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Structure of Antennal Pseudoplacoid Sensilla in the Caddisfly *Philopotamus montanus* Donovan (Trichoptera, Philopotamidae)

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Abstract—The structure of pseudoplacoid sensilla characteristic of Amphiesmenoptera was studied by SEM and TEM methods by the example of the mushroom-like sensilla in *Philopotamus montanus* Don., a member of the primitive family Philopotamidae. These sensilla were found to be different from the externally similar placoid sensilla in the presence of a socket-like depression and a sensillar stem arising from it. The expanded terminal part filled with the dendrites of the sensory neurons has numerous pores on its upper and lower surfaces. The sensillar dendrites have subterminal expansions filled with electron-transparent fluid, while their thin terminal parts have electron-dense central elements. The pseudoplacoid sensillum of *Ph. montanus* comprises three sensory neurons. The mushroom-like pseudoplacoid sensilla of *Ph. montanus* are compared with chemoreceptive sensilla of other insects.

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The antennal sensilla of caddisflies are highly diverse in morphology and distribution over the flagellomeres, i.e., segments of the antennal flagellum (Slifer, 1970; Tozer, 1982; Faucheux, 2004b; Ivanov and Melnitsky, 2011, 2016; Melnitsky and Ivanov, 2011, 2016; Valuyskiy et al., 2017; Melnitsky et al., 2018). The sensory complex of caddisfly antennae comprises over 20 types and subtypes of sensilla, with up to 13 types of various antennal sensory structures present in some species (Ivanov and Melnitsky, 2011, 2016; Melnitsky and Ivanov, 2011, 2016). Essential similarity has been observed between the antennal sensilla in Trichoptera and the related order Lepidoptera (Larsson et al., 2002; Faucheux, 2004a, 2004b; Ivanov and Melnitsky, 2016).

The caddisfly family Philopotamidae is very ancient, being known in the fossil record since the Middle Jurassic (Ivanov and Sukatsheva, 2002). It includes three subfamilies: Philopotaminae Stephens, 1829, Rossodinae Oezdikmen et Darilmaz, 2008, and Chimarrinae Rambur, 1842, and comprises over 1200 species in 25 genera. The subfamily Philopotaminae is the most primitive (Ross, 1956). The morphology of antennal sensilla has been studied in 16 species from all the 3 subfamilies of Philopotamidae (Melnitsky et al., 2018).

Various cuticular structures are non-uniformly distributed on the antennae of caddisflies and follow different arrangement patterns: nonspecific, specific, clustered, and fixed (Valuyskiy et al., 2017; Melnitsky et al., 2018). The pseudoplacoid sensilla have nonspecific distribution, i.e., they do not form distinct clusters but alternate with other types of sensilla on the antennal cuticle (Valuyskiy et al., 2017; Melnitsky et al., 2018). The solitary sensilla, such as styloconic and coronal ones, are characterized by specific (regular) distribution: they are positioned in specific parts of the flagellomere and have the same arrangement on each segment though their

number may vary. The chaetoid sensilla have a fixed position and number on all the flagellomeres. The basal antennal segments in Philopotamidae bear ventrolateral sensory fields, i.e., specialized zones with clusters of curved trichoid sensilla (Melnitsky and Ivanov, 2011). The mean number of sensilla per segment and the diversity of sensory structures in Philopotamidae decrease from the antenna base to its apex (Melnitsky et al., 2018); this trend is also observed in other primitive groups of caddisflies, for instance, the family Rhyacophilidae (Valuyskiy et al., 2017).

The antennae of insects bear numerous trichoid, chaetoid, and other sensilla, and also some unique structures restricted to individual orders. For instance, pseudoplacoid sensilla have been found only in members of the taxon Amphiesmenoptera where they show high morphological diversity. In caddisflies, including *Philopotamus montanus*, these sensilla are absent on the scape and pedicel and are the most numerous at the base of the flagellum (Melnitsky et al., 2018).

