ISSN 0013-8738, Entomological Review, 2017, Vol. 97, No. 3, pp. 383–394. © Pleiades Publishing, Inc., 2017.
Original Russian Text © S.A. Leonovich, S.A. Filimonova, 2017, published in Parazitologiya, 2017, Vol. 51, No. 2, pp. 121–131.

The Quill Mite *Syringophilopsis fringilla* (Fritsch) (Acari: Trombidiformes: Syringophilidae): the Structure of Sensory Organs Providing Feeding of the Parasite in the Feather Quill

S. A. Leonovich and S. A. Filimonova

Zoological Institute, Russian Academy of Sciences, St. Petersburg, 199064 Russia
e-mail: leonssa@mail.ru

Received October 27, 2016

Abstract—The structure of the sensory organs situated on palps and chelicerae of the quill mite *Syringophilopsis fringilla* (Fritsch, 1958) was examined with the use of scanning and transmitting electron microscopy. The tarsal segment of the palps bears 8 sensilla of three types: two contact chemo-mechanoreceptor sensilla, a single chemoreceptor (olfactory) sensillum, and five tactile mechanoreceptor sensilla. All other sensilla situated on basal palpal segments and on cheliceral stylets are represented exclusively by tactile mechanoreceptors. A proprioceptor sensillum was revealed in the movable digit of chelicerae; the modified cilia of dendrites of 5 sensory neurons of this sensillum run inside the inner non-sclerotized core of the stylet and end at different levels in its apical part, attaching to electron-dense rods connected with a sclerotized sheath of the stylet. The authors assume that the proprioceptor sensillum of the stylet detects the strength of the pressure of the stylet of the movable digit on the quill wall during its piercing, and palpal sensilla determine the optimal place for this process.

DOI: 10.1134/S0013873817030113

INTRODUCTION

Quill mites of the genus *Syringophilopsis* (family Syringophilidae) comprise more than thirty species of parasites dwelling in quills of flight feathers of passeriform birds (Hendricks et al., 2013). These mites are monoxenic parasites with the entire developmental cycle occurring inside the quill. All the mites of the family Syringophilidae feed on the host lymph, piercing the quill wall with their mouthparts (Kethley, 1971); some of them are important poultry pests and the headache of many bird fanciers keeping birds in domestic conditions. Syringophilosis, or feather disease, results in breaking of remiges and retrices and the subsequent bird anemia (Skoracki, 2008, Skoracki et al., 2011).

Mite females penetrate into the quill of a developing feather through the “umbiculus superior,” a small aperture at the border between the calamus and the vane. After that they move into the basal part of the quill and search for a feeding site, where they pierce the quill wall with sharp stylets and feed on lymph.

The structure of mouthparts in females of *Syringophilopsis fringilla* (Fritsch, 1958) and their function were studied in detail by Filimonova and Mironov (2010). At the same time, problems concerning detection of place for penetration of reproductive females into a new feather, detection of the piercing site, leaving of the quill by mites, and other problems associated with the structure and functioning of the sense organs in quill mites, in particular, associated with the palps and chelicerae of these arthropods, remain unclear.

Receptors on the palps and chelicerae of mites play the most important role in providing the feeding process (Alberti and Coons, 1999; Dunlop and Alberti, 2008). At the same time, in many groups of Acarina our knowledge on the structure of these receptors remains fragmentary.

The palpal receptors are examined in most detail in representatives of the order Parasitiformes, including the main groups of ixodid ticks (Ixodoidea) (Wallade and Rice, 1982; Ivanov and Leonovich, 1983; Leonovich and Dusbabek, 1991; Leonovich, 2005, etc.), and some representatives of gamasid (mesostigmatic) mites (Liu and Peng, 1990; Leonovich, 1998a; Alberti and Coons, 1999; etc.). In these groups of acarines, the palpal receptors are represented by the chemo-mechanoreceptor sensilla, determining the place for bloodsucking (in ixodid ticks) or an the object for feeding (in free-living gamasid mites). In representatives of Ixodoidea, chemoreceptor sensilla on palps are represented by two types of organs; one of them provides feeding, and the other one, copulation (Leonovich and Dusbabek, 1991; Sonenshine, 2004).

The palpal receptors of acariform mites, a group significantly more voluminous in relation to taxonomy, morphological diversity, and the number of species, comprising 95 superfamilies and about 40 thousand of described species (Mironov and Bochkov, 2009), are studied very fragmentarily (Nuzzaci and Alberti, 1996; Alberti, 1998; Alberti and Coons, 1999; Alberti and Dabert, 2012; Alberti and Kitajima, 2014; etc.). In different groups of mites, a tactile mechanoreceptor and chemo-mechanoreceptor sensilla in different combinations were revealed; mainly, with rare exceptions, the sensory armament of palps is represented by a tactile mechanoreceptor sensilla.

The cheliceral receptors are also studied best of all in representatives of parasitiform acarines (Wallade and Rice, 1977, 1982; Danilov, 1987, 1988; Alberti and Coons, 1999; Di Palma et al., 2006; Phillis III, 2006; Dunlop and Alberti, 2008), especially in ixodid ticks (Ixodoidea). In this group, the cheliceral receptors are represented by "hairless" sensilla (for terminology, see Leonovich, 2005), visible on the cheliceral surface as small pits, groups of pits, or porous areas of small size. "Pits" (funnel-shaped depressions) are connected with tubular bodies, the most characteristic features of tactile mechanoreceptors. Groups of pits are innervated by several sensory neurons with the apical parts of their dendrites ending near the pores situated in pit depressions. Electrophysiological studies have demonstrated that groups of pits belong to tactile chemoreceptors, and porous areas, to thermoreceptors (Wallade and Rice, 1977, 1982). The tactile chemoreceptors of chelicerae in ixodid ticks respond to the genital sex pheromone, providing successful copulation (Sonenshine, 2004), and also respond to phagostimulants, providing feeding of ticks on blood (Soares et al., 2012, 2013).

The cheliceral receptors of acariform mites are studied fragmentarily in several publications (Bruce et al., 1993; Di Palma et al., 2009; Nuzzaci and Alberti 1996; Alberti et al., 2011; Alberti and Dabert, 2012, etc). At the same time, in the majority of the above publications it remains unclear whether dendrites of sensory neurons revealed inside chelicerae are associated with any external structures on the cheliceral surface, i.e., whether they function as exteroceptors, as it was found in ixodid ticks, or not. The pores at the apex of the cheliceral stylet, associated with sensory dendrites, were found in flat mites of the genus *Brevipalpus* (Tenuipalpidae) (Alberti and Kitajima, 2014). The proprioceptors inside chelicera, recording the function of retractor muscles, were described in the soil mite *Archegozetes longisetosus* Aoki, 1958 (Oribatida) (Alberti et al., 2011).

The goal of the present work includes the study of sense organs in the quill mite *Syringophilopsis fringilla*, the parasite of the flight feathers of the finch, namely, the study of receptors associated with mite palps and chelicerae directly responsible for the feeding process, the main process providing survival of a mite in the feather quill.

