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ULTRASTRUCTURE OF THE SALIVARY GLAND COMPLEX IN UNFED LARVAE OF *PLATYTROMBIDIUM FASCIATUM* (C. L. KOCH, 1836) AND *CAMEROTROMBIDIUM PEXATUM* (C. L. KOCH, 1837) (ACARIFORMES : MICROTROMBIDIIDAE)

BY ANDREW B. SHATROV 1

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SUMMARY: Ultrastructure of the salivary glands in the unfed larvae of microtrombidid mites *Platytrombidium fasciatum* (C. L. Koch, 1836) and *Camerotrombidium pexatum* (C. L. Koch, 1837) was examined using transmission electron microscopy. Two pairs of the large salivary glands termed ventral and dorsal occupy a frontal position in the body cavity and are mostly located on the sides of the mouthparts hidden deep under an arched dorsal shield. The dorsal glands possess an intensive rough endoplasmic reticulum situated predominantly on the periphery of the cells as well as numerous electron dense secretory granules spread throughout the cell volume and concentrated around a large central cavity. The ventral glands lie more anterior than the dorsal ones and contain tightly packed electron lucent secretory granules filled with a flocculent material. Due to the position of the ventral glands, their salivary ducts are directed posteriorly on each side of the body and join with the common ducts originating from ducts of the tubular (coxal) glands. After the fusion with ducts of the dorsal salivary glands, the common ducts open into the postero-lateral angles of an atrial (subcheliceral) cavity.

RÉSUMÉ: L’ultrastructure des glandes salivaies de larves affamées des Microtrombidiidæ *Platytrombidium fasciatum* (C. L. Koch, 1836) et *Camerotrombidiium pexatum* (C. L. Koch, 1837) a été étudiée en microscopie électronique à transmission. Deux paires de grandes glandes salivaire (appelées ventrales et dorsales) occupent une position frontale dans la cavité du corps et sont situées de part et d’autre de l’appareil buccal profondément caché sous l’arc du bouclier dorsal. Les glandes dorsales présentent un réticulum endoplasmatique rugueux bien développé disposé préférentiellement à la périphérie des cellules, de nombreux granules de sécrétion électroniquement denses sur tout le volume des cellules et concentrés autour de la cavité centrale intra-alvéolaire. Les glandes ventrales sont en position antérieure par rapport aux glandes dorsales. Elles contiennent des granules sécrétoires électroniquement transparents remplis de substance floconneuse. En raison de la disposition des glandes ventrales, les

1. Zoological Institute Russian Academy of Sciences, 199034, St.-Petersburg, Russia. Fax : (812) 1140444, e-mail : chigger@mail.ru
Introduction

Salivary (podocephalic, prosomal) glands provide a number of important functions directed to the realization of the particular mode of life of different groups of mites. Among trombidiform mites (suborder Actinedida), the anatomical organization of the salivary glands is variously known for adults of Bdellidae (Michael, 1896; Alberti, 1973; Alberti & Storch, 1973), Tetranychidae (Blauvelt, 1945; Jalil, 1969; Mills, 1973; Alberti & Storch, 1974; Mothes & Seitz, 1981; Alberti & Crooker, 1985), Calyptrastomatidae (Vistorin-Theis, 1978), Erythraeidae (Witte, 1978), Smarididae (Witte, 1998), water mites (Cronenberg, 1878; Michael, 1895; Schmidt, 1935; Bader, 1938; Mitchell, 1955), Trombidiidae sensu lato (Pagenstecher, 1860; Henking, 1882; Moss, 1962; Beresanzev, 1980), and, at last, Trombiculidae (Brown, 1952; Mitchell, 1964; Shatrov, 1989a, b, 2000). Only few works deal with the salivary glands of the larval stage of Erythraeidae (Witte, 1978), Trombidiidae (Henking, 1882) and Trombiculidae (Jones, 1950; Voigt, 1971; Shatrov, 1982, 1989c, 1990, 2000). Some of these data are recently summarized in a review work of Alberti & Coons (1999). As it is clearly seen, however, many of these works have been made even in XIX century and now need to be verified due to the modern, e. g. electron microscopical approaches, which, nevertheless, are not widely spread among acarologists (see Alberti & Storch, 1973, 1974; Mothes & Seitz, 1981; Alberti & Crooker, 1985, Alberti & Coons, 1999; Shatrov, 2000).