The ultrastructural organization of the insect sensilla was first described early in the 1960s, with the advent of transmission electron microscopy (Slifer et al., 1959; Slifer and Sekhon, 1961). An insect olfactory sensillum is usually morphologically specialized, with multiple cuticular pores allowing the entry of odorant molecules (Schneider, 1964). These cuticular pores have a complex structure and are associated with dendrites of the olfactory sensory neuron (Steinbrecht, 1996). Until recently, the fine structure of pseudoplacoid sensilla in caddisflies has been practically unknown (Zueva et al., 2011). Yuvaraj and co-authors (2018) showed that the mushroom-like pseudoplacoid sensillum of *Rhyacophila nubila* had very thin cuticle, while the ultrathin section revealed over 25 dendrites in the sensillar lymph. The cited authors also noted that the forked pseudoplacoid antennal sensilla of *Rh. nubila* were morphologically similar to the basiconic sensilla and innervated by more than 20 dendrites, but neither this nor other subtypes of pseudoplacoid sensilla were studied in detail.

MATERIALS AND METHODS

Our study object was *Philopotamus montanus* Donovan (Fig. 1), the type species of the genus *Philopotamus* Stephens. The material was collected by the authors on the Nizhnyaya Luvenga River in Murmansk Province of Russia (67°06′13.0″N, 32°42′30.0″E). For studying the external morphology of sensilla, the material was fixed in 70% ethanol. For histological investigation, living insects were fixed in a solution of 2.5% glutaraldehyde and 1.5% paraformaldehyde in 0.15 M collidine buffer (pH 7.2–7.4) and stored in the buffer for up to 3 months. Then the material was postfixed in 1% osmium tetroxide in 0.15 M collidine buffer, dehydrated in a graded ethanol series and in acetone, and embedded in Epon-812 at elevated temperatures (first 37, then 60°C) for 3 days. Ultrathin sections were examined using a JEOL JEM 100B transmission electron microscope.

Fig. 1. *Philopotamus montanus* Donovan in its natural habitat (Nizhnyaya Luvenga River, Kola Peninsula).

The general morphology of the sensilla was studied using JEOL NeoScope JCM-5000 and Tescan MIRA3 scanning electron microscopes at the Research Park of St. Petersburg State University. The material for SEM was prepared by the standard technique (Melnitsky et al., 2018). The measurements of the sensilla were obtained from series of digital micrographs processed in ImageJ 1.50 software. The morphometric data are presented below as the mean ± standard error.

RESULTS

The antenna of *Philopotamus montanus* consists of about 45 segments. Caddisflies of the family Philopotamidae have 7 types of antennal sensilla arranged in 2 layers (Fig. 2). The upper layer is formed by 4 types of sensilla. The **long trichoid sensilla** are on average

47.5 ± 2.6 μm long, slightly curved, and have a ribbed surface. The **chaetoid sensilla** have a mean length of 31.7 ± 1.5 μm. The **smooth curved trichoid sensilla** have a smooth surface and are on average 17.3 ± 0.9 μm long. The scape additionally bears **Böhm's bristles** which are 18.4 ±1.0 μm long. The lower layer comprises 3 types of sensilla. The **styloconic sensilla** vary in length from 1 to 2 μm and are 1.3 ± 0.1 μm in diameter; the **coronal sensilla** are present in small numbers, no more than 2 per flagellomere, and have a mean length of 1.6 ± 0.1 μm; the **mushroom-like pseudoplacoid sensilla** are numerous, on average 7.5 ± 0.2 μm in diameter, and rise 2 μm above the flagellomere surface. All the pseudoplacoid sensilla in this species are of the mushroom-like type.

The cuticular part of the pseudoplacoid sensillum in *Ph. montanus* (Fig. 2) consists of a wide recessed socket outlined with a raised cuticular ring, and the sensillum body subdivided into a well-developed thick stem and an expanded apical portion. The apical plate of the pseudoplacoid sensillum is shaped as a rounded cap 7.5 ± 0.2 μm in diameter with a concave upper surface and raised margins; sensilla of this type are known as mushroom-like pseudoplacoid sensilla. The sensillum arises from the socket, with its apical plate positioned slightly (by 1–2 μm) above the level of the chitinous socket ring but not extending beyond the tips of the microtrichia. The sensillum surface is covered with numerous radially diverging grooves 0.05 μm wide (Figs. 2, *3*, *4*). These grooves fork very rarely; as the main grooves move farther apart closer to the sensillum margin, isolated intercalary grooves nearly always appear between them. The gaps between the grooves are convex, on average 0.8 ± 0.2 μm wide. The radial grooves are well developed on the upper surface of the sensillum cap and also present on its lower and lateral surface, but they are absent on the stem (Fig. 2, *4*) and on the cap margins where the upper surface continues into the lower one. There are numerous rounded fenestrated depressions (Fig. 2, *3*) positioned at subequal intervals along the grooves, on average 0.23 ± 0.05 μm apart. These depressions are present on both upper and lower surfaces of the sensillum cap.