MATERIALS AND METHODS

Females of *Syringophilopsis fringilla* (Fritsch, 1958) were collected from finches *Fringilla coelebs* Linnaeus, 1758 (Passeriformes: Fringillidae), trapped in the Curonian Spit National Park (Kaliningrad Province) and set free after collection of the material. Mites were winkled out of quills of some (1–2) primaries or secondaries infected with mites. In order to study the mites in the scanning electron microscope (SEM), they were fixed in a 70% ethanol, cleaned in an ultrasonic bath, placed into hexamethyldisilazane (HMDS) (Braet et al., 1997), and air-dried, or were dehydrated in acetone and dried in a Hitachi–2 critical point dryer with the use of liquid carbon dioxide as a working agent. After that, the mites were glued onto aluminum stubs with double-sided sticky film covered with platinum in an Eiko IB-5 vacuum evaporator and examined in a Hitachi S-570 SEM. In order to study the mites in the transmitting electron microscope (TEM), they were fixed in 2.5% glutaraldehyde solution in 0.1M phosphate buffer (pH 7.4), then placed into the fresh solution of fixing fluid and after several days were postfixed in 2% solution of OsO_4 in the same buffer. The material dehydrated in a series of ethanol was embedded in Epon 812 polymer resin. Fine cuts were made in a Leica ultramicrotome, stained in the solution of uranium acetate and lead citrate and examined in the Zeiss LEO 900 and Morgagni 258 electron microscopes. The material examined in SEM and TEM were photographed directly in digital storages. The results of the study are illustrated by electron micrographs obtained in SEM and TEM and also by drawings (Figs. 1–6).

RESULTS

The mites *S. fringilla* are characterized by an elongated body typical of the genus, approximately 1 mm long (Fig. 1*A*). The movable digit of the chelicera (the stylet) can protract from the apex of the hypostome (Fig. 1*B*). A pair of stylets move independently of each other, providing piercing of the quill wall; the inner surface of the stylet is characterized by the presence of a longitudinal groove (Fig. 1*C*). Stylets can be totally retracted into the hypostome and are invisible from the outside (Fig. 1*D*).

Eight sensilla are situated on the apical surface of each palp (Figs. 1*D*, 1*E*), including two long basiconic (*a1* and *a2* in Fig. 1*E*), one short basiconic (*b* in Fig. 1*F*), and five trichoid (*m1–m5* in Fig. 1*F*) sensilla. A pair of trichoid sensilla is visible near the apex of the hypostome (Fig. 1*B*).

Eight groups of receptor neurons are distinctly revealed in a crosscut passing through the apex of the tarsal palpal segment; each group is surrounded by its own enveloping cell (Fig. 2*A*; scheme in Fig. 4*E*). Similar to all mites, the receptor neurons innervating hairs (the external part of the sensilla) are bipolar. Their dendrites bear modified cilia (formula 9 × 2 + 2) on their apices (Fig. 2*A*). The total number of receptor neurons of all the 8 sensilla [(7 + 2) + (7 + 2) + 6 + 2 + 2 + 2 + 2 + 2] constitutes 34 cells (Fig. 2*A*; scheme in Fig. *E*). The palpal nerve uniting axons of sensory cells, running into the nerve ganglion, is formed of 34 axons, strictly corresponding to the number of neurons in all palpal sensilla (Fig. 2*B*).

Comparison of the relative localization of hairs (the external parts of the sensilla) (Fig. 1*E*) and their cells (Fig. 2*A*) makes it possible to determine precisely the number of receptor neurons in each sensillum. The study of the structure of the perceptive apparatus comprising the hairs and the associated apical parts of the sensory cilia) allows determining the modality of each sensillum with a high degree of confidence (Leonovich, 2005).

Each of the most numerous trichoid sensilla *m1–m5* contains 2 receptor neurons surrounded by an enveloping cell (Figs. 1*A*, 1*C*, 2*E*). The external part of the hair of this type of sensilla is hollow in the most basal part (Fig. 2*E*) and solid along the main part (Fig. 2*E*). The cilia of two neurons are enveloped with a cuticular sheath (occasionally named as “the scolopoid sheath” in the literature on sense organs); these cilia terminate at the base of the hair, never penetrating into its cavity (Fig. *D*). In this region, the cuticular sheath forms stiffening ribs (Figs. 2*D*, 2*F*), and tubular bodies are found in the cilia; the presence of these bodies is the most characteristic feature of the tactile mechanoreceptors of mites and ticks (Ivanov and Leonovich, 1983; Leonovich, 2005) (Figs. 2*D*, 2*F*). In the region of tubular bodies, the scolopoid sheath of receptor cilia is connected with the wall of the channel by an accessory membrane; during shifting of the hair, this membrane deforms tubular bodies and switches on generation of action potentials (for more detail, see Leonovich, 2005). The scheme of the structure of the perceptive apparatus in such type of sensilla is represented in Fig. 4*B*. Five palpal sensilla (*m1–m5*) and also sensilla on the apex of the gnathosoma belong to this type (Fig. 1*B*).

Long basiconic sensilla *a1–a2* are innervated by nine neurons each (Figs. 2*A*, 4*E*). Neurons form two groups, consisting of seven and two cells, respectively, enveloped with distal and basal enveloping cells. The proximal parts of the dendrites of the seven-neuron group are enveloped with a common basal enveloping cell (Figs. 2*A*, 4*E*). Proximal parts of the dendrites are filled with mitochondria; the distal parts (cilia) penetrate into an extracellular vacuole, formed by the distal enveloping cell and covered with numerous microvilli (Figs. 2*A*, 4*E*). The structure of the cilium, similarly to that in tactile mechanoreceptor sensilla, is characterized by a 9 × 2 + 2 formula. The dendrites of two and seven neurons in the sensillum form independent groups (Figs. 2*A*, 4*E*) running to the base of the hair in a common channel (Fig. 3*A*). Two cells terminate at the base of the hair, forming tubular bodies (Figs. 3*A*, 3*B*); other cells run into the cavity of the hollow hair (Figs. 3*C*, 3*D*) and then run nearly to the apex. These cilia do not branch. In general, such a structure corresponds to that of the chemo-mechanosensitive sensilla of the acarines.

The short basiconic sensillum (*b* in Fig. 1*F*) is innervated by 6 sensory neurons that are not subdivided into groups and do not form tubular bodies at the base of a short basiconic hair. The cilia of dendrites of sensory neurons branch inside the cavity of a thin-walled hollow hair (Fig. 3*E*).

