Invertebrate Zoology, 2023, 20(2): 241–257

Structure of sensilla on maxillary and labial palps in caddisflies of the genus *Rhyacophila* Pictet, 1834 (Trichoptera: Rhyacophilidae)

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ABSTRACT: A comparative study of the structure and localization of sensilla on the palps of caddisflies from the genus *Rhyacophila*, the family Rhyacophilidae, was carried out for the first time. The structure of maxillary and labial palps in 15 species of the genus *Rhyacophila* was studied by scanning electron microscopy. Seven types and two subtypes of sensilla were found on these head appendages: pointed long trichoid sensilla, blunt chaetoid (gustatory) sensilla (two subtypes), campaniform sensilla, thick basiconic sensilla, petaloid sensilla, leaf-like pseudoplacoid and mushroom-like pseudoplacoid sensilla. The size of chaetoid and pointed trichoid sensilla on palp segments decreases towards the palp apex. Pseudoplacoid sensilla, as a rule, are found only on the terminal segments of the labial and maxillary palps, and in some species they completely disappear. Terminal segments of both pairs of palps have sensory fields formed by aggregations of petaloid sensilla. Apical sensory complexes are localized at the apical end of the maxillary and labial palps. At the top of these sensory areas there is a thick basiconic sensilla, on the lateral surface of the sensory complex there are rudimentary basiconic sensilla. The structure and localization of palpal sensilla, apical sensory complexes, and sensory zones with petaloid sensilla can be used for taxonomy purposes.
How to cite this article: Abu Diiak K.T., Ivanov V.D., Melnitsky S.I., Valuyskiy M.Yu. 2023. Structure of sensilla on maxillary and labial palps in caddisflies of the genus *Rhyacophila* Pictet, 1834 (Trichoptera: Rhyacophilidae) // Invert. Zool. Vol.20. No.2. P.241–257. doi: 10.15298/invertzool.20.2.08

KEY WORDS: Trichoptera, caddisflies, sensilla, palps, Rhyacophilidae, *Rhyacophila*, evolution.

Строение сенсилл максиллярных и лабиальных щупиков ручейников рода *Rhyacophila* Pictet, 1834 (Trichoptera: Rhyacophilidae)

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РЕЗЮМЕ: Впервые проведено сравнительное исследование строения и локализации сенсилл на щупиках ручейников из рода *Rhyacophila* семейства Rhyacophilidae.

Методами сканирующей электронной микроскопии изучено строение максиллярных и лабиальных щупиков у 15 видов из рода *Rhyacophila*. На этих придатках головы обнаружены 7 типов и два подтипа сенсилл: заостренная трихоидная сенсилла, тупоконечная хетоидная (вкусовая) сенсилла (два подтипа), кампаниформная сенсилла, толстая базиконическая сенсилла, лепестковидная сенсилла, листовидная псевдоплакоидная и грибовидная псевдоплакоидная сенсилла. Размер хетоидных и заостренных трихоидных сенсилл на члениках щупиков уменьшается по направлению к вершине щупиков. Псевдоплакоидные сенсиллы, как правило, встречаются только на терминальных члениках лабиальных и максиллярных щупиков, причем у некоторых видов они целиком исчезают. На концевых члениках обеих пар щупиков имеются сенсорные поля, образованные скоплениями лепестковидных сенсилл. Апикальные сенсорные комплексы локализованы на апикальном конце максиллярных и лабиальных щупиков. На вершине этих сенсорных зон расположена толстая базиконическая сенсилла, на латеральной поверхности сенсорного комплекса имеются рудиментарные базиконические сенсиллы. Структура и локализация пальпальных сенсилл, апикальных сенсорных комплексов и сенсорных зон с лепестковидными сенсиллами может использоваться для целей таксономии и систематики.
Как цитировать эту статью: Abu Diiak K.T., Ivanov V.D., Melnitsky S.I., Valuyskiy M.Yu. 2023. Structure of sensilla on maxillary and labial palps in caddisflies of the genus *Rhyacophila* Pictet, 1834 (Trichoptera: Rhyacophilidae) // Invert. Zool. Vol.20. No.2. P.241–257. doi: 10.15298/invertzool.20.2.08

КЛЮЧЕВЫЕ СЛОВА: Trichoptera, ручейники, сенсиллы, строение, щупики, Rhyacophilidae, *Rhyacophila*, эволюция.

Introduction

Maxillary and labial palps, as well as antennae, are sensory appendages of the insect head with a large density of functionally different sensilla having various modalities (Ivanov, 2000). The labial palps are located on the prementum of the labium, and the maxillary palps are located on the stipes of the maxillae. The morphological features of the maxillary and labial palps are widely used in taxonomy of caddisflies (Trichoptera), the order including approximately 17,000 species (Morse, 2022). The first division of the order of caddisflies into suborders was proposed by Kolenati (1851, 1859), who described the suborders where adults have complete (Equipalpia) or incomplete, less than 5, set of maxillary palp segments in males (Inaequipalpia). The principal difference between these suborders was the reduction in the number of segments of the male maxillary palps in the second of the suborders.

Subsequently, A.V. Martynov noted a peculiar annular structure of the terminal segments of the palps in representatives of some families and concluded that according to both imaginal and larval characters all caddisflies can be divided into two separate groups: Annulipalpia and Integripalpia (Martynov, 1924), with the palp structure considered among principal characters. Later (Martynov, 1934) he indicated the presence of sensory pits on the palps as characteristic feature of the suborder Integripalpia, while in the Annulipalpia the characters were the peculiar rounded 2nd segment with long setae, and specific either elongate and annulated or pointed 5th segment of the maxillary palps. Approaches to the division of caddisflies into suborders proposed by A.V. Martynov have been preserved in the modern system (Morse, 1997; Ivanov, Sukatsheva, 2002). At the end of the XX century, John Weaver proposed to distinguish the infraorder Spicipalpia within Annulipalpia; the presence of large apical sensilla on palps was considered as the main apomorphic character (Weaver, 1984). Recently, the authors have shown (Ivanov *et al*., 2018) that the presence of a special sensory zone with large apical sensilla at the apex of the terminal palp segment is not a unique feature of caddisflies from the previously proposed infraorder Spicipalpia including the families Rhyacophilidae, Hydrobiosidae, Glossosomatidae, Hydroptilidae, and Ptilocolepidae (Weaver, 1984, 1992),

because these zones and sensilla were also found in the families Philopotamidae, Stenopsychidae, and in a reduced state in Hydropsychidae outside this infraorder.

The morphological features of the palps of caddisflies have not been sufficiently studied. A variety of early data on the structures and function of the mouthparts including its appendages are summarized by Crichton (1957). Structure of head including its appendages was described for 2 species of Rhyacophilidae by Klemm (1966). The external morphology of the palps of caddisflies was studied in representatives of 16 families and the structure of the head appendages of *Philopotamus ludificatus* McLachlan, 1878, including the sensilla on the palps, was studied in more detail (Ljungberg, Hallberg, 1992; Kubiak *et al*., 2015). In a recent study, the structure of the apical regions of the maxillary and labial palps was studied in 80 species from 26 families of caddisflies (Ivanov *et al*., 2018). It has been shown that in the families Rhyacophilidae, Hydrobiosidae, Glossosomatidae, Ptilocolepidae, Stenopsychidae, and Philopotamidae, the last segment of the maxillary and labial palps has morphologically distinct apical sensory complexes in the form of elongated cone-shaped or cylindrical protrusions. It was also shown that the apical sensory zone has only thick basiconic sensilla remain on its surface. In some groups of caddisflies, one larger apical sensilla of terminal zone is strikingly different from other thick basiconic sensilla of this zone (Melnitsky, Ivanov, 2010; Ivanov *et al.*, 2018). The cuticular structures on the surface of apical sensory zone demonstrate significant differences in structure both at the level of suborders and superfamilies, and at lower taxonomic levels. Functions of receptors on the palps of caddisflies have hardly been studied and are proved mainly by observations of movements of the haustellum in response to the tests of sugar or salt solutions interacted with terminal sensilla (Frings, Frings, 1949).

The nomenclature of insect sensilla is developed incompletely due to transitions between different types of sensilla (Ivanov, 2000; Ivanov *et al*., 2018). We use here the classification based on the traditional nomenclature which we followed earlier (Ivanov, Melnitsky, 2011, 2016; Melnitsky, Ivanov, 2011a, 2016; Valuyskiy *et al*., 2017) to maintain uniformity and provide comparison with antennal sensilla. The majority of the sensilla on palps appear to belong to the same types as on antenna; the petaloid and thick basiconic sensilla are specific for palps of the mouthparts, and the campaniform sensilla are absent on antennae. Structural details of these sensilla are discussed below.