In general, the higher trombidiiform mites belonging to the cohort Parasitengona, tend to have a most developed salivary gland complex consisting of up to five pairs of alveolar glands in some water mites (Bader, 1938) and even six pairs of alveolar glands in the trombidiid mite Allothrombium lerouxi Moss (Moss, 1962), from which two pairs are located in the gnathosoma. In all cases, the salivary glands of each side of the body are found arranged regularly on the main (common) salivary duct formed by a duct of a special tubular (coxal) gland functioning in osmoregulation (see Alberti & Coons, 1999). Such a disposition of glands supposedly plays a role in a particular mixing of salivary ferments providing a process of extra-oral digestion (Thor, 1904, Mitchell, 1970; see also Cohen, 1995, 1998), highly characterized for mites from the cohort Parasitengona. A pair of glands occupying a most ventral position may open by an own duct. Besides paired glands, an unpaired tracheal gland was also shown in water mites (Cronenberg, 1878; Michael, 1895; Schmidt, 1935; Bader, 1938), tetranychids (Blauvelt, 1945; Alberti & Storch, 1974; Mothes & Seitz, 1981) and bdellids (Michael, 1896; Alberti & Storch, 1973). In larvae, full number of alveolar glands, four pairs, was found in Erythraeidae (Witte, 1978) and Trombiculidae (Voigt, 1971; Shatrov, 1982, 1989c, 1990, 2000), and a reduced gland complex consisting of two pairs of alveolar glands was demonstrated in representative of Trombidiidae — Trombidium fuliginosum Herm. (Henking, 1882). The revealing of only two pairs of glands in the trombiculid mite Neotrombicula autumnalis (Shaw) (Jones, 1950) was obviously erroneous. In accordance with the electron microscopical investigations, most of the glands are apparently serous (protein-secreting), although some glands may be also mucous with the glycoprotein secretion (Alberti & Storch, 1973, 1974; Alberti & Coons, 1999, Shatrov, 2000).

As it is known, trombiculid larvae, in contrast to all other Parasitengona, parasitize vertebrates, especially mammals, whereas trombidiid ones, like other members of this group, attack various invertebrates, in particular arthropods. Due to this reason, it is of great interest to compare the organization of the salivary gland complex in larvae of these two groups and try to reveal its possible adaptations to the parasitic way of life on vertebrate and invertebrate hosts.
as well as some evolution trends. In that ground, the main purpose of this communication is to provide a detailed ultrastructural examination of the alveolar salivary glands and their comparative analysis in unfed larvae of the microtrombidiid mites *Platytrombidium fasciatum* (C. L. Koch, 1836) and *Camerotrombidium pexatum* (C. L. Koch, 1837).

**Material and Methods**

Larvae used in this study were obtained from adult mites captured from the soil surface in the 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. Dr. J. MAKOL from the Agricultural University of Wroclaw (Poland) kindly agreed to make the identification of the mite species.

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 in 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 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 and in longitudinal planes were then 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 were stained with toluidine blue and investigated under an Amplival light optical microscope.

**Results**

Unfed larvae of both species possess two pairs of large simple alveolar salivary glands, which can be termed dorsal and ventral. The salivary glands occupy a comparatively large body volume under a giant arched dorsal shield (see SHATROV, 2001) and lie mostly on the sides of the mouthparts deep inserted into the body (Figs. 1, 2). Whereas the ventral glands are entirely located on the level of the mouthparts, the dorsal glands occupy a more posterior position in the body cavity partly flanking the brain.

The salivary glands are composed of a single acinus built up from few large acinar cells arranged around an intra-alveolar (central) cavity, from which a salivary duct originates (Figs. 1-3). External margins of the glands are predominantly flat without conspicuous infoldings of the plasma membrane and delimiting basal lamina.