Taking into account a very small size of the basiconic hair, revealing of pores in the walls of this hair in a crosscut seems to be a big success (Fig. *F*). On the

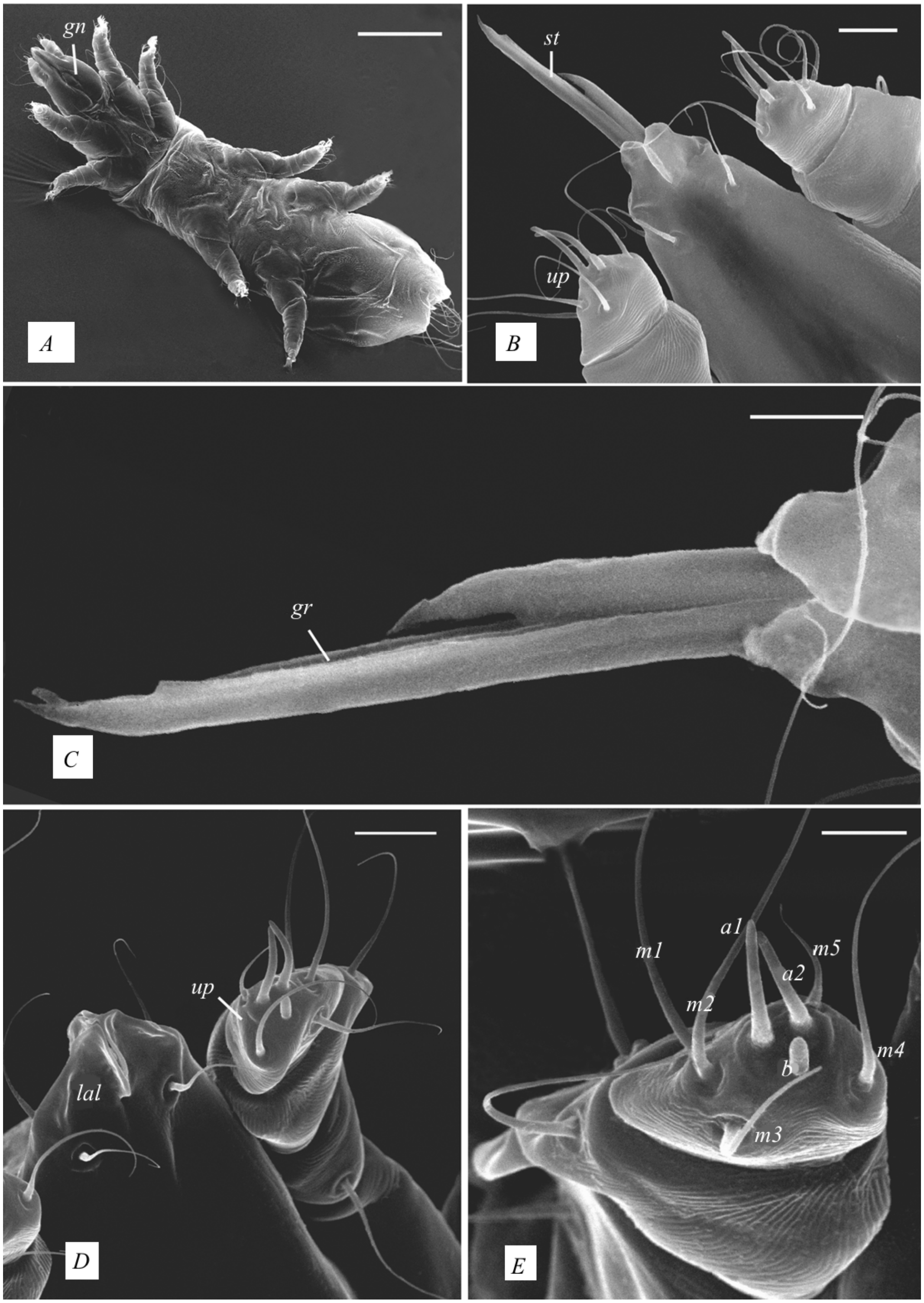

Fig. 1. Structure of palps and chelicerae of *Syringophilopsis fringilla* female in a scanning electron microscope: (*A*) female in ventral view; (*B*) gnathosoma in ventral view; (*C*) partly projecting stylets; (*D*) lateral lips of malapophysae concealing retracted stylet and tarsal segment of left palp; (*E*) apical surface of palptarsus with 8 sensilla of three types. Sensilla of palpal organ: *a1*–*a2*, basiconic hairs of two contact chemo-mechanoreceptive sensilla; *b*, short hair of distant (olfactory), sensillum; *m1*–*m5*, tactile (mechanoreceptor), sensilla; *gn*, gnathosoma; *gr*, groove on movable digit of chelicera; *lal*, lateral lips of malapophysae; *st*, stylet; *up*, apical palpal segment. Scale: (*A*) 200 μm; (*B*) 20 μm; (*C*) 10 μm; (*D*) 15 μm; (*E*) 8 μm.