Our paper is devoted to the morphology of sensilla on the palps of caddisflies of the genus *Rhyacophila* from the archaic family Rhyacophilidae. Recent studies in the field of molecular taxonomy (Thomas *et al*., 2020) place this family near the base of the integripalpian branch of the Trichoptera. The basal position of this family on the phylogenetic tree of the order Trichoptera and the general archaic structure of adults in Rhyacophilidae make these insects a key object for reconstructing the ground plan of the palp surface in caddisflies. The family Rhyacophilidae is widespread in the Palearctic, Nearctic, and Oriental zoogeographic regions and comprises more than 830 species, the vast majority of which belong to the genus *Rhyacophila* Pictet, 1834 (Melnitsky, Ivanov, 2011b). The oldest representative of the genus, *Rhyacophila antiquissima* Botosaneanu et Wichard, 1983, is known from Cretaceous Taimyr amber. The modern fauna of the family includes 5 genera, with the vast majority of species (more than 800) belonging to the genus *Rhyacophila* Pictet, 1834. According to the morphology of the genital structures of males, four evolutionary branches are distinguished in the genus *Rhyacophila*: *vulgaris*, *philopotamoides*, *divaricata* and *naviculata*, which in turn, they include more than 70 groups of species (Schmid, 1970).

Species of the family Rhyacophilidae have an unusually high diversity of antennal sensilla, which tend to form unique subtypes (Valuyskiy *et al*., 2017). With this in mind, this publication will evaluate the diversity of palpal sensilla in different species and compare sensory structures on antennae and palps, including their size and location in different members of the family under study.

Material and methods

MATERIAL. Representatives of 15 species from the genus *Rhyacophila* were studied: *Rhyacophila armeniaca* Guerin-Meneville, 1844; *Rh. cupres-*

sorum Martynov, 1913; *Rh. dorsalis* (Curtis, 1834); *Rh. fasciata aliena* Martynov, 1916; *Rh. forcipulata* Martynov, 1926; *Rh. nubila* Zetterstedt, 1840; *Rh. nephroida* Sun et Yang, 1998 (branch vulgaris, group *anatina*); *Rh. tristis* Pictet, 1834 (branch philopotamoides, group *tristis*); *Rh. lepnevae* Levanidova, 1977 (branch philopotamoides, group *sibirica*); *Rh. sibirica* McLachlan, 1879 (branch philopotamoides, group *sibirica*); *Rh. angulata* Martynov, 1910 (branch naviculata, *angulata* group); *Rh. kaltatica* Levanidova et Schmid, 1977 (branch divaricata, group *kaltatica*); *Rh. chayulpa kaligandaki* Melnitsky, 2005 (branch divaricata, group *chayulpa*); *Rh. shingripa tatopani* Melnitsky, 2005 (branch divaricata, group *nabochepa*); *Rh. stigmatica* (Kolenati, 1859) (an isolated separate group *stigmatica*). The division of the genus *Rhyacophila* into branches and groups of species is accepted here according to the proposals by Schmid (1970). In a recent study based on molecular data, the special position of the *stigmatica* group within the genus under consideration was noted (Mclaughlin *et al*., 2019). In our opinion, based on the details of the genitalia (parameres, IX and X segments), representatives of the *stigmatica* group may have relations with members of the divaricata and vulgaris branches even if they are considered within the separate *stigmatica* branch. The subsequent comparative analysis of sensilla will be carried out according to this assumption.

Material was taken from the collections of the Department of Entomology of St. Petersburg State University sampled in Russia, Kazakhstan, Nepal, Vietnam and Austria. Insects were stored in 90% ethanol. The positions and movements of the palps were observed both on living material in nature and in the laboratory, and on insects stored in ethanol.

MICROSCOPY. The study was made using light and scanning electron microscopy (SEM). The photograph of the head was taken with a Nikon D5300 camera with a Tamron SP 90 mm macro lens. The photographs of the palps were obtained using a Leica DM 1000 microscope with a Leica EC 3 camera in incident light and subsequent combination of a series of overlay palp photographs. SEM data on the palp surface were obtained with Tescan MIRA3 and Hitachi TM3000 scanning electron microscopes at the Resource centers of St. Petersburg State University "Development of molecular and cellular technologies" and "Resource center for microscopy and microanalysis". The preparation of palps for SEM included the mounting of the dried palps on microscope holders, gold sputtering, and was described in detail earlier (Abu Diiak *et al*., 2021).

MEASUREMENTS AND COUNTING OF THE SENSILLA. Measurement of sensilla size and calculation of their number were performed using the ImageJ 1.52r program. Calibration of the length measurement modules was carried out according to the size ruler in the images using the "Set scale" command. After that, length measurements were made for each type of sensilla (or the largest diameter for pseudoplacoid ones) using the "Straight line" / "Segmented line" functions and the "Measure" tool. The obtained numerical values with an accuracy of hundredths were transferred to an Excel spreadsheet for further processing. The mean length, standard deviation, and standard error of the mean were calculated from 10 measurements of each type of sensilla, independently on the maxillary and labial palps. The number of sensilla was counted using the ImageJ multi-point tool on images of the lateral and medial surfaces of each palp segment. The average number of sensilla in the field of view was calculated from five samples of each of the segments.

Results

GENERAL STRUCTURE OF PALPS. The maxillary palps consist of five segments (Fig. 1A, C, E, F), while the labial palps are three-segmented (Fig. 1A, B, D). The 1st and 2nd segments of the maxillary palps are approximately the same length (100–220 μm in the studied species), they are shorter than the others, with the 1st segment cylindrical and the 2nd rounded. The 3rd, 4th and 5th segments are elongated, cylindrical, with obliquely truncated apices of the 3rd and 4th segments. The third and fifth segments are usually equal in length (300–600 μm), and the 4th one is much shorter (200–400 μm). There is an apical sensory complex 35–40 μm long at the apex of the 5th segment, consisting of thick basiconic sensilla located on a conically protruding area with a slightly corrugated cuticle without microtrichia (Figs 2I–K; 3C–D).

The 1st and 2nd segments of the labial palps have a narrow base and a widened distal part; the 1st is the shortest (up to 140 μm in length), while the 2nd and 3rd segments are approximately the same in length (380–420 μm). The 2nd segment has a strong basal constriction and a subapical notch. The 3rd segment is more or less cylindrical and narrow. The labial apical sensory complex at the tip of the 3rd segment is shorter than on the maxillary palp, its length does not exceed 30 μm (Figs 2I–K; 3E–F). Comparative sizes of segments of the oral appendages of *Rh. nubila* and *Rh. kaltatica* are shown in Figure 1.

At rest, the maxillary palps are elevated in such a way that their two basal segments are directed forward, the 3rd is turned forward and upward, the 4th is forward and downward at right angles to the 3rd, and the last is downward at various angles, usually downward and backward parallel to the 3rd segment (Fig. 1A). The labial palps, located on the outgrowth of the labium (palpiger), at rest are direct-

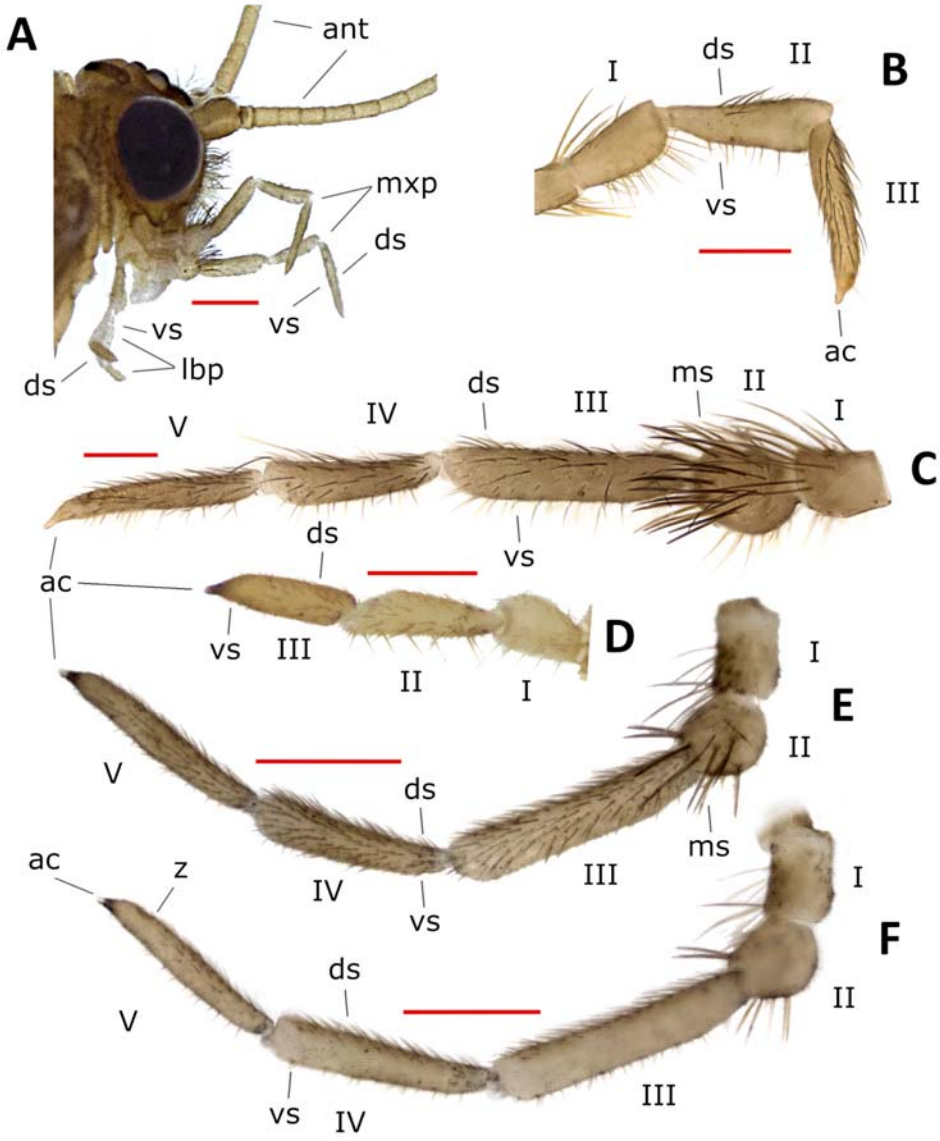

Fig. 1. Structures of head and palps in the caddisfly species *Rhyacophila nubila* Zett (A–C) and *Rh. kaltatica* (D–F), optical images. A — head, right lateral view; B, D — labial palps; C, E, F — maxillary palps, medial (C, E) and lateral (F) view.