The TEM micrographs (Figs. 3, 4) show that each pseudoplacoid sensillum has a complex structure. Its inner parts are filled with dendrites that have local vacuolar expansions and form a tubular layer under the cap surface. These dendrites extend from 3 bipolar neurons in 3 bundles densely packed inside an extracellular tube; the latter probably consists of loose and thin cuticle, similar to the tubes of other olfactory sensilla. The bodies and axons of three bipolar sensory neurons are located at a lower lever. The auxiliary trichogen, thecogen, and tormogen cells lie outside the chitinous tube and the neuron bodies.

The sensillar cuticle is monolayered and very thin (0.17 ± 0.01 μm) as compared with the regular surface of the antennal segment. The outer part of the sensillar socket has multilayered thick cuticle (2–3 μm). As can be seen in the sections, the antennal cuticle outside the sensillum consists of endocuticle comprising 3 thick dark lower layers and a series of 6–8 thin dark upper layers with lighter intervals between them; these series are separated by a wide light gap approximately at half the depth of the endocuticle layer. The exocuticle lies above the endocuticle and is not divided into layers. The cuticle of the sensillum reveals no layered structure; therefore, the cover of both the stem and the cap is formed by exocuticle. The cuticular cover of the sensilla is connected only to the uppermost (i.e., oldest) layers of the endocuticle whereas other layers are interrupted closer to the sensillum.

The numerous grooves perforated with very narrow pores (0.01 μm in diameter) are easily discernible in the cuticular sensillum wall. Outside the fenestrated depressions, the groove bottom has single pores by which the internal sensillar structures come into contact with the ambient air (Figs. 3, *2*, *3*). The rounded fenestrated depressions reveal groups of pores separated by small cuticular gaps (Fig. 3, *3*); thus, these depressions correspond not to single cuticular pores but to pore clusters no more than 0.3–0.5 μm in diameter. We have observed no traces of the pore-tubule system, i.e., tubules extending from the pores inside the sensillum; the pores open directly into the sensillum cavity. At the same time, in some places outside the grooves the lower cuticle layer appears non-uniform, with rows of recesses located at the same level as the bottoms of the fenestrated depressions. These recesses are surrounded with dense cuticle and look similar to the pores, but they are covered with a layer of cuticle on the outside and have no visible connection with the ambient air.

The pseudoplacoid sensillum contains a small amount of sensillar lymph, which in TEM sections forms granular electron-dense matrix not entering the pores. The