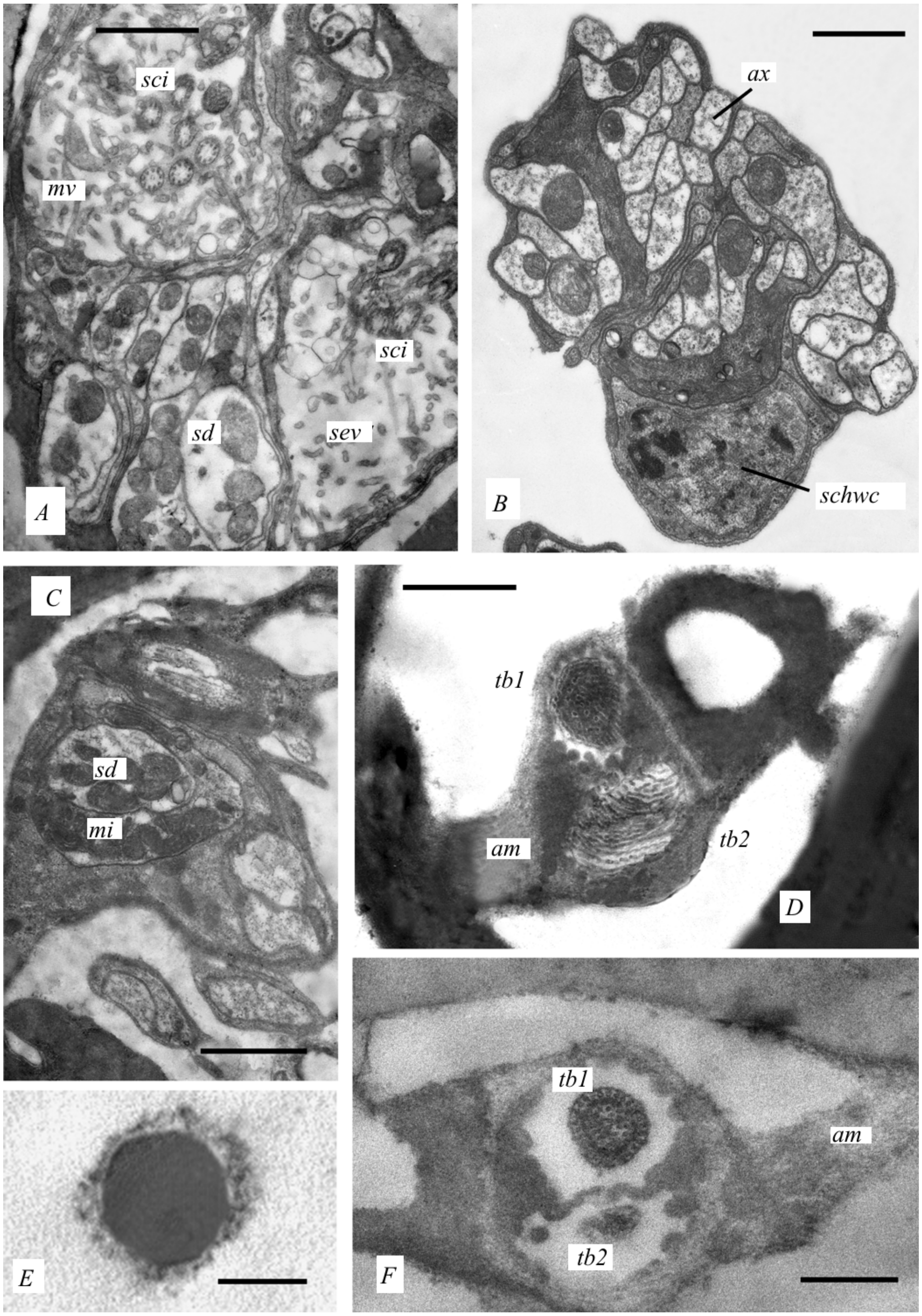

Fig. 2. Palpal receptors of *S. fringilla* in a transmitting electron microscope. (*A*) cross section through palpal sensilla near palpal tip; (*B*) transverse section of palpal nerve; (*C*) dendrites of tactile mechanoreceptor sensilla; (*D*) tubular bodies of mechanoreceptor neurons at sensillar base; (*E*) rod-shaped hair of tactile sensillum of palpal organ; (*F*) accessory membrane (*am*) and mode of their attachment to cuticular sheath of tubular bodies (*tb*) basally of attachment site; *ax*, axons of receptor neurons; *mv*, microvilli of sheath cell; *mi*, mitochondria; *schwc*, Schwann's cell; *sci*, sensory cilia of apical part of sensory dendrite; *d*, dendrite of receptor neuron. Scale: (*A*, *B*) 1 µm; (*C*, *D*, *E*) 0.3 µm; (*F*) 1 µm.

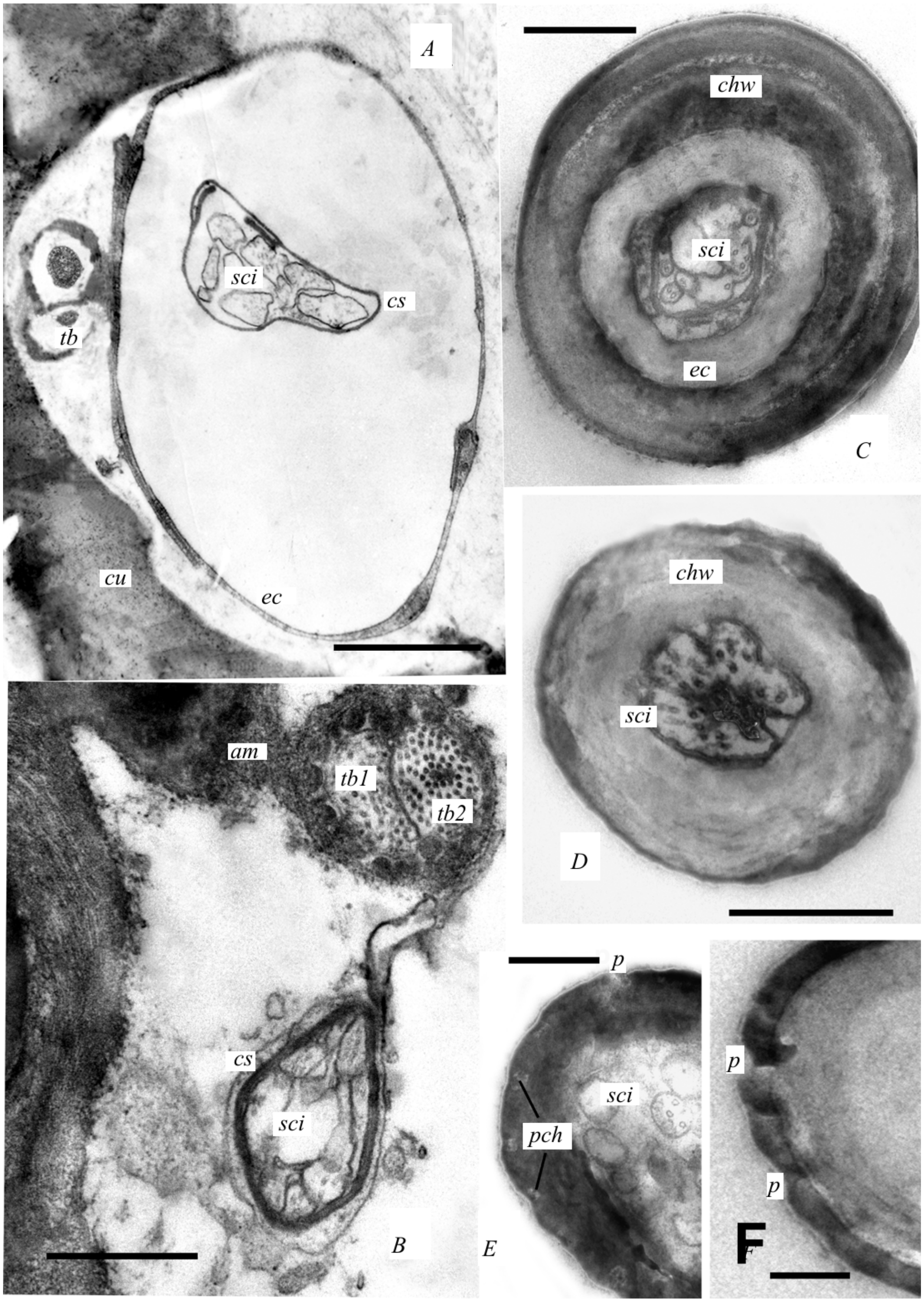

Fig. 3. Apical (receptor) parts of palpal sensilla. (*A*) transverse section under the base basiconic hair *a1*; (*B*) the same, sensillum *a2*; (*C*, *D*) transverse crosscuts of type a sensilla in basal (*C*) and apical (*D*) areas; (*E*, *F*) sections of hair parts of type *b* sensillum. (*cs*) cuticular sheath (theca) around cilia of sensory dendrites; (*ec*) enveloping cell; (*chw*) cuticular wall of sensillar hair; (*p*) pore. Other designations as in Figs. 1 and 2. Scale: (*A*) 0,5 µm; (*B*, *C*, *E*, *F*) 0,1 µm; (*D*) 0,05 µm.