Abbreviations: roman numerals — segment numbers; ac — apical sensory complex; ant — antennae; ds — dorsal surface; lbp — labial palps; ms — group of blunt chaetoid sensilla on medial surface of the segment II; mxp — maxillary palps; vs — ventral surface; z — position of the sensory zone with petaloid sensilla. Scale bars: A — 500 μm; B–F — 200 μm.

Рис. 1. Структура головы и щупиков у видов *Rhyacophila nubila* Zett (A–C) и *Rh. kaltatica* (D–F), оптические снимки. A — голова, вид справа; B, D — лабиальные щупики; C, E, F — максиллярные щупики, вид с медиальной (C, E) и латеральной (F) стороны.

Обозначения: римские цифры — номера сегментов; ac — апикальный сенсорный комплекс; ant — антенны; ds — дорсальная поверхность; lbp — лабиальные щупики; ms — группа тупоконечных хетоидных сенсилл на медиальной поверхности второго сегмента; mxp — максиллярные щупики; vs — вентральная поверхность; z — положение сенсорной зоны с лепестковидными сенсиллами. Масштаб: A — 500 μm; B–F — 200 μm.

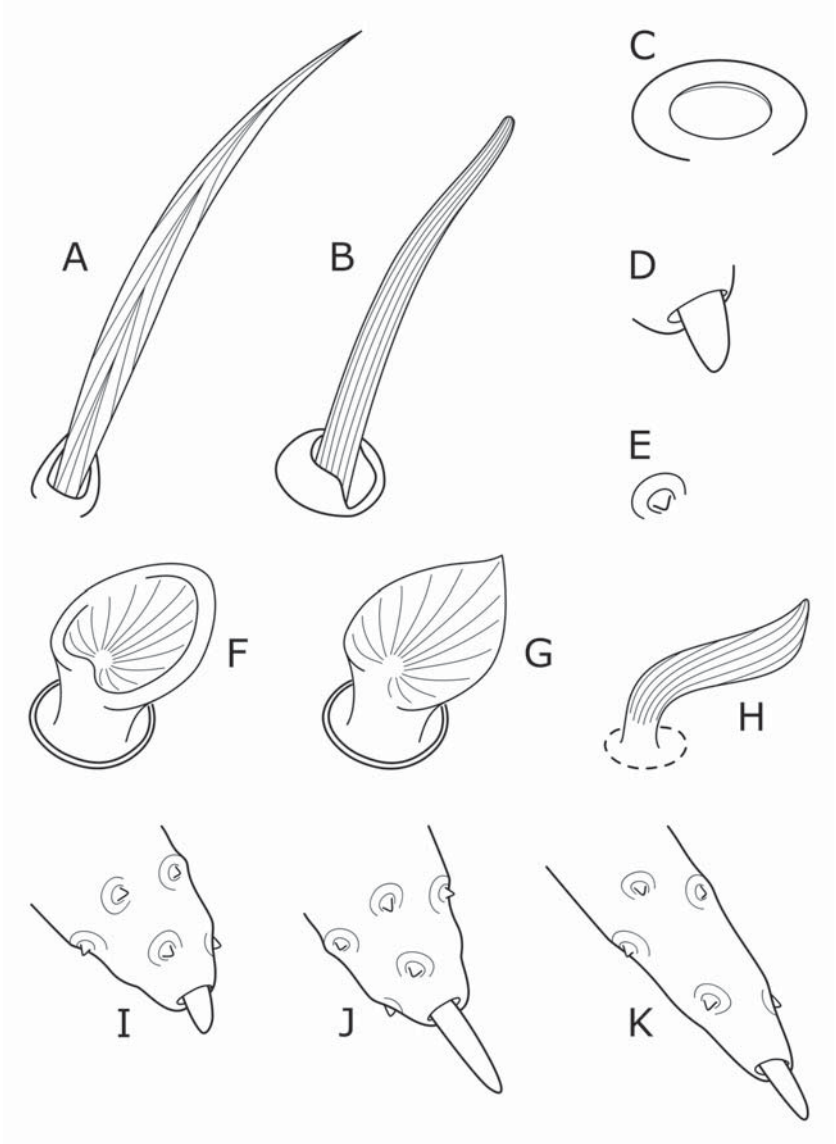

Fig. 2. Schemes of sensilla on maxillary and labial palps in caddisflies of the genus *Rhyacophila*. A — pointed long trichoid sensillum; B — blunt chaetoid (gustatory) sensillum; C — campaniform sensillum; D — apical thick basiconic sensillum; E — thick basiconic sensillum on the lateral surface of apical sensory complex; F — mushroom-like pseudoplacoid sensillum; G — leaf-like pseudoplacoid sensillum; H — petaloid sensillum; I — apical sensory complex without modifications; J — apical sensory complex with elongated apical thick basiconic sensillum; K — elongated apical sensory complex.

Рис. 2. Схемы сенсилл на максиллярных и лабиальных щупиках у ручейников рода *Rhyacophila*. A — длинная трихоидная сенсилла; B — тупоконечная (вкусовая) хетоидная сенсилла; C — кампаниформная сенсилла; D — апикальная толстая базиконическая сенсилла; E — толстая базиконическая сенсилла на боковой поверхности апикального сенсорного комплекса; F — грибовидная псевдоплакоидная сенсилла; G — листовидная псевдоплакоидная сенсилла; H — лепестковидная сенсилла; I — апикальный сенсорный комплекс без модификаций; J — апикальный сенсорный комплекс с удлиненной апикальной толстой базиконической сенсиллой; K — удлиненный апикальный сенсорный комплекс.