The dorsal glands occupy a more dorsal and posterior position than the ventral ones (Fig. 3). Their maximum measurements are 42 µm in width, 54 µm in height and 60 µm in length in *Pl. fasciatum* larvae and 37, 57 and 40 µm respectively in *C. pexatum* larvae. The cells have irregular outlines either flat or slightly folded. The cell margins are frequently marked by a narrow strip of clear cytoplasm free of organelles (Figs. 4, 5), like in the midgut cells of microtrombidiid larvae (SHATROV, 2003), and may be flanked by cisterns of rough endoplasmic reticulum (Figs. 6, 7). Lateral walls of the cells are tightly opposed each other without conspicuous intercellular space. The cells of the dorsal glands contain numerous electron-dense round inclusions (secretory granules) 1.2-1.7 µm in average diameter variously grouped in different parts of the cells (Figs. 4, 5). These granules concentrate around a large central cavity with deep lateral lacunas (Fig. 8). A remaining part of the cell volume is typically filled with an intensive rough endoplasmic reticulum in a form of long cisterns and sometimes whorls arranged predominantly along the basal and lateral cell borders (Figs. 4, 5). The ends of cisterns and their parts in the vicinity of Golgi zones may be somewhat widened. It is interesting to note that cisterns of the rough endoplasmic reticulum are found to encompass some granules and, on the other hand, may branched from the perinuclear cistern (Fig. 6). Comparatively large Golgi zones situated normally not far from nuclei are poorly organized and nearly do not contain regular cisterns (Figs. 6, 7). The Golgi zones, frequently in a form of small “clouds”, have an
electron-light ground cytoplasm and are loosely packed with small vesicles, among which larger and denser condensed vacuoles may be sometimes observed (Fig. 7). The large nuclei with somewhat wavy outlines and a large centrally located nucleolus occupy a middle position in the cell (Figs. 4, 5). The measurements of nuclei and nucleoli are around 6.5x4.8 and 3.7x2.9μm respectively in both species studied. Mitochondria are not numerous and show a matrix of moderate density as well as loosely packed transverse cristae. Mitochondria are oval to elongate in shape and spread either freely in the cell volume or are located in the vicinity of the Golgi zones (Fig. 6). The cytoplasm of the cells is dense with large amounts of free ribosomes (Fig. 7).

The ventral glands are somewhat smaller than the dorsal ones and occupy more ventral and frontal position in the body cavity (Figs. 2, 3), flanking the mouthparts (Fig. 1). From their postero-dorsal sides the ventral glands are tightly contiguous with the dorsal salivary glands (Figs. 3, 4). The measurements of the ventral glands are 28μm in width, 38μm in height and 38μm in length in Pl.fasciatum larvae and 38, 33 and 40μm respectively in C.pexatum larvae. These glands are filled with tightly packed round to oval secretory granules, which are electron-lucent partly containing loosely organized flocculent material (Figs. 10-12). On their periphery, granules typically bear a narrow rim of more dense material (Fig. 12). The diameter of these granules mostly ranges within 1.2-1.9μm in both species. Nuclei are only rarely located freely within the cell volume (Fig. 10), but are mainly situated on the periphery of the glands (Fig. 11) frequently flattened against the basal membrane. The long axis of the nuclei varies within 4-5μm. The cytoplasm is lighter than that of the dorsal glands and instead the rough endoplasmic reticulum contains only some amount of free ribosomes, separate vesicles (Fig. 12) and small cisterns of supposedly smooth endoplasmic reticulum. Small scarce mitochondria with a matrix of moderate density are dispersed freely throughout the cells. Conspicuous Golgi complexes were not clearly identified in the cells of the ventral glands, although associations of small vesicles and distended profiles of short tiny cisterns in some parts of the cells supposedly indicate a particular synthetic activity in the ventral glands (Fig. 12). The cell margins are not much folded and difficult to recognize being mostly hidden among the many inclusions.