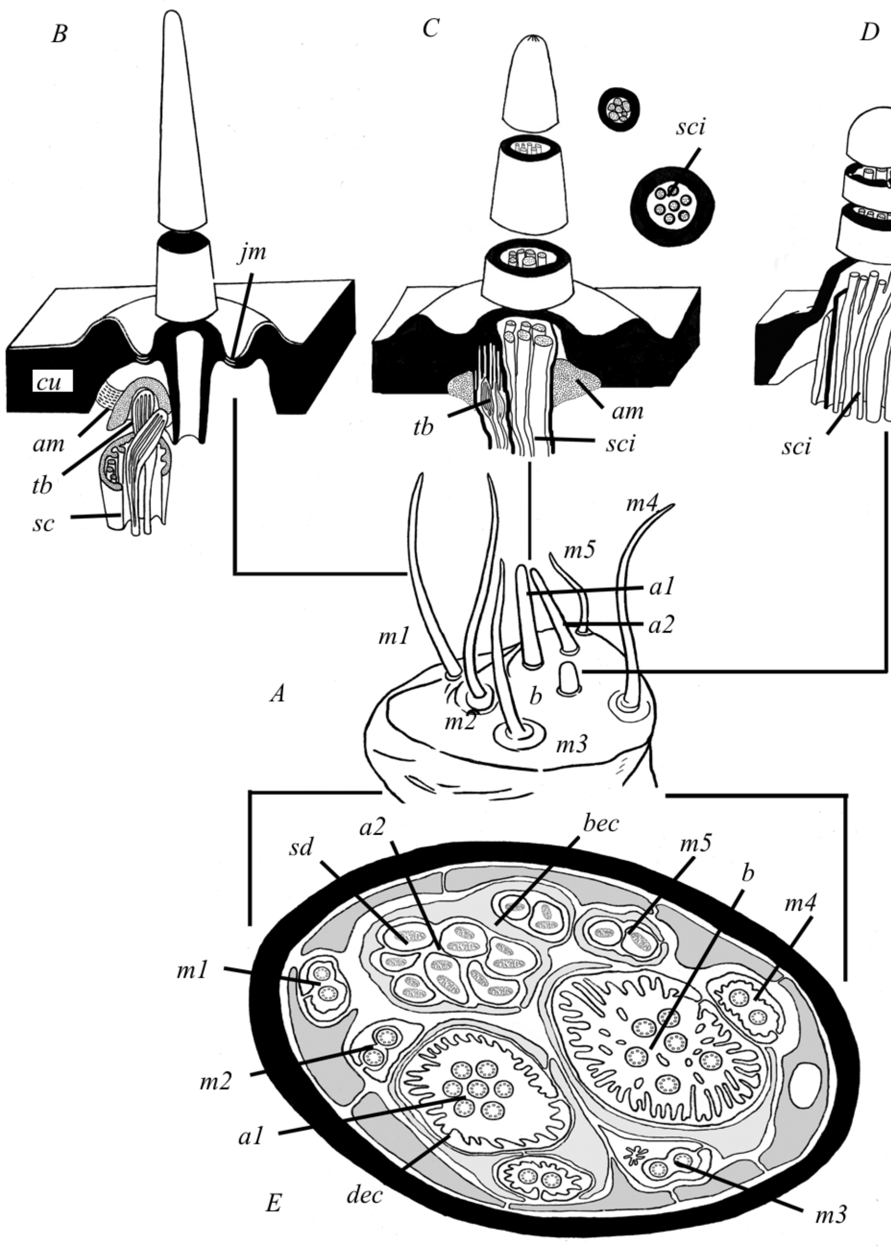

Fig. 4. Scheme of fine structure of palpal sensilla in the quill mite *Syringophilopsis fringilla*; (*A*) arrangement of three types of sensilla (*a*, *b*, *m*) on apical palpal surface; (*B–D*) fine structure of palpal sensilla: (*B*) tactile mechanoreceptor sensillum (*m1–m5*); (*C*) basiconic chemoreceptor sensillum of type *b* (*a1–a2*); (*D*) basiconic olfactory sensillum of type *b*; (*E*) receptory cilia and enveloping cells of palpal sensilla (crosscut) in apical part of tarsal segment. Designations: (*bec*) basal enveloping cell; (*dec*) distal enveloping cell; (*jm*) joint membrane. Other designations as in Figs. 1–3.

whole, such a structure corresponds to that of the olfactory sensilla of mites and ticks and belongs to single-walled porous sensilla (for more detail, see Leonovich, 2005).

The movable digit of chelicerae is subdivided into two parts: the basal part, or the lever, and the distal part, or the stylet itself. In the resting state, the movable digit resembles a half-opened pocketknife, where the lever is the handle and the stylet, the blade. It is the muscles of the lever which ensure protracting of the stylet (Filimonova and Mironov, 2010).

We found some sensory structures in the transverse sections through the stylet of the quill mite. In particular, in the region of the lever, in its remote from the