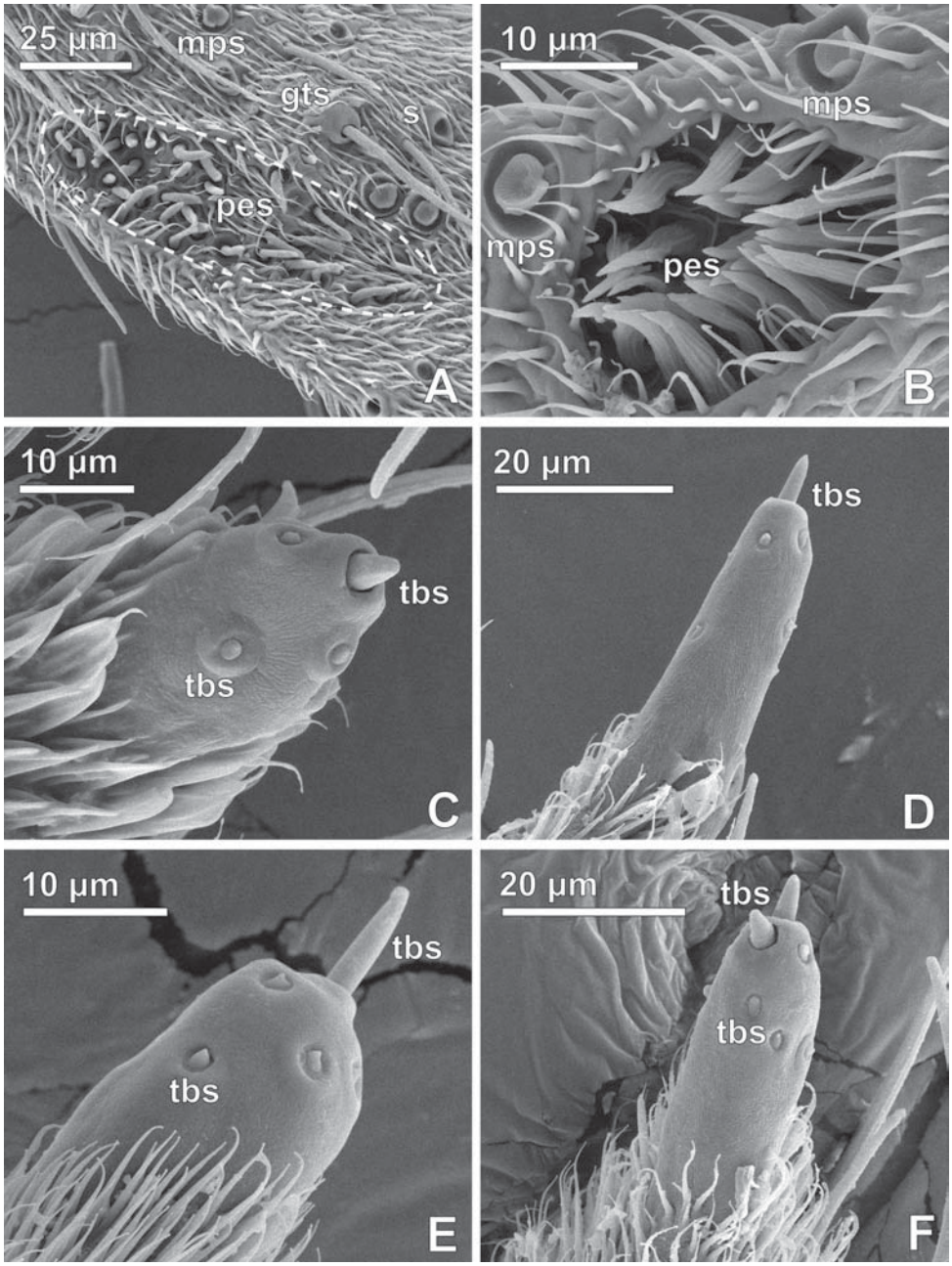

Fig. 3. Palpal sensory fields and apical sensory complexes in caddisflies of the genus *Rhyacophila*. A — sensory field of petaloid sensilla on the fifth segment of maxillary palp in *Rh. armeniaca* female; B — sensory field of petaloid sensilla on the fifth segment of maxillary palp in *Rh. kaltatica* male; C — apical sensory complex of maxillary palp in *Rh. forcipulata* male; D — apical sensory complex of maxillary palp in *Rh. lepnevae* male; E — apical sensory complex of labial palp in *Rh. aliena* male; F — apical sensory complex of labial palp in *Rh. lepnevae* male.

Abbreviations: gts — blunt chaetoid (gustatory) sensilla; mps — mushroom-like pseudoplacoid sensilla; pes — petaloid sensilla; s — empty sockets of pointed long trichoid sensilla; tbs — thick basiconic sensilla. Dashed line shows approximate border of a sensory field.

ed downward and backward, their apical segments are turned forward due to a bend in the articulation of the 2nd and 3rd segments. During activity, including feeding on water droplets and testing of substrate, insects can straighten previously bent palps and move them up and down and to the sides. The preferred position of maxillary palps then is forward with sideward movements, the labial palps extended obliquely backwards. We consider that the dorsal surface of the segments is directed upwards with the palp of both the maxillary and labial pair of appendages fully extended, the ventral surface directed downwards in this position, and recognize medial and lateral surfaces directed inside and outside, respectively.

The cuticle of the palps is less sclerotized than the head capsule and antennae, which is noticeable by the paler coloration. The degree of sclerotization varies: most of the surface has a dense cuticle, while the areas adjacent to the joints are weakened, pale and more flexible. The truncated oblique apical portions of the 3rd and 4th segments of the maxillary and 2nd labial palps facilitate a significant bending of the maxillary palp during movements downwards and backwards, and that of the labial palp, forwards.

STRUCTURE AND DIVERSITY OF SENSILLA. The classification of sensilla previously proposed by the authors (Ivanov *et al*., 2018) is used in this work. In males and females of the studied species, 7 types and 2 subtypes of sensilla were found in maxillary and labial palps (Figs 2–4): pointed long trichoid sensilla (lts), blunt chaetoid (gustatory) sensilla (two size subtypes), otherwise called in the literature thick-walled gustatory trichoid sensilla (gts), thick basiciconic sensilla (tbs), campaniform sensilla (cfs), petaloid sensilla (pes), leaf-like pseudoplacoid (lps), and mushroom-like pseudoplacoid sensilla (mps). Under a light microscope (Fig. 1), the difference in thickness and sclerotization of the sensilla is clearly visible; the most sclerotized of them form groups of black hairs visible to the naked eye on the dorsomedial surfaces of the 2nd and partly 1st segments of the maxillary palps. Lighter, shorter and flexible sensilla are situated ventrally on the same segments.

Pointed long trichoid sensilla (Figs 2A; 4A) are located on all segments of the maxillary and labial palps and have a ribbed surface without visible pores, elongated sockets, and pointed apices. These include both the longest and flattened hair-like sensilla and shorter and weakly sclerotized sensilla. The sizes of these sensilla are variable in a wide range within the studied species (Table 1; Fig. 5A). These sensilla are numerous on dorsal parts of palp segments.

Blunt chaetoid (gustatory) sensilla (Figs 2B; 4C–D) are present on all segments of both pairs of palps. These hair-like sensilla have a longitudinally striated ribbed lateral surface, a round cross section, and a rounded apex, without an apical pore. The mouthpart appendages bear two size subtypes of these sensilla in all studied species. At the base of the maxillary palps, on the 1st and 2nd segments, there are very large dark chaetoid sensilla collected in dorsomedial clusters (Fig. 1, ms). The cluster on the 2nd segment is most pronounced. Large blunt chaetoid sensilla are strongly thickened and have the 8-shaped sockets narrowed in the middle. The average length of these sensilla on the maxillary palps of *Rh. nubila* is 179.2 ± 7.0 μm, in other species it varies from 112 to 213 μm (Table 1).

Chaetoids of the smaller subtype on subsequent segments of maxillary palps and on all segments of labial palps occupy the whole surface of each segment, but their highest number is observed on the medial surface. Sensilla of this subtype have rounded sockets. Their size in *Rh. nubila* is 46.2 ± 3.6 μm on labial and 48.8 ± 2.3 μm on maxillary palps. The size of small gustatory palpal sensilla varies greatly in studied species; comparison of the lengths of these sensilla is shown in Table 1 and Fig. 5B.

In *Rh. nubila* the largest number of blunt chaetoid sensilla is observed on the second segment of the maxillary palps (60.3 ± 5.8), the smallest on the first segment of the labial palps (22.4 ± 7.9) (Fig. 6A–B). Medial surfaces of the 3rd–5th maxillary palp segments and of all segments of the labial palps bear more sensilla of this type than the lateral surfaces (Fig. 6C–D). The number of blunt chaetoid sensilla on the medial side of first and second segments of maxillary palps is less than on the lateral side (Fig. 6C).

Рис. 3. Сенсорные поля и апикальные сенсорные комплексы на щупиках у ручейников рода *Rhyacophila*. A — сенсорное поле лепестковидных сенсилл на пятом членике максиллярного щупика самки *Rh. armeniaca*; B — сенсорное поле лепестковидных сенсилл на пятом членике максиллярного щупика самца *Rh. kaltatica*; C — апикальный сенсорный комплекс максиллярного щупика самца *Rh. forcipulata*; D — апикальный сенсорный комплекс максиллярного щупика самца *Rh. lepnevae*; E — апикальный сенсорный комплекс лабиального щупика самца *Rh. aliena*; F — апикальный сенсорный комплекс лабиального щупика самца *Rh. lepnevae*.

Обозначения: gts — тупоконечные (вкусовые) хетоидные сенсиллы; mps — грибовидные псевдоплакоидные сенсиллы; pes — лепестковидные сенсиллы; s — пустые сокеты длинных трихоидных сенсилл; tbs — толстые базиконические сенсиллы. Пунктирная линия показывает примерные границы сенсорного поля.