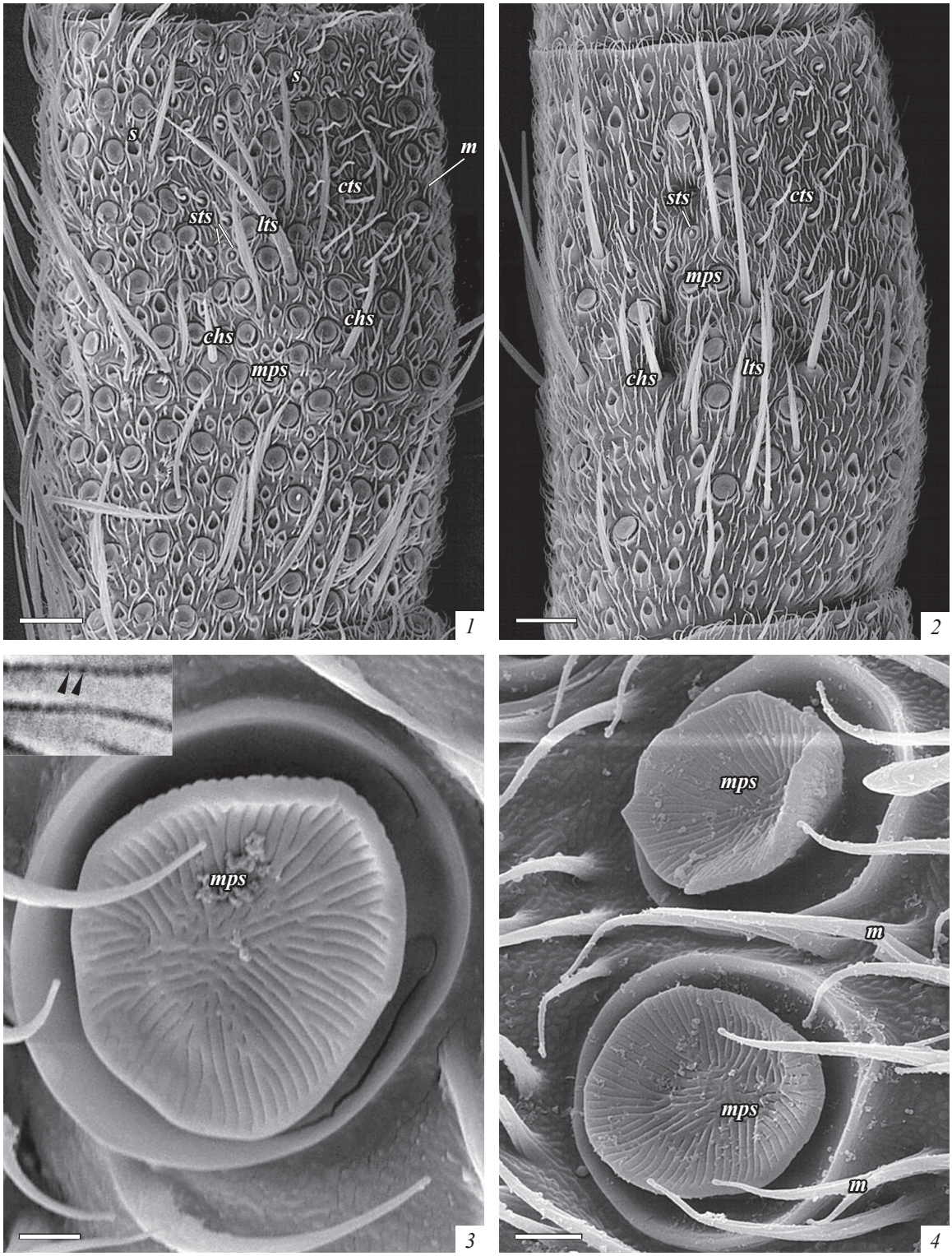

Fig. 2. *Philopotamus montanus* Donovan, SEM: (*1*) sensory structures on the ventral side of the 10th flagellomere in male; (*2*) sensory structures on the ventral side of the 10th flagellomere in female; (*3*) pseudoplacoid sensilla on the antennal surface in male; (*4*) pseudoplacoid sensilla on the antennal surface in female; *chs*, chaetoid sensilla; *cts*, curved trichoid sensilla; *lts*, long trichoid sensilla; *m*, microtrichia; *mps*, pseudoplacoid sensilla; *s*, sockets of detached long trichoid sensilla; *sts*, styloconic sensilla. Inset in (*3*): grooves on the sensillar cap, with depressions marked with arrows. Scale bars 20 μm in *1*, *2*; 5 μm in *3*, *4*.