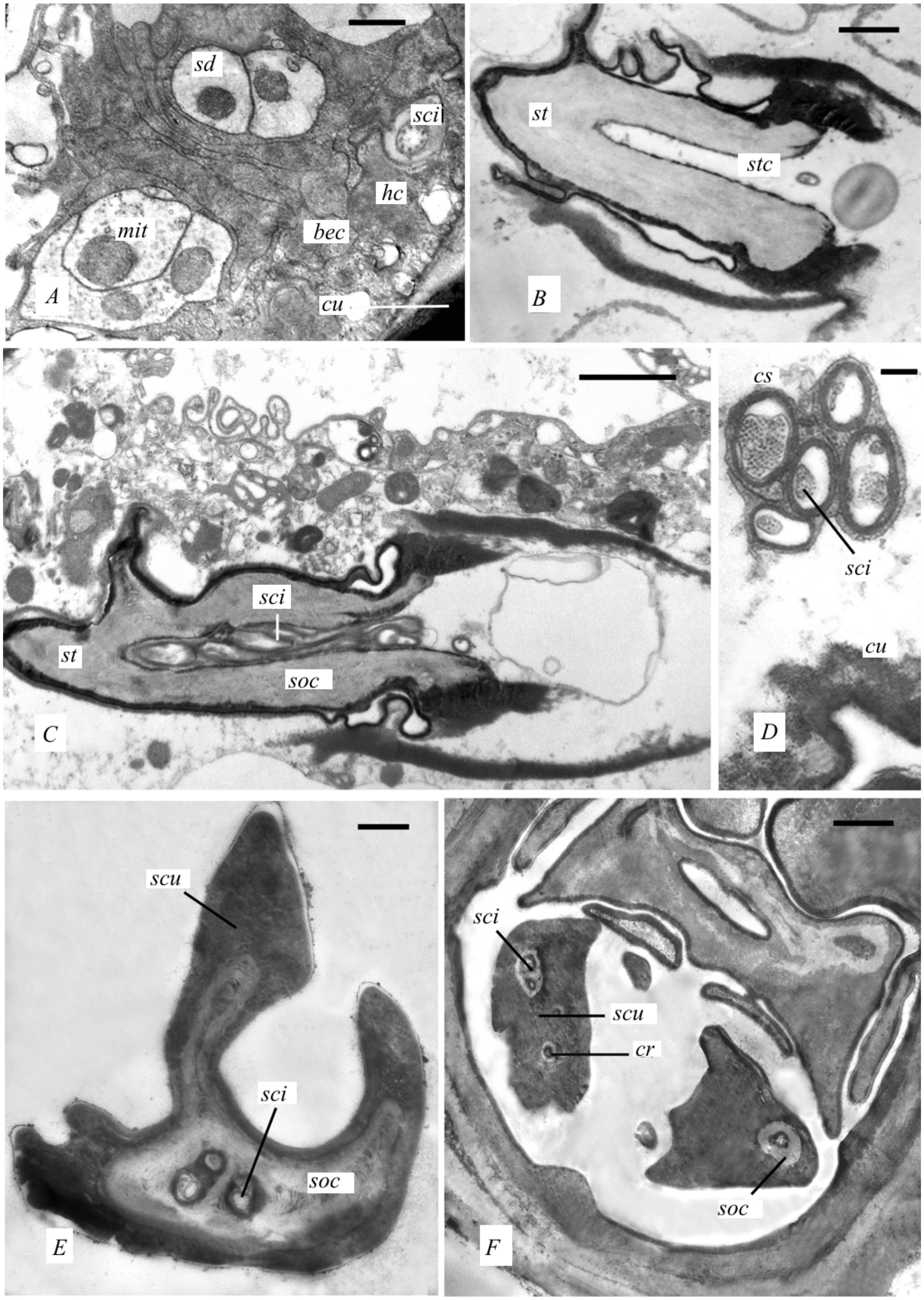

Fig. 5. Fine structure of the stylet sensillum in the quill mite *Syringophilopsis fringilla* in transmitting electron microscope: (*A*) dendrites and cilia of receptor neurons of stylet sensillum; (*B*) proximal part of the stylet without sensory elements and with inner cavity (crosscut *7* in Fig. 6); (*C*) oblique section through stylet (between crosscuts *6* and *7* in Fig. 6); (*D*) sensory cilia of dendrites near cuticular wall of the lever; (*E*) transverse section of the stylet (section *5* in Fig. 6); (*F*) transverse section of mouthparts with a pair of stylets (cuts *2* and *3* in Fig. 6). (*stc*) stylet cavity; (*sci*) modified sensory cilia; (*cr*) cuticular rod; (*soc*) “soft” non-sclerotized cuticle; (*scu*) sclerotized cuticle of the stylet. Other designations as in Figs. 1–4. Scale: (*A*) 0.6 μm; (*B*, *C*) 2 μm; (*D*, *E*) 0.5 μm; (*F*) 1 μm.

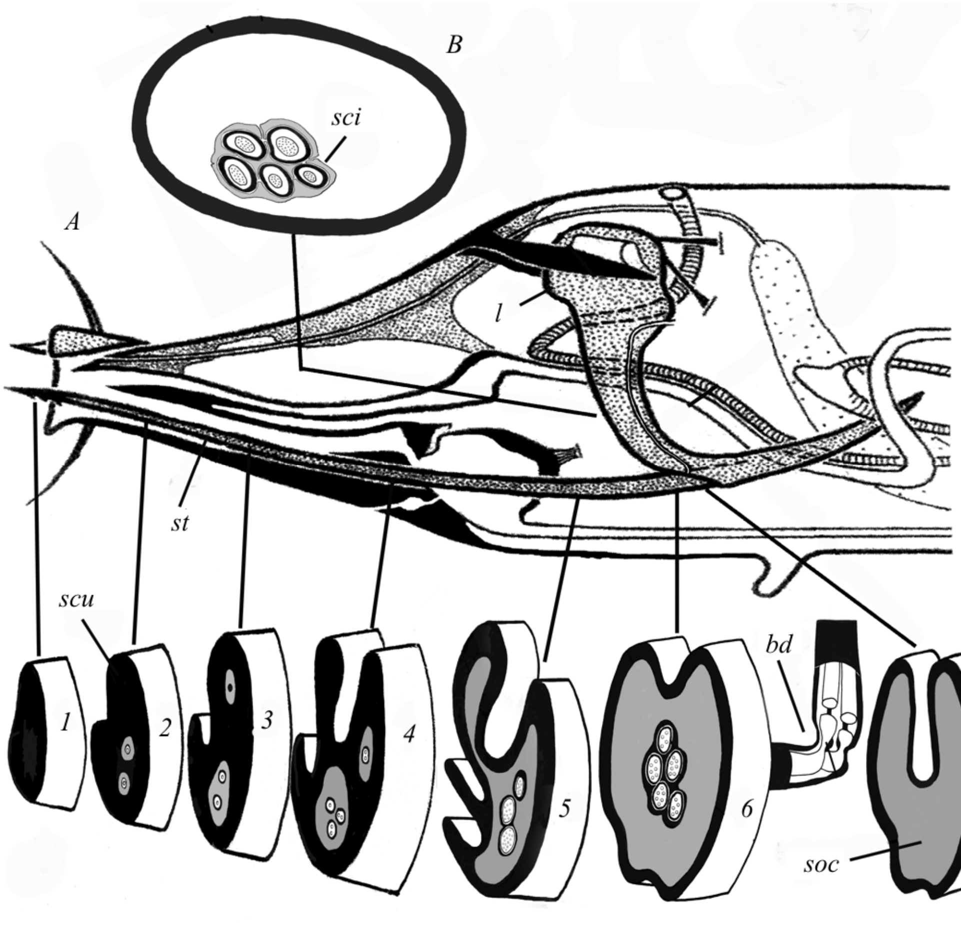

Fig. 6. Scheme of arrangement of mouthparts in *S. fringilla* (from Filimonova and Mironov, 2010, with changes) (*A*) and the structure of the stylet sensillum *B*, *C*); (*A*) scheme of mouthparts, demonstrating arrangement the basal part (lever) and distal part (stylet) of the movable digit of chelicera. (*B*) cilia of dendrites of sensory neurons in the lever, enveloped in a common cuticular sheath; (*C*) series of crosscuts through the stylet from the most distal (*1*) to the most basal (*7*) sections. (*bd*) bend of sensory cilia in retracted stylet; (*l*) lever of the stylet. Other designations as in Figs. 1–5.

surface part, we revealed distinct dendrites of sensory neurons, forming cilia on their distal surfaces (Fig. 5*A*).

The sensory cilia of five neurons were found in the proximal part of the lever (Fig. 5*D*); these cilia were also found in the stylet (Fig. 5*C*). At the same time, no sensory structures were found in the proximal part of the stylet, in the place of its “bend” (the place of attachment to the lever) (Fig. 5*B*). The dendrites of sensory neurons penetrate into the stylet in the place of attachment of “the handle” to “the blade” (Figs. 5*C*, 6*A*, 6*D*).

It should be noted that we did not manage to trace the connection between the cilia of sensory neurons, running in the cavity of the lever, and the basal parts of dendrites, revealed approximately in the same region (Fig. 5*A*); therefore, we cannot state that perikarya of sensory neurons are situated near the basal wall of the lever. Probably, the neuron perikarya are situated closer to the ganglion, and those revealed by us belong to some other sensillum. It should be noted, however, that for the establishing of the probable modality of a sensillum and of its functional significance, localization of the perikarya doesn’t really matter.

Inside the stylet, the receptor cilia in their own cuticular (scolopoid) sheaths run in the central, weakly sclerotized core of the stylet (Figs. 5*E*, 5*F*, 6*D*). In a series of crosscuts, it has been shown that receptory cilia did not approach the outer wall of the stylet; all of them terminated in its cavity at different levels (Figs. 5*F*, 6*D*). The apex of each cilium is attached to a rigid cuticular rod, connecting the cilium with the sclerotized outer part of the stylet (Figs. 5*D*, 6*D*).