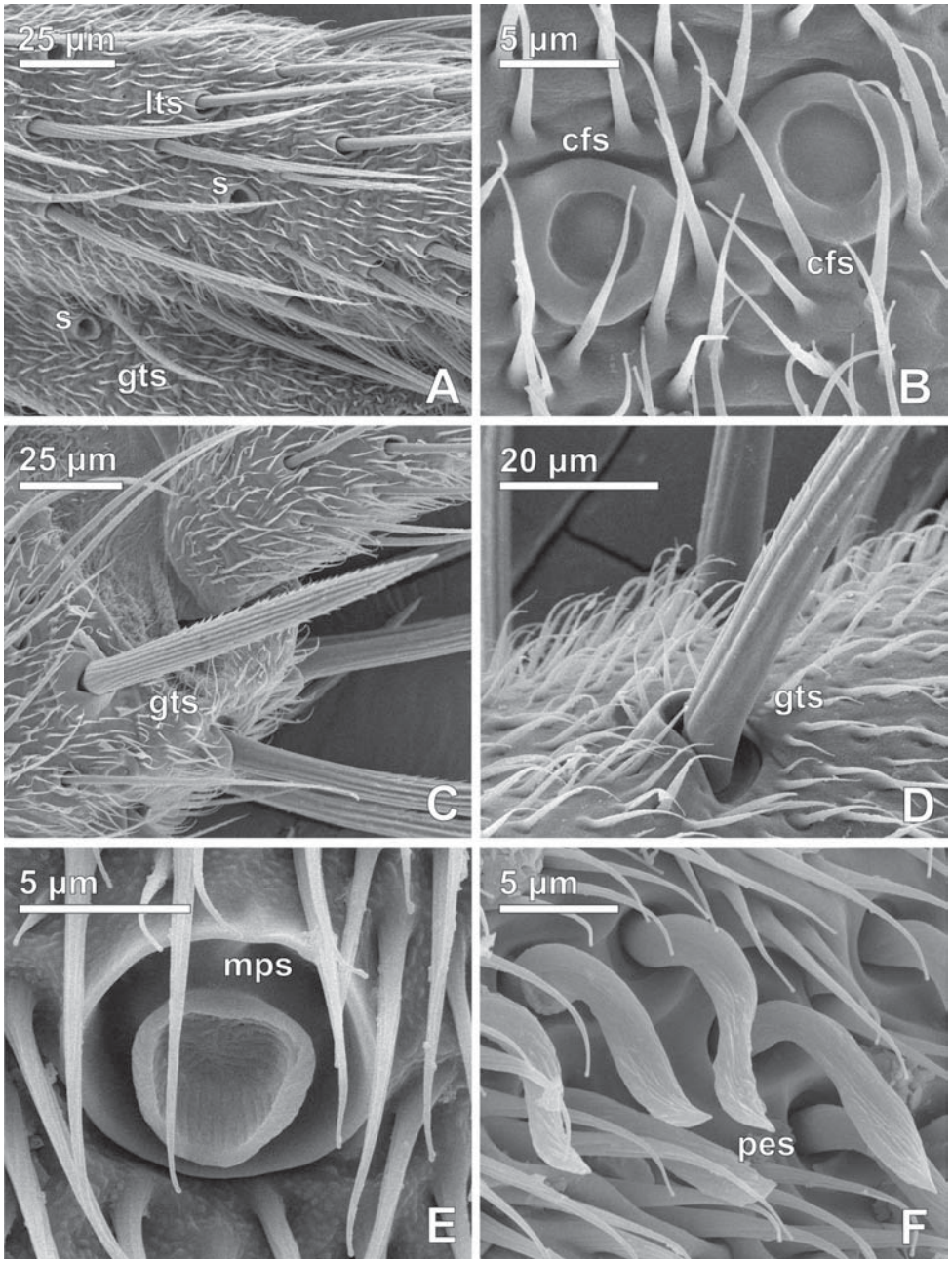

Fig. 4. Sensilla on maxillary and labial palps in caddisflies of the genus *Rhyacophila*. A — lateral surface of the fourth segment of maxillary palp in *Rhyacophila aliena* male; B — campaniform sensilla on the first segment of labial palp in *Rh. kaltatica* female; C — blunt chaetoid (gustatory) sensillum on the second segment of maxillary palp in *Rh. stigmatica* female; D — the base of blunt chaetoid (gustatory) sensillum on the second segment of maxillary palp in *Rh. aliena* male; E — mushroom-like pseudoplacoid sensillum on the fifth segment of maxillary palp in *Rh. aliena* male; F — petaloid sensilla on the fifth segment of maxillary palp in *Rh. armeniaca* male.

Table 1. Minimal and maximal size of sensilla (μm) in the studied species of the genus *Rhyacophila* (males). Length of cuticular part is taken for most of sensilla types except for the pseudoplacoid sensilla where the size refers to the cap diameter.

Таблица 1. Минимальный и максимальный размер сенсилл (μm) у изученных видов рода *Rhyacophila* (самцы). Длина кутикулярной части сенсиллы использована для большинства типов, кроме псевдоплакоидных сенсилл, где указан диаметр.

	Labial palps		**Maxillary palps**	
	Min	**Max**	**Min**	**Max**
lts	36.5 ± 1.7 *Rh. shingripa tatopani*	102.9 ± 4.3 *Rh. fasciata aliena*	29.8 ± 2.2 *Rh. chayulpa kaligandaki*	102.2 ± 3.5 *Rh. stigmatica*
gts-l	–	–	112.1 ± 7.8 *Rh. kaltatica*	212.6 ± 15.7 *Rh. lepnevae*
gts-s	25.7 ± 4.8 *Rh. fasciata aliena*	69.1 ± 8.2 *Rh. dorsalis*	29.7 ± 2.1 *Rh. chayulpa kaligandaki*	69.8 ± 4.0 *Rh. shingripa tatopani*
tbs	3.3 ± 0.5 *Rh. tristis*	7.0 ± 1.1 *Rh. fasciata aliena*	3.9 ± 1.1 *Rh. sibirica*	7.4 ± 1.0 *Rh. fasciata aliena*
pes	6.6 ± 0.2 *Rh. shingripa tatopani*	11.8 ± 0.4 *Rh. stigmatica*	6.9 ± 0.2 *Rh. tristis*	12.5 ± 0.4 *Rh. forcipulata*
mps	2.6 ± 0.3 *Rh. kaltatica*	8.0 ± 0.5 *Rh. fasciata aliena*	2.9 ± 0.2 *Rh. kaltatica*	6.8 ± 0.2 *Rh. forcipulata*
cfs	3.6 ± 0.2 *Rh. stigmatica*	4.6 ± 0.2 *Rh. armeniaca*	4.0 ± 0.2 *Rh. lepnevae*	5.3 ± 0.3 *Rh. armeniaca*

Abbreviations: cfs — campaniform sensilla; gts-l — blunt chaetoid (gustatory) sensilla of the longer subtype; gts-s — blunt chaetoid (gustatory) sensilla of the shorter subtype; lts — pointed long trichoid sensilla; Max — maximal size of sensilla; Min — minimal size of sensilla; mps — mushroom-like pseudoplacoid sensilla; pes — petaloid sensilla; tbs — apical thick basiconic sensilla.

Обозначения: cfs — кампаниформные сенсиллы; gts-l — тупоконечные (вкусовые) хетоидные сенсиллы более длинного подтипа; gts-s — тупоконечные (вкусовые) хетоидные сенсиллы более короткого подтипа; lts — длинные трихоидные сенсиллы; Max — максимальный размер сенсилл; Min — минимальный размер сенсилл; mps — грибовидные псевдоплакоидные сенсиллы; pes — лепестковидные сенсиллы; tbs — апикальные толстые базиконические сенсиллы.

Abbreviations: cfs — campaniform sensilla; gts — blunt chaetoid (gustatory) sensilla; lts — pointed long trichoid sensilla; mps — mushroom-like pseudoplacoid sensilla; pes — petaloid sensilla; s — empty sockets of pointed long trichoid sensilla.

Рис. 4. Сенсиллы на максиллярных и лабиальных щупиках у ручейников рода *Rhyacophila*. A — латеральная поверхность четвертого сегмента максиллярного щупика самца *Rhyacophila aliena*; B — кампаниформные сенсиллы на первом членике лабиального щупика самки *Rh. kaltatica*; C — тупоконечная (вкусовая) хетоидная сенсилла на втором сегменте максиллярного щупика самки *Rh. stigmatica*; D — основание тупоконечной (вкусовой) хетоидной сенсиллы на втором сегменте максиллярного щупика самца *Rh. aliena*; E — грибовидная псевдоплакоидная сенсилла на пятом членике максиллярного щупика самца *Rh. aliena*; F — лепестковидные сенсиллы на пятом членике максиллярного щупика самца *Rh. armeniaca*.

Обозначения: cfs — кампаниформные сенсиллы; gts — тупоконечные (вкусовые) хетоидные сенсиллы; lts — длинные трихоидные сенсиллы; mps — грибовидные псевдоплакоидные сенсиллы; pes — лепестковидные сенсиллы; s — пустые сокеты длинных трихоидных сенсилл.