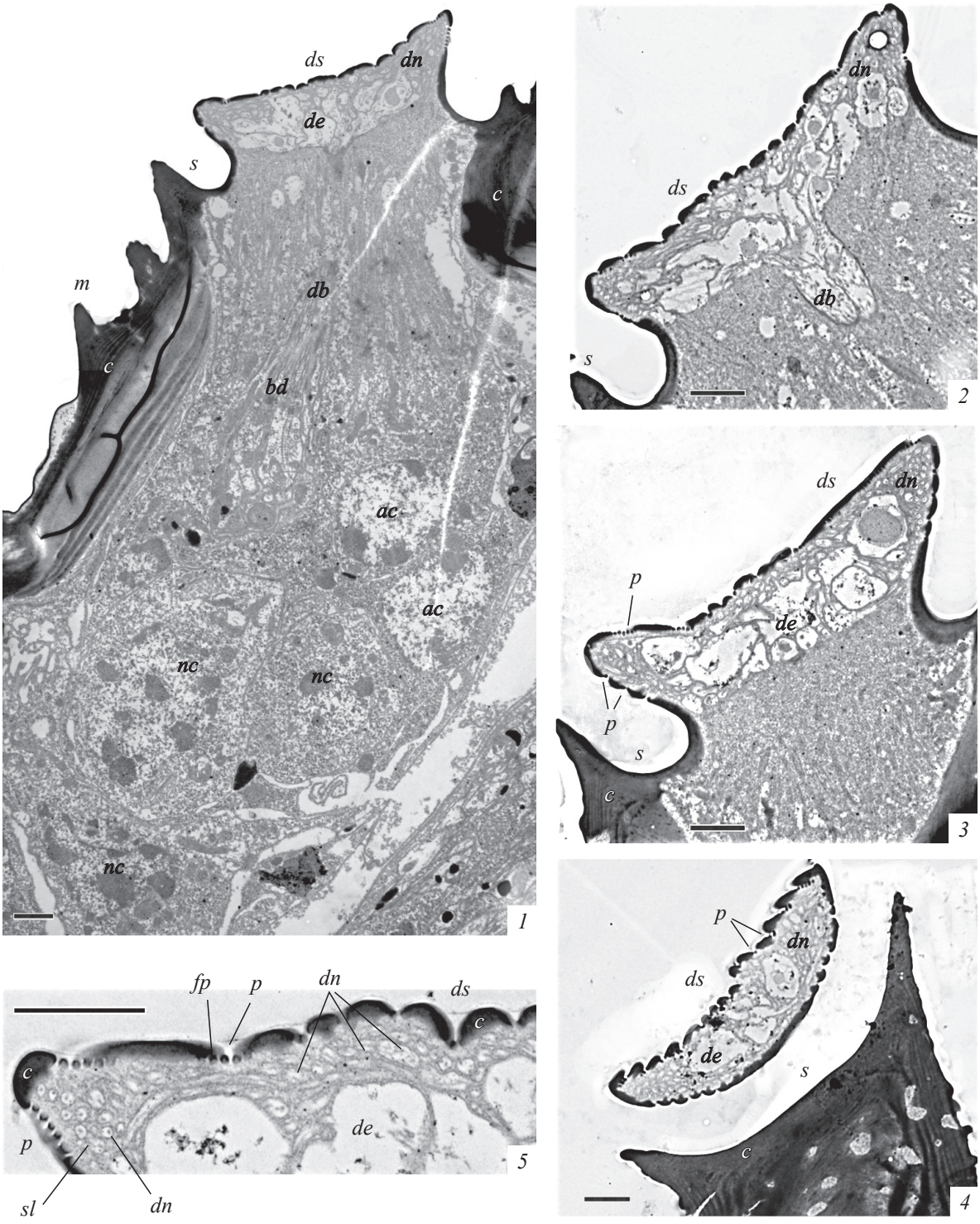

Fig. 3. *Philopotamus montanus* Donovan, TEM of antennal pseudoplacoid sensilla in male: (*1*) total view, longitudinal sagittal section; (*2–4*) sections through the upper part of pseudoplacoid sensillum: (*2*) sagittal; (*3*) parasagittal; (*4*) through the cap margin; (*5*) part of sensillar cap with pores; *ac*, nuclei of auxiliary cells; *bd*, basal parts of dendrites; *c*, cuticle; *db*, dendrite bundle in the extracellular sheath; *de*, apical expansions of dendrites; *dn*, terminal dendritic processes in sensillar lymph; *ds*, dorsal surface of sensillar cap; *fp*, false pore; *m*, microtrichia; *nc*, nuclei of neurons; *p*, pore; *s*, socket; *sl*, sensillar lymph. Scale bars 1 μm in *1–4*; 0.5 μm in *5*.