DISCUSSION

Our investigations have demonstrated that palps of the quill mite *S. fringilla* bear 8 sensilla of three types: five tactile mechanoreceptor sensilla of different length, two basiconic chemo-mechanoreceptor sensilla, and a single olfactory sensillum.

S. fringilla (family Syringophilidae, superfamily Cheyletoidea) belongs to the parvorder Eleutherengona of the infraorder Prostigmata (Mironov and Bochkov, 2009). The palpal receptors were studied in detail in bloodsucking representatives of the other parvorder (Anystina) of the same infraorder, namely, in representatives of the family Trombiculidae (genera *Walchia, Helenicula, Microtrombicula, Ascoschoengastia, Leptotrombidium, Myotrombicula, Odontacarus*, *Euschoengastia, Hirzutiella,* and *Ericotrombidium)* (Leonovich, 1994). In chigger larvae, several tactile mechanoreceptor sensilla are present (4 in *Walchia;* 5 in *Helenicula;* 6 in *Microtrombicula* and *Ascoschoengastia* and 7 in *Leptotrombidium, Myotrombicula, Odontacarus* and *Euschoengastia*), and also, in all the studied species, a single solenidion (palptarsala) (Goff et al., 1982), according to its structure belonging to single-wall wall-pore sensilla with thin walls, i.e, olfactory organs (Leonovich, 2005). Besides, a single eupatidium was found on palps in representatives of the genera *Hirzutiella* and *Ericotrombidium*. This is a smooth short seta, according to its fine structural features belonging to single-wall chemoreceptor sensilla with non-branched cilia of sensory dendrites in the setal cavity, also lacking mechanoreceptor neurons with tubular bodies at the base (Leonovich, 1994).

It should be noted that in representatives of parasitiform mites and ticks, sensory armament of palps includes contact chemoreceptor sensilla of two types, differing morphologically and functionally (Leonovich and Dusbabek, 1991; Leonovich, 1998; Alberti and Coons, 1999). With the help of contact chemo-mechanoreceptor sensilla, parasitiform acarines (ixodid ticks and gamasid mites) detect feeding objects (bloodsucking acarines, the place for bloodsucking) and also the sex partner. The olfactory sensilla of the solenidion type are absent on the palps of parasitiform acarines (Leonovich, 2005).

We can make an assumption that in the quill mite *S. fringilla* it is the palpal sensilla which play the main role both in the search for the umbilicus superior in the developing feather and in detection of a place for quill wall piercing. Probably, this is the reason for the presence of two chemo-mechanoreceptor sensilla on palps of these ticks together with solenidion and tactile mechanoreceptors, typical of Eleutherengona.

A propos, it should be noted that the structure of the palpal organ within the infraorder Prostigmata (at least in the examined representatives of the parvorders Anystina and Euletherengona) is, on the whole, similar; at the same time, it strongly differs from that revealed in mesostigmatic acarines (Leonovich, 1998b; Coons and Alberti, 1999). This fact can be used as an indirect confirmation of the existing taxonomic views (Mironov and Bochkov, 2009).

The stylet sensillum of the quill mite is also characterized by a very original structure. The “inner” cheliceral sensilla are examined in most detail in ixodid ticks. In all the known cases, cheliceral sensilla, i.e. sensilla with dendrites and receptory cilia running in the cuticle of the chelicera terminate as some surface structure (a pit, a porous field, etc.) in the lateral surface of the stylet wall, serving as chemo- thermo-, or proprioceptors; at the same time, the proprioceptor sensilla contain tubular bodies oriented perpendicular to the lateral surface of the stylet; in other words, they are modified specialized exteroceptors (Danilov, 1987, 1988; Leonovich 2005; Soares et al., 2013).

In our work, on a series of crosscuts examined in the transmitting electron microscopes, it was unambiguously demonstrated that apices of 5 cells of the stylet sensillum do not run to the lateral surface of the movable digit of chelicera, but terminate in the weakly sclerotized inner layer, attaching to the rigid cuticular rods connected with a sclerotized cuticle (Fig. 6).

It is possible to find sui generis analogies of such a structure of the apical part of cilia of receptor dendrites in some types of insect chordotonal sensilla, where the apical parts of weakly differentiated cilia running in a cuticular sheath are rigidly fixed by means of a special cuticular cap connected with the sclerotized cuticle of the integument (Yack, 2004). In some cases, such sensilla function as stretch and tension receptors (Lee and Craig, 2009).

In our case, such a structure can also work as a proprioceptor determining the strength of the pressing of the stylet on the inner wall of the feather quill. During piercing, minute deformations in the subproximal part of the stylet are quite probable (it should be noted that in this part of the stylet its sclerotized walls are rather thin and its core is filled with friable weakly sclerotized cuticle) (Fig. 5*F*). The sensory dendrites terminate in the stylet cuticle at different levels Fig. 6*D*); thus, the degree of pressure of the quill wall on the piercing stylet may be determined (the stronger is the deformation, the greater number of sensory cells is stimulated).

Thus, the fine structure of the palpal receptors and the stylet in a representative of quill mites of the family Syringophilidae was examined by means of electron microscopy for the first time and their probable role in the process of feeding of the mite inside the feather quill was analyzed on the basis of morphological data.