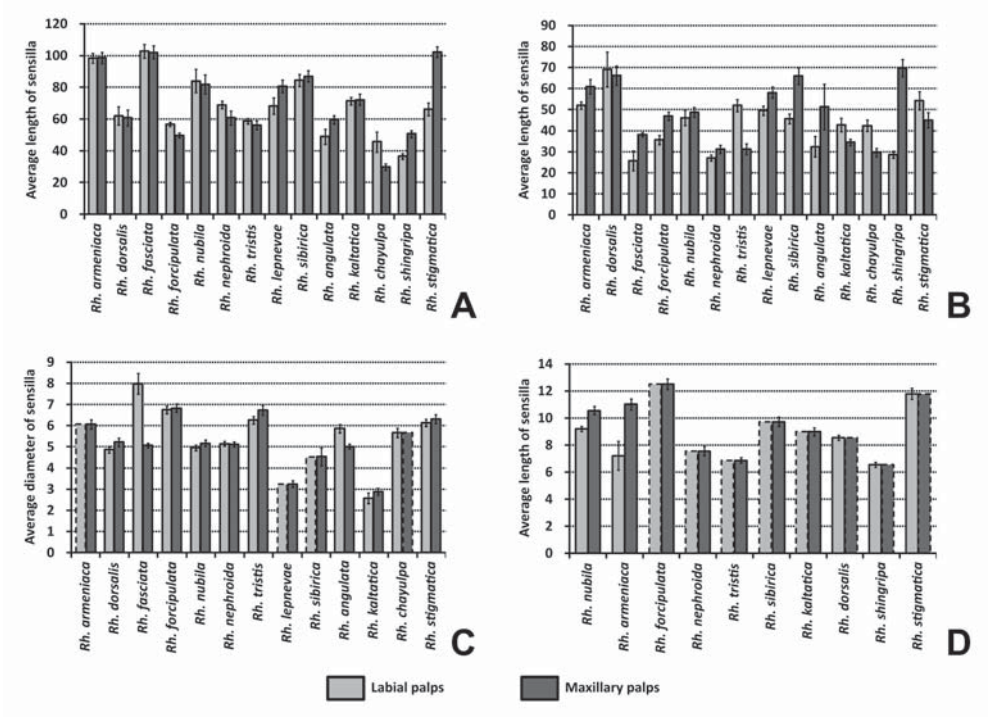

Fig. 5. Size of palpal sensilla in caddisflies of the genus *Rhyacophila*, μm. A — pointed long trichoid sensilla; B — smaller subtype of blunt chaetoid (gustatory) sensilla; C — mushroom-like pseudoplacoid sensilla; D — petaloid sensilla. Dashed lines show the absence of the given sensilla type on labial or maxillary palps.
Рис. 5. Размер сенсилл на щупиках у ручейников рода *Rhyacophila*, μm. A — длинные трихоидные сенсиллы; B — короткий подтип тупоконечных (вкусовых) хетоидных сенсилл; C — грибовидные псевдоплакоидные сенсиллы; D — лепестковидные сенсиллы. Пунктирная линия показывает отсутствие данного типа сенсилл на лабиальных или максиллярных щупиках.

Thick basiconic sensilla (Figs 2D–E, I–K; 3C–F) were found in all studied species only on the last segments of both pairs of palps as part of the apical sensory complexes. These are short cone-shaped structures without surface pores. The labial palps sensilla of this type in *Rh. nubila* are 3.8 to 6.5 μm long and those on the maxillary palps are from 5.8 to 7 μm. The length of these sensilla in males of other species is shown in Table 1. The average size of thick basiconic sensilla on the labial palps in all studied species is 4.1 μm (4.2 μm in males and 4 μm in females), on the maxillary palps — 5.1 μm (5.2 μm in males and 5 μm in females). In addition to thick basiconic sensilla, which are part of the apical sensory complex, some species also have thick basiconic sensilla at the base of the sensory complex (*Rh. forcipulata*, *Rh. kaltatica*).

Petaloid curved sensilla (Figs 2H; 3A–B; 4F) are present only on the distal region of the terminal segments in both pairs of palps. These sensilla are elongated and curved, their surface covered with longitudinal or spiral furrows. This type of sensilla was found in 9 species on maxillary (*Rh. fasciata aliena*, *Rh. armeniaca*, *Rh. forcipulata*, *Rh. kaltatica*, *Rh. lepnevae*, *Rh. nephroida*, *Rh. nubila*, *Rh. sibirica*, *Rh. tristis*) and in 6 species on labial palps (*Rh. armeniaca*, *Rh. lepnevae*, *Rh. nubila*, *Rh. stigmatica*, *Rh. dorsalis*, *Rh. shingripa*). Compared to other types, the petaloid sensilla are relatively short (about 10 μm in *Rh. nubila*), and their sizes vary in a wide range in the studied species (Table 1; Fig. 5D).

Mushroom-like pseudoplacoid sensilla (Figs 2F; 4E) have a flat apical part attached to a short stalk and bearing furrows with pores radiating from the center. The diameter of these sensilla shows a significant variation in studied species (Table 1; Fig. 5C). These structures were found on the terminal segments of both pairs of palps in all the studied species, except for females of *Rh. tristis*, although males of this species have these sensilla. Numerous sensilla of this type are found in males *Rh. stigmatica* on 2nd segments of the labial and 3rd–4th segments of the

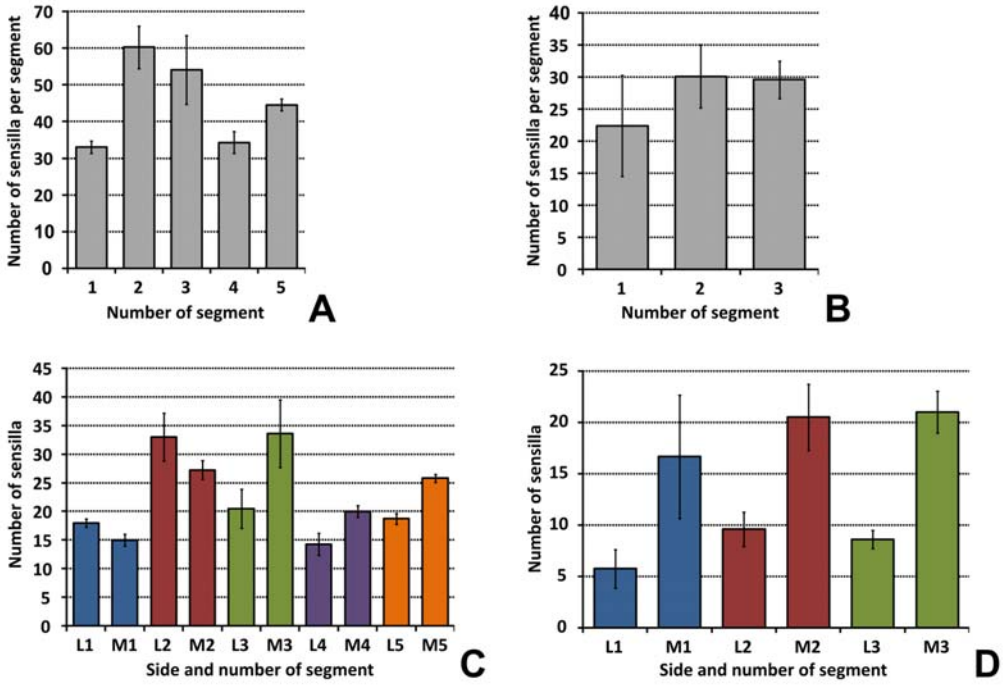

Fig. 6. Quantitative distribution of blunt chaetoid (gustatory) sensilla on palps of *Rhyacophila nubila* male. A — number of sensilla on maxillary palp segments; B — number of sensilla on labial palp segments; C — number of sensilla on lateral and medial sides of maxillary palp segments; D — number of sensilla on lateral and medial sides of labial palp segments.

Abbreviations: L — lateral side of the segment; M — medial side of the segment.

Рис. 6. Количественное распределение тупоконечных (вкусовых) хетоидных сенсилл на щупиках *Rhyacophila nubila*. A — количество сенсилл на сегментах максиллярных щупиков; B — количество сенсилл на сегментах лабиальных щупиков; C — количество сенсилл на медиальной и латеральной сторонах сегментов максиллярных щупиков; D — количество сенсилл на медиальной и латеральной сторонах сегментов лабиальных щупиков.

Обозначения: L — латеральная сторона сегмента; M — медиальная сторона сегмента.

maxillary palps; in females, solitary sensilla are found only on 3rd–4th segments of the maxillary palps. Males of *Rh. nephroida* have a few mushroom-like pseudoplacoid sensilla also on the 4th segment of the maxillary palps.

Leaf-like pseudoplacoid sensilla (Fig. 2G) are found only on terminal segments in *Rh. chayulpa kaligandaki*. These sensilla are very similar in structure to mushroom-like pseudoplacoid sensilla, differing from them in the shape of the apical part, which has a pronounced leaf-like shape; the maximum length of the apical leaflet is 5.7 ± 0.2 μm, and the width is 5.2 μm.

Campaniform sensilla (Figs 2C; 4B) occur irregularly on first and second segments of both pairs of palps singly or in small groups (up to 4 sensilla). These sensilla have a thin, pore-free cuticle surrounded by a raised cuticular ridge. The comparison of the average diameter of these sensilla is shown in Table 1.