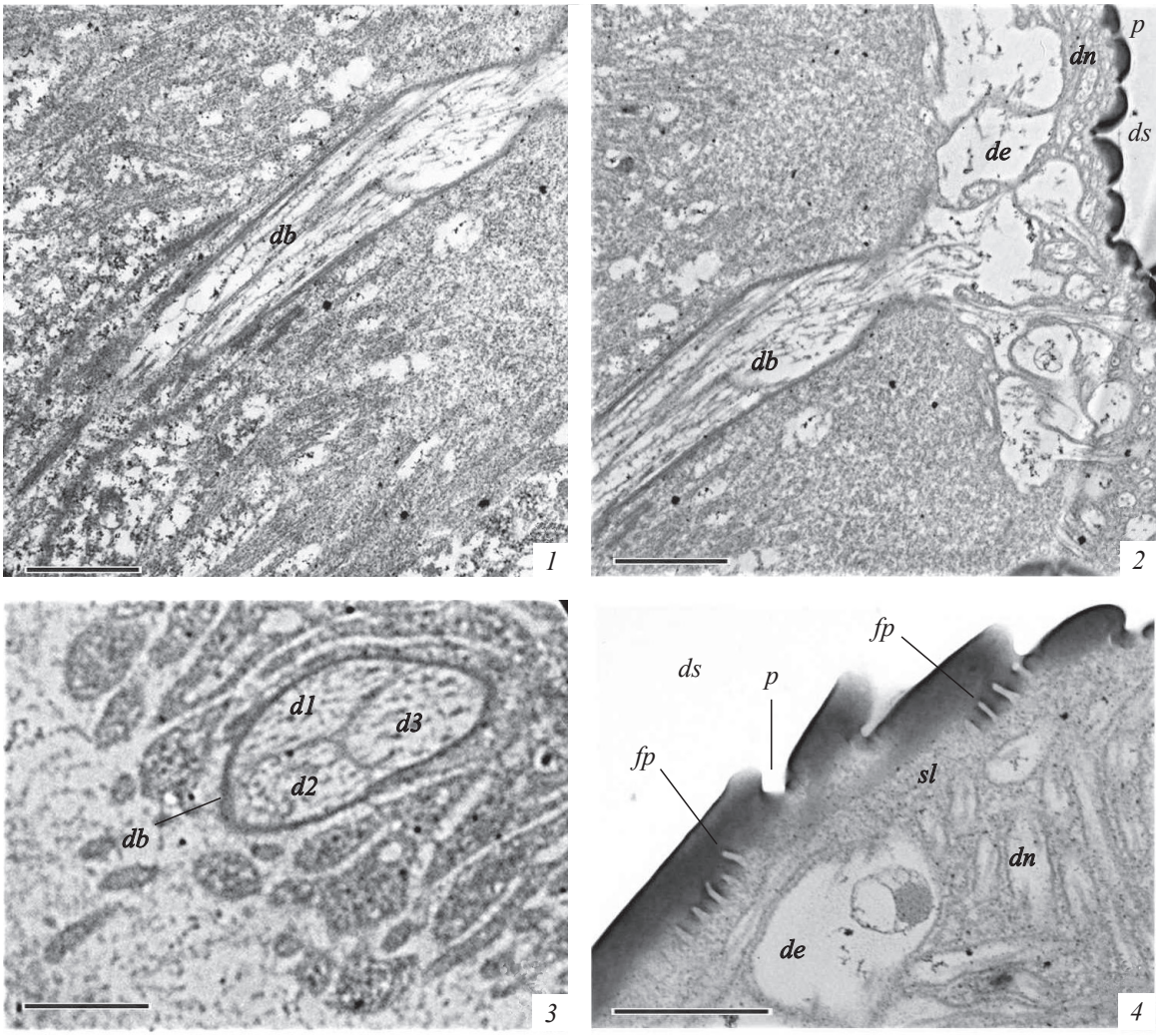

Fig. 4. *Philopotamus montanus* Donovan, TEM of antennal pseudoplacoid sensilla in male: (*1*, *2*) sagittal section through the dorsomedian part of sensillum with dendrites in the sheath: (*1*) basally; (*2*) apically; (*3*) cross-section of dendrites in the sheath; (*4*) section through the cap surface with false pores; *d1*, *d2*, *d3*, individual dendrites in the bundle; other designations as in Fig. 3. Scale bars 1 μm in *1–3*; 0.5 μm in *4*.

