is not apparently observed in the young microtrombidiid adult mites obviously collecting in spring soon after their hatching from the quiescent tritonymphs.

In accordance with the anatomical observations obtained previously for various groups of the Parasitengona, both the larvae (VOIGT, 1971; SHARAMLOVÁ, 1978; SHATROV, 1995) and adult mites (CRONEBERG, 1878; MICHAEL, 1895; THOR, 1904; BADER, 1938; BROWN, 1952; MITCHELL, 1955, 1964; VISTORIN-THEIS, 1978), no distinct subdivision into different portions of the long curved tube of the coxal glands was identified with certainty. Among the Parasitengona, only some water mites demonstrate the presence of the distal bladder (MICHAEL, 1895; ALBERTI & STORCH, 1977), whereas the coxal glands of calyptostomatids are found to have a proximal sacculus of a tubular form (VISTORIN-THEIS, 1978). The latter contradicts to the assumption that the Parasitengona generally lacks the proximal sacculus (ALBERTI & STORCH, 1977; WITTE, 1991). Apart from the Parasitengona, the proximal sacculus is also absent in the Tetranychidae (BLAUVELT, 1946; MILLS, 1973; ALBERTI & STORCH, 1974; MOTHESS & SEITZ, 1980; 1981; ALBERTI & CROOKER, 1985), where the coxal glands are found composed of a simple tubule, and in the Myobiidae. In the latter case, a rather thin curved tubule of the gland is followed by a dilated distal bladder serving, supposedly, for reabsorption of fluids (FILIMONOVA, 2004). In other Actinedida (MICHAEL, 1896; ALBERTI, 1973; ALBERTI & STORCH, 1974, 1977; ALBERTI & COONS, 1999) and Oribatida (MICHAEL, 1883; WOODRING & COOK, 1962; WOODRING, 1973; ALBERTI & STORCH, 1977; ALBERTI *et al.*, 1997; ALBERTI & COONS, 1999) the proximal sacculus is typically present, which is followed by the variously curved and sometimes very long tube. In representatives of the Acaridida, where Malpighian tubules have evolutionary developed, the so-called supracoxal glands may be significantly modified or even reduced (PRASSE, 1967; RHODE & OEMICK, 1967; BRODY *et al.*, 1976; WHARTON & FURUMIZO, 1977; ALBERTI & COONS, 1999).

Due to the morphological evidences available, the organization of the coxal glands corresponds to that of transport and osmoregulatory epithelia (PEASE, 1956; SMITH & LITTAU, 1960; ANDERSON & HARVEY,

1966; DIAMOND & TORMEY, 1966; COONS & AXTELL, 1971; SEITZ, 1975; KUKEL & KOMNICK, 1989; etc.) that indicates their significant role in the processes of osmoregulation and water excretion in arthropods, in particular ticks and mites (LEES, 1946; RASMONT *et al.*, 1958; SCHMIDT-NIELSEN, 1968; WOODRING, 1973; ALBERTI, 1979; EL SHOURA & ROSHDY, 1985; EVANS, 1992; ALBERTI & STORCH, 1999; etc.). Indeed, the glandular walls are built up of the prismatic epithelial cells contacting each other by means of the apical closing junctions. The cells are provided with basal labyrinth and apical microvilli, which greatly increase the cell surface and determine polarity of the cells transporting solutions and taking part in ion/water exchange. Particular mechanisms involving in this process still remain unclear. Long microvilli in the proximal tube may indicate the invert polarity and transport of solutions from the lumen of the gland to the haemolymph (BERRIDGE & OSCHMAN, 1969; BERRIDGE, 1970). However, in thrips *Frankliniella occidentalis*, Malpighian tubules, closely attached to the hind gut and provided with intensively developed microvilli on the apical cell surface, are thought to promote reabsorption of water and solutions from the gut into the tubules (DALLAI *et al.*, 1991). With respect to the coxal glands, it is generally accepted that in their proximal portions, provided with microvilli, only filtration and active transport of solutions from the haemolymph into the gland lumen and formation of the primary urine are realized, whereas ion exchange and osmoregulation proper, i.e. selective sorption and reabsorption of solutes are carried out in the distal tubular portions (SCHMIDT-NIELSEN *et al.*, 1968; WOODRING, 1973; ALBERTI & COONS, 1999). It is interesting to note that in oribatids, the length of the glands depends on the salinity of the medium – in fresh-water and terrestrial mites the glands are longer than in mites inhabiting saline waters (WOODRING, 1973).

It is clear, however, that in the higher trombidiform mites like Parasitengona, feeding by the liquid semi-digested substances, the main function of the coxal gland is focused on the removing of the exceeding water from the organism, whereas particular functional dynamics of this process are different in the different gland zones. This function of the gland seems to be higher in active periods of life such as feeding

larvae and adult mites (the volume of both the gland and the lumens are greatly increased), whereas in unfed animals and quiescent instars it may be decreased (collapsed lumen of the gland like in unfed microtrombidiid larvae) (SHATROV, 2000, 2006). It is highly characteristic for the Parasitengona that the functions of the ion/water balance on the one hand and the excretion proper on the other, are progressively divided in time and space between the coxal glands and the specialized excretory organ – derivative of the posterior portions of the midgut (MICHAEL, 1895; BADER, 1938; MITCHELL, 1955, 1964, 1970). Nearly the same situation may be observed in the plant-feeding tetranychid mites, although the midgut and the hindgut are still connected to each other in this group (MCENROE, 1961, 1963; MOTHESE & SEITZ, 1980; ALBERTI & CROOKER, 1985). In the Acariformes, the reduction of the proximal sacculus of the coxal glands is thought as a progressive tendency (ALBERTI & STORCH, 1977; ALBERTI & COONS, 1999), whereas the integration of the coxal glands within the podocephalic gland complex is progressively carried out in the Parasitengona. The latter situation may provoke the reduction of the distal bladder in the majority representatives of this group. In this case, the absorbing water, passing through the gland, inevitably takes part in the saliva composition (MITCHELL, 1970).

The soft-body Parasitengona, especially large adult mites as well as unfed larvae, are very sensitive to loss of water and are forced to preserve water in the organism and to remove only obvious exceeding amount of water. On the other hand, fresh-water and terrestrial mites, to provide an adequate salt balance, have to in any way remove particular amount of both electrolytes and water, but more water than electrolytes. In these processes, functions of both sorption and reabsorption are very important. The latter inevitably leads to the coxal glands strongly developed in the general mite organization with the progressive reduction of the distal bladder and their association within the podocephalic system. In the latter case, the secreted water apparently comes into the host or victim injury constituting a closed circulation of ions and water between of the mite and the victim organisms.

The present data shows that the coxal glands in the adult microtrombidiid mites agree with the general

evolutionary tendencies of the higher trombidiform mites with the progressive reduction of both proximal sacculus and the distal sac. A strong development of the gland, especially its posterior portions and the proximal tube with the intense microvillous border and dilated lumen, apparently indicate that in these terrestrial soil-dwelling boreal mites a large amount of water is in any way pumping through its epithelium of the gland providing an appropriate salt/water balance of the mite organism.

ACKNOWLEDGEMENTS

This study is supported by a grant N 06-04-48538-a from the Russian Foundation for Fundamental Research. I am very thankful to the engineers of the Department of Electron Microscopy of the Zoological Institute of the Russian Academy of Sciences, A.E. Tenison and P.I. Genkin, for their qualified assistance with the electron microscopy.

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