SENSORY FIELDS. Sensory fields or isolated sensory zones formed exclusively by petaloid sensilla were found in 6 species on the labial palps and in 9 species on the maxillary palps (Figs 3A–B; 7D; 8C–D). The sensory fields of maxillary and labial palps are usually located on the morphologically dorsal surface of the terminal segment. The position of sensory fields is labile and may be shifted to dorsolateral or dorsomedial surface. The sensory field sometimes can be wide and long and pass through the entire terminal segment (*Rh. shingripa tatopani*); mostly they have a shape of a short strip (*Rh. fasciata aliena*, *Rh. armeniaca*, *Rh. forcipulata*, *Rh. lepnevae*, *Rh. nubila*, *Rh. stigmatica*, *Rh. dorsalis*) or a rounded submerged zone (*Rh. kaltat-*

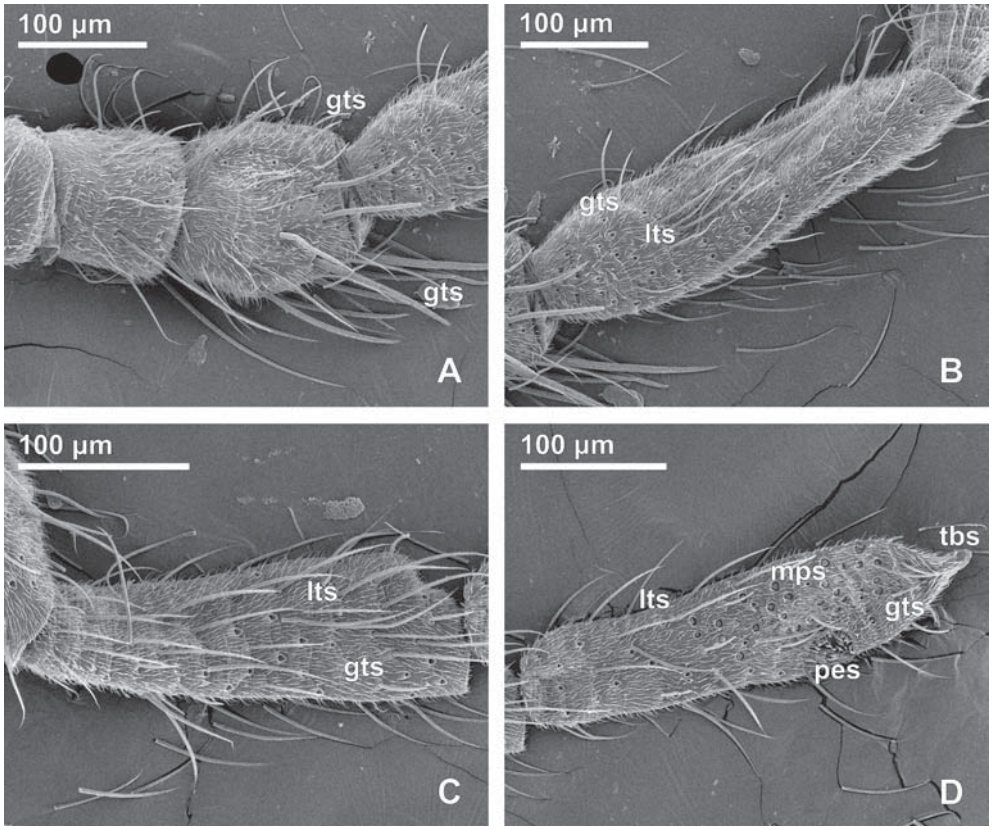

Fig. 7. Lateral surface of the maxillary palp segments of *Rh. kaltatica* male. A — first and second segments; B — third segment; C — fourth segment; D — fifth segment.
Abbreviations: cfs — campaniform sensilla; gts — blunt chaetoid (gustatory) sensilla; lts — pointed long trichoid sensilla; mps — mushroom-like pseudoplacoid sensilla; pes — petaloid sensilla; tbs — thick basiconic sensilla.
Рис. 7. Латеральная поверхность сегментов максиллярного щупика самца *Rh. kaltatica*. A — первый и второй сегменты; B — третий сегмент; C — четвертый сегмент; D — пятый сегмент.
Обозначения: cfs — кампаниформные сенсиллы; gts — тупоконечные (вкусовые) хетоидные сенсиллы; lts — длинные трихоидные сенсиллы; mps — грибовидные псевдоплакоидные сенсиллы; pes — лепестковидные сенсиллы; tbs — толстые базиконические сенсиллы.

ica, *Rh. nephroida*, *Rh. sibirica*, *Rh. tristis*) in the distal part of the terminal palpal segment. Sensory fields were found both on two pairs of palps in females of *Rh. lepnevae* and *Rh. armeniaca*, as well as in males of *Rh. nubila*. In some species, the sensory fields are reduced to small groups of a few petaloid sensilla. On the labial palps, small fields are found in males (5 sensilla) and females (13 sensilla) of *Rh. stigmatica* (Fig. 8C–D) and female *Rh. lepnevae* (5 sensilla). On the maxillary palps, a small field consisting of 5 sensilla is noted in *Rh. nephroida*. Quite often, the surface of the palps at the locations of the sensory fields has very thin cuticle causing a strong surface deformation when palps are dried before coating for electron microscopic studies. Optical images of the surface reveal the presence of chitinous rings of a thicker cuticle around compact sensory fields on the maxillary palps (Fig. 1F).

APICAL SENSORY COMPLEXES. The apices of both the maxillary and labial palps are provided with specific apical sensory complexes in all studied species (Figs 2I–K; 3C–F). Each such complex is a separate protruding area of the surface, devoid of microtrichia and covered with specialized sensilla occurring only within these complexes. The apical sensory complex has one larger thick basiconic sensilla at the apex and several (5–15) very short basiconic sensilla on the lateral surfaces.

Length of apical sensory complex at apex of labial palp in *Rh. nubila* is from 21 to 33 µm, and the width is about 20 µm at the base and 12 µm at the tip.

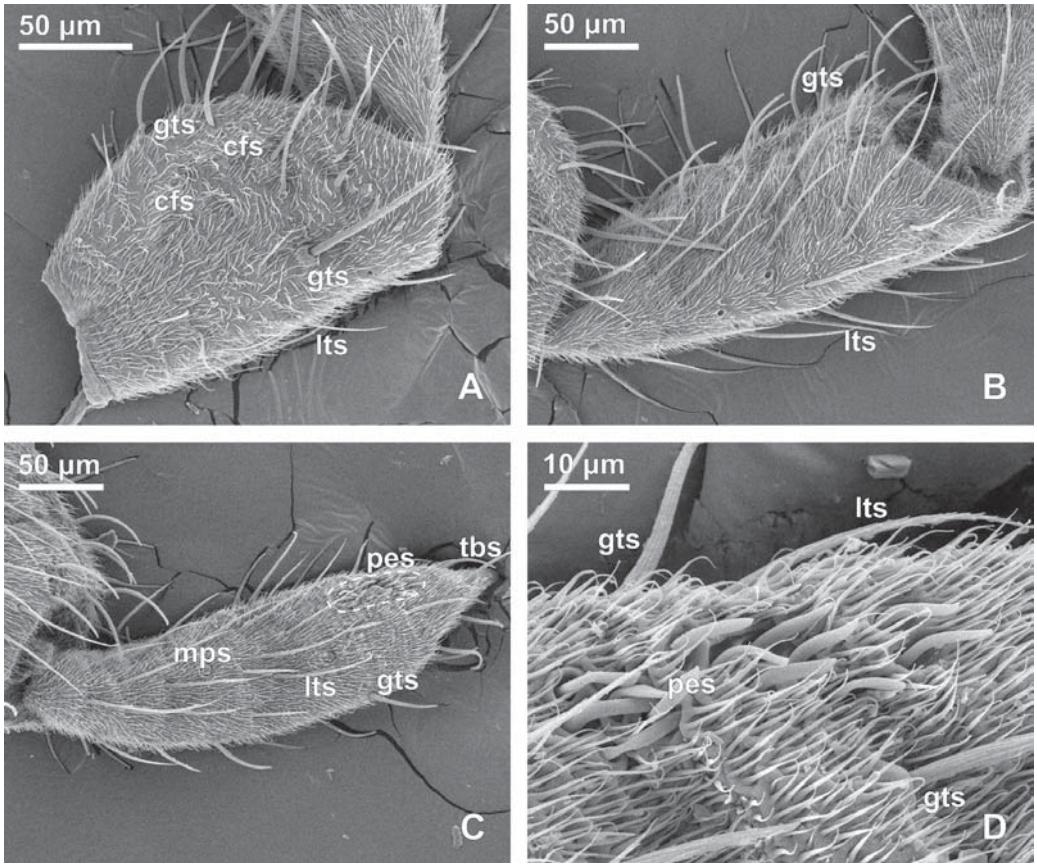

Fig. 8. Lateral surface of the labial palp segments of *Rh. stigmatica* female. A — first segment; B — second segment; C — third segment; D — sensory field of petaloid sensilla on the third segment.
Abbreviations: cfs — campaniform sensilla; gts — blunt chaetoid (gustatory) sensilla; lts — pointed long trichoid sensilla; mps — mushroom-like pseudoplacoid sensilla; pes — petaloid sensilla; tbs — thick basiconic sensilla. Dashed line shows approximate border of a sensory field.
Рис. 8. Латеральная поверхность сегментов лабиального щупика самки *Rh. stigmatica*. A — первый сегмент; B — второй сегмент; C — третий сегмент; D — сенсорное поле лепестковидных сенсилл на третьем сегменте.
Обозначения: cfs — кампаниформные сенсиллы; gts — тупоконечные (вкусовые) хетоидные сенсиллы; lts — длинные трихоидные сенсиллы; mps — грибовидные псевдоплакоидные сенсиллы; pes — лепестковидные сенсиллы; tbs — толстые базиконические сенсиллы. Пунктирная линия показывает примерные границы сенсорного поля.