terminal parts of dendrites look as thin tubes with electron-dense cores, and in cross-sections, as rings with dark central spots. In some places inside the sensillum cap the dendrites strongly expand to form reservoirs with electron-transparent fluid; the terminal parts of dendrites arise dorsolaterally from these reservoirs with wide bases. The reservoirs sometimes contain rounded dark inclusions (Figs. 3, *4*, *5*). Below the cap surface the dendrites become thinner and branch. The branching of dendrites is rare if present, so that the dendritic layer inside the cap is mostly formed by a small number of densely packed, gradually tapering dendritic processes. The basal parts of the dendrites reach the sensillar lymph as a narrow bundle enclosed in a chitinous tube, i.e., the dendritic sheath. The proximal parts of the dendrites of all the neurons below the dendritic sheath are thick. Sections through the dendritic sheath (Figs. 4, *1–3*) show that there are only three dendrites entering the sensillum. In some cases (Fig. 3, *4*) vacuolar expansions are formed already at the level where the dendrites leave the sheath. The bodies of three bipolar neurons with large nuclei are located deep below the cuticle surface; they are densely packed and enveloped by the auxiliary cells. The basal part of the sensillum has the structure quite typical of other olfactory sensilla. There is almost no free space between the clusters of neurons and auxiliary cells belonging to the adjacent sensilla; therefore, the distribution of sensilla over the antenna surface may be determined by the limited space needed to accommodate the cell bodies.

DISCUSSION

Yuvaraj and co-authors (2018) published the TEM micrograph of a single section through the cap margin of the mushroom-like pseudoplacoid sensillum of *Rhyacophila nubila* Zett. and noted that over 25 dendrites immersed in the sensillar lymph were found in one section. Our micrographs revealed only a few receptor cells (Fig. 4). We never observed the branching of dendrites in our material, and it is possible that dendrites do not actually branch but form a dense tangle giving the impression of numerous branches. The surface of pseudoplacoid sensilla has grooves with rounded depressions (Fig. 2, *3*). These depressions resemble the pore openings, but cross-sections of the cap (Figs. 3, *5*; 4, *4*) show that the depressions actually contain clusters of pores whereas single pores may also lie in the grooves outside the depressions. The pore size is about 0.01 μm, which is at the lower size limit for pores found in the olfactory sensilla of insects; similar pores occur in the sensilla of lepidopterans and beetles (Schneider and Steinbrecht, 1968). Apart from the open pores, there are false pores inside the cuticle layer. These are recesses in the inner cuticle surface resembling the true pores in size and position; however, they are covered with a cuticle layer and have no external opening (Fig. 4, *4*). Such false pores may form aggregations resembling the clusters of true pores inside the fenestrated depressions; in some cases they are adjacent to pore clusters and look as their extensions (Fig. 3, *5*).

Pseudoplacoid sensilla belong to the single-walled type of insect sensilla (Steinbrecht, 1996); yet we have not observed the characteristic pore tubules extending in a divergent bundle from the pore opening inside the sensillum and probably involved in transport of hydrophobic odorants to the dendrites of the receptor cells (Steinbrecht, 1997). Moreover, the dense arrangement of dendrites leaves almost no place for sensillar lymph, the hydrophilic medium through which stimulant molecules have to travel to reach the dendritic membrane receptors. Densely packed dendritic processes and thin cuticle were also found in the sensilla of primitive moths, for instance, *Micropteryx calthella* (L.) from the family Micropterigidae (Hallberg and Hansson, 1999).

Pseudoplacoid sensilla differ from placoid ones in the presence of a socket, a stem, and a dilated cap perforated with pores on both the upper and the lower surface (Fig. 5). The placoid sensilla of hymenopterans are the most different from the pseudoplacoid sensilla of caddisflies in their internal structure. In particular, the placoid sensilla of the bumblebee *Bombus lapidarius* (L.) are innervated by 13–20 neurons and have no cuticular dendritic sheath (Agren and Hallbeig, 1996). The placoid sensilla of chalcid wasps have pore tubules (Barlin and Vinson, 1981) and also thicker cuticle of the porous plate. The placoid sensilla of the honeybee *Apis mellifera* L. include from 12 to 18 sensory cells and have pores 0.01 μm in diameter (Slifer and Sekhon, 1961). Only two sensory cells were found in the placoid sensilla of the diving beetle *Acilius sulcatus* (L.) (Ivanov, 1969). The placoid sensilla of the Asiatic rhinoceros beetle *Oryctes rhinoceros* L. have thick cuticle with large pores and pore tubules, considerable amounts of sensillar lymph, a dendritic sheath, and only two neurons responding to the ether and alcohol components of pheromones (Renou et al., 1998).