Pictures of the cell degradation with swollen and empty cytoplasm, condensed cisterns of endoplasmic reticulum and pycnomorphic nuclei may be seen in the cells of the dorsal (Fig. 8) and occasionally in the ventral glands. The dorsal glands possess a large intra-alveolar cavity lined by long slim and branched processes of the myoepithelial cells (Fig. 8). The latter, as is generally accepted (Kierszenbaum, 2002), form the initial portion of the secretory duct also producing its cuticle (Fig. 9). The intra-alveolar cavity looks like a loose basket provided with deep lateral lacunae. Here the secretions are extruded from the cells via the merocrine extrusion. Conversely, the central cavity of the ventral glands is much smaller, irregularly shaped and without conspicuous lacunae (Fig. 11). Nevertheless, ducts of the both glands have the same structure and are organized similar to that found for the salivary glands of trombiculid larvae (Shatrov, 1982, 1989c, 1990). In the wide initial portion of the ducts, irregularly shaped cavities may be seen in their walls between the two membranes forming the internal and external borders of the duct wall. In the unfed larvae, a secretion does not seem to squeeze out of the glands and, correspondingly, was found neither in the intra-alveolar cavities, nor in the ducts spaces.

Figs. 1-3. 1. — Semi-schematic drawing of transverse section of Camerotrombidium pexatum larva on the level of the hypostomal base showing ventral salivary glands (VSG) lying on the sides of mouthparts with palps (palpal trochanter) (PP), chelicerae (Ch), pharynx (Ph) and atrial cavity (AC). Note an arched dorsal shield (DSh) covering the anterior part of the body. 2. — Semi-schematic drawing of transverse section of Camerotrombidium pexatum larva on the level of the middle portion of gnathoexoa (GC) with the same elements as in Fig. 1. Note dorsal salivary glands (DSG) with large central cavities. 3. — Schematic drawing of longitudinal section of generalized larva showing an approximate disposition of the gland complex of one side of the body and the course of salivary ducts. Note that the coxal gland (CG) forms the common salivary duct, which in due course joins with ducts of the ventral (VSG) and dorsal (DSC) salivary glands and opens to the atrial cavity, that is indicated by a cut line. DSh: dorsal shield.
Due to the unusual arrangements of the glands in the microtrombidiid larvae, in comparison with mites having glands mostly located behind the mouthparts, the courses of the excretory ducts are also unusual. The ducts of the ventral glands go initially backwards (Fig. 3) and soon after leaving the glands meet the ducts of tubular (coxal) glands, which are thought to form a common salivary duct of each side of the body (Alberti & Coons, 1999). Then, the common duct goes upwards and joins the duct of the dorsal gland running to the medial and ventral direction (Fig. 3). After the fusion, the common duct of each side of the body open to the most posterior angles of the atrial (subcheliceral) cavity. The latter is organized more complex than that found in trombiculid larvae and has a number of chambers on its course within the mouthparts. A detailed description of the atrial cavity, which is associated within the mouthparts, is beyond the scope of this paper and will be described in a separate work.

Discussion

As seen from this investigation, microtrombidiid larvae, in comparison with adult mites of the superfamily Trombidioidae, Trombidiidae sensu lato, where at least four pairs of alveolar glands are observable (Moss, 1962; Beresanzev, 1980), have a salivary gland complex consisting of the only two pairs of large glands. These glands are simple alveolar composed of a large single acinus that is a general characteristic for mites belonging to the suborder Actinedida, a large branch of Acariform mites, gene-

Representatives of other terrestrial Parasitengona, such as Calypostomatidae (Vistorin-Theis, 1978), Erythraeidae and Smaridae (Witte, 1978, 1998) and Trombiculidae (Brown, 1952; Mitchell, 1964; Voigt, 1971; Shatrov, 2000), both their larvae and adult mites, seem to possess an equal number of four pairs of the alveolar prosomal salivary glands. A large group of water mites (Hydrachnidia) appear to take a separate position among Parasitengona, because they may have not only an unstable number of the alveolar glands from 2 to 5 pairs (Croneberg, 1878; Michael, 1895; Schmidt, 1935; Bader, 1938; Mitchell, 1955), but even an unpaired, so called tracheal gland (Michael, 1895; Schmidt, 1935; Bader, 1938). The latter is dorsally located and is known to provide lipid secretion. Other trombidi-