REFERENCES

1. Alberti, G., "Fine Structure of Receptor Organs in Oribatid Mites (Acari)", in *Arthropod Biology: Contributions to Morphology, Ecology and Systematic*, *Biosystematics and Ecology*, *Series 14* (1998), pp. 27–77.
2. Alberti, G. and Coons, L.B., "Acari: Mites," in *Microscopic Anatomy of Invertebrates.* Vol. 8 C. *Chelicerate Arthropoda*, Ed. by Harrison F.W. and Foelix, R.F (Wiley & Sons, Chichester, 1999), pp. 515–1217.
3. Alberti, G. and Coons, L.B., "*Acari: Mites*," in *Microscopic Anatomy of Invertebrates.* Vol. 8 C. *Chelicerate Arthropoda*Ed. by Harrison F.W. and Foelix, R.F. (Wiley & Sons, Chichester, 1999), pp. 515–1217.
4. Alberti, G. and Dabert, J., "Fine Structure of the Feather Mite *Falculifer rostratus* (Buchholz 1869) (Acari, Falculiferidae). Gnathosoma, Digestive System and Supracoxal Glands," Zoologica **158**, 1–150 (2012).
5. Alberti, G. and Kitajima, E.W., "Anatomy and Fine Structure of *Brevipalpus* Mites (Tenuipalpidae)—Economically Important Plant-Virus Vectors," Zoologica **160**, 1–192 (2014).
6. Alberti, G., Heethoff, M., Norton, R.A., Schmelzle, S., Seniczak, A., and Seniczak, S., "Fine Structure of the Gnathosoma of *Archegozetes longisetosus* [Corrected] *aoki* (Acari: Oribatida, Trhypochthoniidae)," Journal of Morphology **272**, 1025–79 (2011).
7. Braet, F., De Zanger, R., and Wisse, E., "Drying Vells for SEM, AFM and TEM by Hexamethyldisilazane: a Study on Hepatic Endothelial Cells," Journal of Microscopy **186** (1), 84–87 (1997).
8. Bruce, W.A., Kethley, J.B., and Kaliszewski, M.J., "Morphology of the Gnathosoma of *Pyemotes tritici*: Cheliceral Stylets and an Associated Cheliceral Structure (Acari: Pyemotidae)," International Journal of Acarology **19**, 127–136 (1993).
9. Coons, L.B. and Alberti, G., "Acari: Ticks," in *Microscopic Anatomy of Invertebrates. Vol. 8B*, Ed. by Harrison, F.W. and Foelix, R.F. (Wiley-Liss, New-York, 1999), pp. 267–514.
10. Danilov, S.N., "Cheliceral Sensilla of the Ixodid Tick *Hyalomma asiaticum*," Parazitologiya **87** (1), 60–62 (1987).
11. Danilov, S.N., "Structure of Cheliceral Sensilla in Ixodid Ticks *Haemaphysalis punctata* and *Ixodes persulcatus*," Parazitologiya **22** (5), 361–365 (1988).
12. Di Palma, A., Nuzzaci, G., and Alberti, G., "Morphological, "Ultrastructural and Functional Adaptations of the Mouthparts in Cheyletid Mites (Acari: Actinedida: Cheyletidae)," International Journal of Acarology **35**, 521–532 (2009).
13. Dunlop, J. A. and Alberti, G., "The Affinities of Mites and Ticks: a Review," Journal of Zoological Systematics and Evolutionary Research **46**, 1–18 (2008).
14. Filimonova, S.A. and Mironov, S.V., "Functional Morphology of the Gnathosoma in the Quill Mite *Syringophilopsis fringilla* Fritsch (Acari: Prostigmata: Syringophilidae)," Zoologischer Anzeiger—A Journal of Comparative Zoology **249**, 165–180 (2010).
15. Goff, M.J., Loomis, R.B., Welbourn, W.C., and Wrenn, W.J., "A Glossary of Chigger Terminology (Acari, Trombiculidae)," Journal of Medical Entomology **19**, 221–238 (1982).
16. Hendricks, S.A., Flannery, M.E., and Spicer, G.S., "Cophylogeny of Quill Mites from the Genus Syringophilopsis (Acari: Syringophilidae) and Their North American Passerine Hosts," Journal of Parasitology **99** (5), 827–34 (2013).
17. Ivanov, V.P. and Leonovich, S.A., "Sensory Organs," in *An Atlas of Ixodid Tick Ultrastructure*, Ed. by Balashov, Yu.S. (Entomological Society of America Special Publication, 1983), pp. 191–220.
18. Kethley, J.B., "Population Regulation in Quill Mites (Acarina: Syringophilidae)," Ecology **52**, 1113–1118 (1971).
19. Lee, R.M.K.W. and Craig, D.A., "Fine Structure of the Sense Organs on the Labella and Labium of the Mosquito *Aedes aegypti* (L.)," The Open Entomology Journal **3**, 7–17 (2009).
20. Leonovich, S.A., "Morphology of Specialized Setae of Body Appendages in Chigger Mites of the Family Trombiculidae," Parazitologiya **28** (6), 445–451 (1994).
21. Leonovich, S.A., "Palpal Receptor Organ in Gamasid Mites (Mesostigmata, Gamasina)," Parazitologiya **32** (3), 258–263 (1998a).
22. Leonovich, S.A., "Search Receptors in Bloodsucking Ticks and Mites of the Order Parasitiformes," Parazitologicheskii Sbornik **34**, 83–96 (1998b).
23. Leonovich, S.A., *Sensory Systems of Parasitic Ticks and Mites* (Nauka, St. Petersburg, 2005) [in Russian].
24. Leonovich, S.A. and Dusbabek, F., "Pheromone Receptive Subsystem in Ticks: Correlation between Stimulus Conducting Structures and Evolution of Behavior," in *Modern Acarology* (SPB Publishers, the Hague, 1991), pp. 53–58.

25. Liu, T.P. and Peng, Ying-Shin, “Palpal Tarsal Sensilla of the Female Mite, *Varroa jacobsoni* Oudemans (Acari: Varroidea),” Canadian Entomologist **122**, 295–300 (1990).
26. Mironov, S.V. and Bochkov, A.V., “Modern Conceptions Concerning the Macrophylogeny of Acariform Mites (Chelicerata, Acariformes),” Zoologicheskii Zhurnal **88** (8), 922–937 (2009) [Entomological Review **89**, 975–992 (2009)].
27. Nuzzaci, G. and Alberti, G., “Internal Anatomy and Physiology,” in *Eriophyoid Mites—Their Biology, Natural Enemies and Control, Vol. 6.*, Ed. by Lindquist, E.E., Sabelis, M.W., and Bruin J. (Elsevier, Amsterdam, 1996), pp. 101–150.
28. Phillis, III W.A., “Ultrastructure of the Chelicerae of *Dermanyssus prognephilus* Ewing (Acari: Dermanyssidae),” International Journal of Acarology **32**, 85–91 (2006).
29. Skoracki, M., “Quill Mites (Acari: Syringophilidae) of the Palaearctic Region,” Zootaxa **2840**, 1–415 (2011).
30. Skoracki, M., Flannery, M.E., and Spicer, G.S., “Quill Mites of the Genus *Syringophilopsis* Kethley, 1970 (Acari: Syringophilidae) from North American Birds,” Folia Parasitologica **55**, 291–300 (2008).
31. Soares, S.F., Louly, C.C.B., Neves, C.A., Marion-Poll, F., and Borges L.M.F., “Detection of Phytoecdysteroids by Gustatory Sensilla on Chelicerae of the Brown Dog Tick *Rhipicephalus sanguineus*,” Physiological Entomology **37**, 241–249 (2012).
32. Soares, S.F., Louly, C.C., Marion-Poll, F., Ribeiro, M.F., and Borges L.M., “Study on Cheliceral Sensilla of the Brown Dog Tick *Ripicephalus sanguineus* (Latreille, 1806) Involved in Taste Perception of Phagostimulants,” Acta Tropica **126**, 75–83 (2013).
33. Sonenshine, D.E., “Pheromones and Other Semiochemicals of Ticks and Their Use in Tick Control,” Parasitology **129**, 405-425 (2004).
34. Wallade, S.M. and Rice, M.J., “The Sensory Nervous System of the Adult Cattle Tick *Boophilus microplus* (Canestrini). Part III. Ultrastructure and Electrophysiology of the Cheliceral Receptors,” Journal of the Australian Entomological Society **453**, 142–156 (1977).
35. Wallade, S.M. and Rice, M.J., “The Sensory Basis of Tick Feeding Behaviour,” in *Physiology of Ticks*, Ed. by Obenchain, F.D. and Galun, R. (Pergamon Press, Oxford, 1982), pp. 71–118.
36. Yack, J. E., “The Structure and Function of Auditory Chordotonal Organs in Insects,” Microscopy Research and Technique **63**, 315-337 (2004).