The apical sensory complex on the maxillary palps is longer (from 35 to 40 μm), but has approximately the same width (from 20 μm at the base to 9 μm at the apex) as on the labial palps. The shortest apical sensory complexes are observed in males of *Rh. kaltatica*: 13.3 μm on the labial and 16.7 μm on the maxillary palps; the longest sensory complexes on the labial palps are found in males of *Rh. lepnevae* (40 μm), on maxillary palps — in males of *Rh. lepnevae* (46.7 μm) and *Rh. sibirica* (47 μm).

Discussion

The antennae and palps of insects are the main chemoreceptor organs, so it is interesting to compare the structure of the sensory surfaces of these appendages. Eight types of sensilla were found on the antennae of caddisflies: long trichoid, curved trichoid, chaetoid, pseudoplacoid, basiconic, coronal, coeloconic, and styloconic (Ivanov, Melnitsky, 2011, 2016; Mel-

nitsky, Ivanov, 2011a, 2016; Melnitsky *et al*., 2018; Valuyskiy *et al*., 2017, 2019, 2020). Pseudoplacoid sensilla are the most diverse and form numerous subtypes within the order: forked, ribbed, mushroom-like, bilobed, stellate, dentate, spear-like, leaf-like, multiforked, dissected, horn-like, T-shaped, and auricillic (Ivanov, Melnitsky, 2011, 2016; Melnitsky, Ivanov , 2011a; Valuyskiy *et al*., 2017, 2020; Abu Diiak *et al*., 2021).

A comparison of the characteristics and diversity of the palpal sensilla with the antennal sensilla shows significant differences in the organization of sensory surfaces. Previously, the authors studied the structure of the antennal surface in 25 species of caddisflies from the family Rhyacophilidae (Valuyskiy *et al*., 2017). The studied species of this family have 13 types and subtypes of antennal sensilla: long trichoid, thin curved trichoid, chaetoid, auricillic, styloconic, basiconic, coronal sensilla, Boehm's bristles, and various types of pseudoplacoid sensilla: mushroom-like, leaf-like, dissected, forked and multiforked (Valuyskiy *et al*., 2017). Seven types of sensilla were found on the palps, including campaniform, thick basiconic and petaloid sensilla, which were not found on the antennae of Rhyacophilidae and caddisflies in general (Ivanov, Melnitsky, 2011, 2016; Melnitsky, Ivanov, 2011a; Valuyskiy *et al*., 2017). Thus, the total diversity of sensilla on the antennae of caddisflies of the genus *Rhyacophila* is higher than on the palps. Three types of sensilla are common to these head appendages: long trichoid, blunt chaetoid, and mushroom-like pseudoplacoid sensilla.

Comparison of sensilla on appendages in *Rh. nubila* shows that antennal sensilla are represented by 8 types and 2 subtypes of sensilla: long trichoid, chaetoid, curved trichoid, auricillic, basiconic, coronal, Boehm's bristles, mushroom-like pseudoplacoid, and forked pseudoplacoid sensilla. Both subtypes of pseudoplacoid sensilla cover the entire surface of the antenna and are characterized by a nonspecific arrangement, with mushroom-like pseudoplacoid sensilla predominating on the basal segments of the antennae, and forked sensilla on the apical segments. A sharp change in the predominant subtype occurs in the region of segments 5–7 (Valuyskiy *et al*., 2017). Only mushroom-like subtype of all variety of the pseudoplacoid sensilla is found on the palps, and exclusively on terminal segments. Three types of pseudoplacoid sensilla are present on the antenna of *Rh. lepnevae*: forked, multiforked, and mushroom-like (Valuyskiy *et al*., 2017), while the palps have only mushroom-like sensilla. Only one type is noted on the palps in other species having more than one type of pseudoplacoid sensilla on the antennae: mushroom-like or, in *Rh. chayulpa kaligandaki*, leaf-like. It was noted previously that different subtypes of pseudoplacoid sensilla can be formed by transformation of the original mushroom-like subtype of pseudoplacoid sensilla (Ivanov, Melnitsky, 2011, 2016; Melnitsky, Ivanov, 2011a; Valuyskiy *et al*., 2017, 2020). Thus, only the initial subtype of pseudoplacoid sensilla is present on the palps.

Sizes of long trichoid and chaetoid sensilla on palps of different species (long trichoid 30–103 μm, chaetoid 26–213 μm) vary more than on antennae (long trichoid 40–66 μm, chaetoid 25–45 μm) (Valuyskiy *et al*., 2017). The diameter of the mushroom-like pseudoplacoid sensilla on palps (2.6–8.0 μm) is also more variable than on antennae (5.2–8.4 μm).

An interesting fact is the complete absence of thin curved trichoid sensilla on the labial and maxillary palps; these sensilla are probably of attractant-perceiving olfactory type (Melnitsky, Ivanov, 2011a). Curved trichoid sensilla are the main component of the antennal sensory fields in caddisflies (Ivanov, Melnitsky, 2011, 2016); sometimes pseudoplacoid sensilla are added to them as part of the sensory fields (Melnitsky, Ivanov, 2011a). The sensory fields on the terminal segments of the palps are formed exclusively by petaloid sensilla, which are absent on the antennae.

Apical sensory complexes are present in both sexes in the studied species. There is one (rarely two) terminal sensillum and 5–15 lateral much shorter basiconic sensilla. A fundamentally similar structure of apical complexes is observed in species from different groups of the genus *Rhyacophila*. The main differences of these complexes can be found in their length and in the number of small basiconic sensilla on the lateral surfaces of the complex. The peculiar thick basiconic sensilla are not found on the antennae of caddisflies and are observed only on the apical sensory complexes in some species of Hydrobiosidae, Rhyacophilidae, Glos-

sosomatidae, Ptilocolepidae, Stenopsychidae, and Philopotamidae (Ivanov *et al*., 2018). The antennae, in turn, lack apical sensory complexes.

Distribution of the blunt chaetoid sensilla on palp surfaces shows an apparent disparity; numbers of sensilla on medial palp surfaces are significantly higher than on lateral sides except for 2 basal segments of the maxillary palps (Fig. 6C, D). Deficiency of sensilla on medial surfaces of basal maxillary palp segments is compensated by enormous development of these sensilla exceeding all others in length and sclerotization (Fig. 1C, E). In this instance the reduced numbers might be caused by deficiency of space available for sensilla. Such a distribution of sensilla presumes the dominant receiving of chemical stimuli from the space between the palps, not from substrate below as one might expect provided the presumable gustatory function in food seeking and testing. An alternative hypothesis might be the participation of these sensilla in other behaviour like courtship and mating, when some body parts of other insect like abdomen or head are nearby the palps. Further experiments are necessary for understanding of their function and significance.

A detailed analysis of the functional significance of various sensilla requires physiological and ethological research methods and is beyond the scope of this work. Observations show that at rest and during movement with folded palps, the apical complexes and groups of petaloid sensilla are directed downwards towards the substrate, since morphologically the dorsal surface is directed downwards. Presumably, in this position, these sensilla can perceive volatile substances evaporating from the surface: the smell of vegetation, fermentation products of sugars in sweet solutions for nutrition, odorous chemical marks of their own or other species. When feeding, the palps are spread apart; the sensory fields are far from food. The strong development of groups of thick and long sclerotized chaetoid sensilla on the dorsomedial surfaces is puzzling. During feeding, these groups of gustatory sensilla are far from the surface from which the insect licks food with its short haustellum. It is possible that these contact (gustatory) chemoreceptors evaluate the nature of the food before eating. The use of these sensilla in other behavioral acts, for example, in mating, cannot be ruled out. Special experiments are needed to further study the functions of the sensilla.

The data obtained show that, despite the difference in the functions of the antennae and palps, their sensory surfaces have common features: a number of similar types of sensilla, similar principles of distribution of sensilla, including sensory fields, although they are formed by different types of receptors. Comparing the organization of sensory surfaces in different species of the large genus *Rhyacophila*, one should note the uniformity of the general structure with slight variations in certain species. Thus, the sensory structures of the mouthpart appendages demonstrate stability and structural unity within an extensive and diverse genus. Structural features of the sensory surface of the Rhyacophilidae palps can probably be used as a starting point for the reconstruction of the ground plan of the order of caddisflies in the course of further study of related families.

Compliance with ethical standards

CONFLICTS OF INTEREST: The authors declare that they have no conflicts of interest.

Acknowledgements. The authors express their gratitude to Prof. N.Yu. Kluge for help in photographing the palps. The work was carried out within the framework of projects No. 112-28656 and No. 109-24431 of the Resource Centers of St. Petersburg State University “Development of Molecular and Cell Technologies” and “Resource Center for Microscopy and Microanalysis”. The study was financially supported by the Russian Science Foundation (project No. 22-24-00259).

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Responsible editor E.N. Temereva