Figs. 4-7. 4 — General view of right dorsal salivary gland of Camerotrombidium pexatum larva showing large oval nuclei (N) with large nucleoli (Nu) as well as a developed rough endoplasmic reticulum (RER) and electron dense secretory granules (SG) scattered throughout the cell volume. Note part of ventral salivary gland (VSG) tightly adjoined to dorsal gland and hypoderms (Hd) underlying cuticle of dorsal shield. BL: basal lamina; HS: haemacoelic space. Scale bar — 3 μm. 5. — Portion of left dorsal salivary gland of Platycternidium fasciatum larva in its posterior part filled with secretory granules (SG), rough endoplasmic reticulum (RER) and large nuclei (N) with nucleoli (Nu). L: lipid inclusions. Scale bar — 2 μm. 6. — Near-nuclear region in dorsal gland of Platycternidium fasciatum larva with irregular Golgi zones (G) and secretory granule (SG) surrounded by cistern of rough endoplasmic reticulum (RER). Note that cisterns of RER have a connection with perinuclear cistern and also flank the cell margins (CM). M: mitochondria; N: nucleus; Nu: nucleolus. Scale bar — 0.5 μm. 7. — Golgi zone (G) in dorsal salivary gland of Camerotrombidium pexatum larva near the cell margins (CM). Note condensed vacuole (CV) and ribosomes (R). Scale bar — 0.2 μm.
cerehalic glands, open to the main secretory duct, the podocephalic canal, formed from the duct of the tubular (coxal) glands of each side of the body. The ducts of these three pairs of glands join with the duct of the tubular gland due to the particular sequence one after another, whereas one pair of the infracapitular, or ventral glands discharge their secretion through the own separate duct.

As seen from this consideration, among the higher trombidiiform mites, only trombiculids seem to possess a constant number of the alveolar glands, four pairs, and this number and the general composition of the glands do not change in all active instars of their life cycle (Brown, 1952; Mitchell, 1964; Voigt, 1971; Shatrov, 2000), in both parasitic larvae and free-living deutonymphs and adult mites. In the case of obvious structural dissimilarities of the corresponding glands in larvae and adults, their homology may be easily determined by the particular course of their ducts. Thus, the parasitism of larvae on vertebrates did not affect the number of the salivary glands in the Trombiculidae. The salivary gland complex in this group despite a high morphological and ecological specialization of its representatives appears to preserve invariable in the course of evolution and are very close to the morphological prototype of this organ system generally accepted for the Actinedida (Alberti & Coons, 1999).

In contrast to other related mites, in particular Trombiculidae, where the larvae have the prognathous gnathosoma as a conspicuous tagma, the microtrombidiid larvae possess the hypognathous gnathosoma deeply inserted into the body with the strongly overhanging giant dorsal shield. Due to such unusual body architecture, the margins between tagmata mostly disappear and the salivary glands take a position not behind the mouthparts, but on each side of them in a voluminous body cavity surrounding the gnathosoma nearly up to its frontal sucker (Shatrov, 2001). Thus, the mouthparts, the salivary glands, the brain (synganglion) and even a frontal part of the midgut of larvae are proved finely protected against the compression by an arched and strongly chitinous dorsal shield. This adaptation may have supposedly elaborated only during the course of parasitism of larvae on invertebrates, in particular arthropods, when the larvae are feeding under a threat of squeezing between the hard cuticular squamae of the host. Nevertheless, the reason for the reduction of the number of glands in larvae, in contrast to adult mites, up to the two pairs is still unknown. Such a reduction, in the case of a similar systematical position of the potential victims of the postlarval instars and hosts of the larvae may be explained by the tendency to the optimization of the salivary ferments actions in larvae, and may play, on the other hand, an evolutionary role in the course of oligomerization of the functional salivary units in the larval stage. For this reason, the microtrombidiid larvae appear to be more derived than the trombiculid ones. It is clear at the same time that no any homology between individual glands can be proved in larvae of Trombiculidae and Microtrombidiidae.