The pseudoplacoid sensilla of Amphiesmenoptera may have originated from placoid or basiconic sensilla. The latter are widespread in Holometabola whereas placoid sensilla have been found within this group only in Coleoptera and Hymenoptera. As a rule, the cuticular part of a placoid sensillum is shaped as a rounded or oblong plate. The basiconic and trichoid sensilla in insects are very diverse in morphology and ultrastructure. The number of receptor cells in the olfactory sensilla varies greatly in members of different orders of insects: from 1 in Lepidoptera and Diptera to 50 in Orthoptera (Schneider and Steinbrecht, 1968).

In our previous studies, the pheromone glands and associated abdominal cuticular structures in caddisflies of the family Philopotamidae were found to be largely similar to the corresponding structures in moths of the family Eriocraniidae (Ivanov and Melnitsky, 1999; Melnitsky, 2004). The sternal glands of caddisflies and primitive lepidopterans produce and release pheromones which play an important role in chemical communication of Amphiesmenoptera (Ivanov and Melnitsky, 2002). Besides, it was shown that members of the above families had similar components in their pheromone blends (Ivanov and Melnitsky, 2014). Comparison of the composition, structure, and distribution of antennal sensilla in Philopotamidae and Eriocraniidae revealed considerable differences between these families (Melnitsky et al., 2018; Yuvaraj et al., 2018). In particular, long trichoid sensilla in Philopotamidae are replaced by

Fig. 5. Structure of the placoid (*A*) and pseudoplacoid (*B*) sensilla: *ac*, nuclei of auxiliary cells; *an*, axons of sensory neurons; *bd*, basal parts of dendrites; *c*, cuticle; *db*, dendrite bundle in the extracellular sheath; *de*, apical expansions of dendrites; *dn*, terminal dendritic processes in sensillar lymph; *ds*, dorsal surface of sensillar cap; *hp*, hypoderm cells; *m*, microtrichia; *nc*, nuclei of neurons; *s*, socket; *sp*, grooves on the cap surface with depressions and pores; *tc*, trichogen auxiliary cell; *th*, thecogen auxiliary cell; *tm*, tormogen auxiliary cell.

shorter and wider scales in Eriocraniidae. Curved trichoid sensilla in these moths, similar to caddisflies, form sensory fields in a specific position near the proximal margin of the flagellomere. Mushroom-like pseudoplacoid sensilla on the flagellomeres of *Philopotamus montanus* and other species of this family are probably homologous to the auricillic sensilla in Eriocraniidae. It may be assumed that the auricillic sensilla of Lepidoptera are also a subtype of the pseudoplacoid sensilla of Amphiesmenoptera.

Amphiesmenoptera reveal the highest structural diversity of pseudoplacoid sensilla. Nine types of these structures have been found in caddisflies: mushroom-like, bifurcate, forked, serrate, corniculate, stellate, leaf-like, multiforked, and dissected (Melnitsky and Ivanov, 2011; Valuyskiy et al., 2017). In some caddisfly families the apical parts of pseudoplacoid sensilla vary in shape; size-based subtypes may appear within individual species and develop into unique structural types of sensilla in the course of subsequent evolution (Valuyskiy et al.,

2017). Mushroom-like sensilla have been found in many caddisfly families possessing pseudoplacoid sensilla, with the exception of Phryganeidae, Goeridae, Oeconesidae, and Sericostomatidae (Melnitsky and Ivanov, 2011). They are widespread in different evolutionary lineages of Trichoptera and also occur in some taxa of Lepidoptera, in particular the families Micropterigidae, Agatiphagidae, Eriocraniidae, and Lophocoronidae (Faucheux, 2004a, 2004b; Melnitsky et al., 2018). Pseudoplacoid sensilla are present in primitive members of both orders and evidently belong to the ground plan of Amphiesmenoptera.

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