Due to the ultrastructural evidences and appearance of the secretory granules, the dorsal glands of the microtrombidiid larvae may be characterized as serous with the protein secretion (Pinkstaff, 1980; Kierszenbaum, 2002). All dorsally located podocephalic glands in Bdellidae and Tetranychidae are also

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Figs. 8-12: 8. — Central part of right dorsal salivary gland of *Camerotrombidium pexatum* larva showing large intra-alveolar cavity (IC) with lateral lacunas surrounded by tightly packed electron-dense secretory granules (SG). Note nuclei (N) on the periphery and degenerated cell (DC) in the bottom. MC: muscle cell. Scale bar — 3 μm. 9. — Basal portion of secretory duct of dorsal gland of *Camerotrombidium pexatum* larva formed by thick duct wall (DW) provided by system of cavities. Note nuclei (N) of myoepithelial cells. HS: haemocoelic space. Longitudinal section of larva. Scale bar — 1 μm. 10. — Frontal portion of ventral salivary gland of *Camerotrombidium pexatum* larva situated underneath a marginal part of dorsal shield with thick selerotized cuticle (CDSn). Note tightly packed electron-lucent secretory granules (SG) and scattered nuclei (N). HS: haemocoelic space partly dividing the gland mass. Hc: haemocyte. Scale bar — 3 μm. 11. — Main portion of right ventral salivary gland of *Platytrombidium fasciatum* larva with narrow intra-alveolar cavity (IC), nucleus on the periphery (N) and electron-lucent secretory granules (SG) filling the gland volume. Note hypodermis (Hd) underneath cuticle of dorsal shield (CDSn). SCu: soft cuticle. Scale bar — 2 μm. 12. — Internal part of ventral gland of *Camerotrombidium pexatum* larva with secretory granules (SG) filled with flocculent material with a denser rim on the periphery. Small clear vesicles and tiny cisterns in the lower side indicate a supposed synthetic activity of the gland. M: mitochondrion; R: ribosomes. Scale bar — 0.5 μm.
protein secreting with variously expressed electron dense granules and prominent Golgi complexes (Alberti & Storch, 1973, 1974; Alberti & Coons, 1999). As concerns the ventral glands, the number of the fine morphological evidences, such as the electron lucent inclusions, the absence of conspicuous Golgi zones and intensive rough endoplasmic reticulum, clearly indicate these glands as mucous glands with glycoproteins secretion (Kierszenbaum, 2002). For this reason, the ventral glands of the microtrombidiid larvae are structurally comparable, on the one hand, with the tracheal gland of bdellids and tetranychids and, on the other hand, with the silk glands of T. urticae (Alberti & Storch, 1973, 1974; Alberti & Coons, 1999). At the same time, however, in adults of trombiculid and trombidiid mites the paired ventral glands with an apparent protein, but not a glycoprotein secretion occupy such ventral position (Shatrov, 2000). These ventral glands are a probable homologue of the infracapitular gland of bdellids (Alberti & Coons, 1999) due to its own separate excretory duct, which is also characterized by a protein secretion. It is now known that in adults of the microtrombidiid mites the only gland with the mixed secretion is the large paired gland located most posteriorly (Shatrov, unpublished data). The all remaining three pairs of glands, including ventrally located ones having also an own secretory duct, seem to be protein or at least mixed secreting. Such inversion of the ventral gland ultrastructure in the larval stage, in comparison with adult mites, not to mention about a different course of their excretory ducts, may indicate a special function of this gland having elaborated during the evolution of the parasitic life on arthropod hosts. This particular function is still remaining unknown.

To summarize, the microtrombidiid larvae possess only two pairs of the large simple alveolar salivary glands, which appear to be strongly differentiated regarding to their functions. These functions provide a successful feeding of parasitizing larvae on arthropod hosts. These glands discharge their contents to the common salivary duct of each side of the body, and for this reason may be anatomically considered as podocephalic glands.

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