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Research Article

Sensory structures on mouthpart palps in Trichoptera: ground plan and basal evolution trends*

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Abstract

Comparative study of sensory structures on maxillary and labial palps in 71 species from 14 families by scanning electron microscopy and light microscopy revealed significant diversity of sensory structures. Seven principal types of sensory structures were found: pointed trichoid, blunt chaetoid, campaniform, thin basiconic, thick basiconic, petaloid, and pseudoplacoid sensilla. Pointed trichoid and blunt chaetoid sensilla occur on every palp segment. First and, especially, second segments of maxillary palps have bunches of very large blunt chaetoid sensilla on medial surfaces. Campaniform sensilla were found only on basal segments. Pseudoplacoid sensilla are common on the terminal segments of both labial and maxillary palps except for Ptilocolepidae and Hydroptilidae. The petaloid sensilla forming the sensory fields are found in groups surrounded by the soft cuticle, generally in depressions, on the apical segments either on maxillary and labial palps in Hydrobiosidae and Rhyacophilidae, only on labial palps in other studied Integripalpia, or on apical labial palp segment and third and fourth maxillary palp segments in Annulipalpia. The pointed tips of both maxillary and labial palps in lower families have apical sensory complexes looking like small conical outgrowths without microtrichia, each with one large thick basiconic sensilla on its tip and several shorter thick basiconic sensilla on lateral surfaces. We consider these seven types of sensilla along with the apical sensory complex and the assemblage of the petaloid sensilla as a part of Trichoptera ground plan. This primitive diversity changes in evolution so the apical sensory complex, the fields of petaloid sensilla, the groups of very long blunt trichoid sensilla of basal segments, and the pseudoplacoid sensilla disappear in some advanced instances, more often on the maxillary palps. Interspecific variations of sensilla might be important for species discrimination, while the distribution of certain sensory structures is important for higher taxonomy.

Key Words

apical sensory complex, labial palp, maxillary palp, sensilla, sensory field, Trichoptera

Introduction

Structure of the mouthpart appendages of adult caddisflies plays a special role in the taxonomy of this order. Presence of sexual dimorphism in the structure of the maxillary palps was used in the first subdivision of the order Trichoptera into suborders (Kolenati 1851, 1859). Further transformations of the system of this order (Martynov 1924, 1934; Weaver 1984) continued to use the structure of the mouthpart palps, among other features, to divide the order Trichoptera into suborders. These characters were associated primarily with the number of palp segments, the degree of annulation, the presence of pits, and the development of a terminal point on the last segment of the maxillary or labial palp. The obvious function of the palps is sensory. Martynov (1934) suggested these functions for both the pits and the acute apices of the palps; however, special studies of the palp sensilla have not been conducted until recent decades.

The very first comparative study of sensilla on the surface of the palps of the mouthparts of caddisflies

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(Ljungberg and Hallberg 1992) showed the abundance and diversity of sensilla on the mouth appendages of caddisflies. This study showed the presence of five sensilla types in 23 species from 16 families. Those authors combined several sensilla nomenclatures for description of the sensilla found on palps. Those authors found sensilla chaetica (equal to both the trichoid and the chaetoid sensilla of the present study), sensilla campaniformia (the campaniform sensilla), apical cone complex with larger and smaller pegs (the apical sensory complex with thick basiconic sensilla), wall-pore sensilla (the pseudoplacoid sensilla) and poreless sensilla (the petaloid sensilla) to be present on palps of the studied species. Their terminology is corrected as shown above in the subsequent discussion for better comparison with the structural types used in other sensilla studies (e.g., Valuyskiy et al. 2017, 2020) to provide more stable nomenclature and permit wider comparison.

The scope of this paper is to outline the ground plan of palp sensory structures and provide some insights into their modes of evolution in the phylogenetically basal families of Trichoptera according to the publications combining data on morphology and genomics (Thomas et al. 2020; Holzenthal et al. 2007a, b). Our recent publications (Ivanov et al. 2018, 2023a, b; Abu Diiak et al. 2023a, b, c; Melnitsky et al. 2023; Puyto et al. 2023) provide more information on the subject including extended lists of studied species and thorough descriptions of sensilla morphology and distribution. The analysis includes mostly data on more basal families –Rhyacophilidae, Hydrobiosidae, Glossosomatidae, Ptilocolepidae, Philopotamidae, and Stenopsychidae. The data on the crown families are less complete and used mostly for the tracing the evolution trends.

Material and methods

The palp sensory structures of 71 species from 14 families of caddisflies were studied: Rhyacophilidae (2 genera, 19 species), Glossosomatidae (4 genera, 7 species), Ptilocolepidae (1 genera, 1 species), Hydroptilidae (4 genera, 4 species), Phryganeidae (4 genera, 5 species), Hydrobiosidae (3 genera, 3 species), Philopotamidae (4 genera, 6 species), Stenopsychidae (1 genus, 2 species), Hydropsychidae (8 genera, 11 species), Psychomyiidae (2 genera, 3 species), Ecnomidae (1 genus, 1 species), Polycentropodidae (4 genera, 5 species), Dipseudopsidae (2 genera, 3 species), and Xiphocentronidae (1 genus, 1 species). Representatives of basal Lepidoptera were also studied for comparison: *Micropterix maschukella* Alpheraky, 1876 (Micropterigidae) and *Eriocrania cicatricella* (Zetterstedt, 1839) (Eriocraniidae).

The palp sensilla were studied mainly by scanning electron microscopy (SEM). The palps or heads of the studied specimens were removed, dried, mounted on specimen holders with sticky conductive tape, and covered with 20 nm gold layer in Leica EM SCD500 coater. The photographs were obtained with Tescan MIRA3, Hitachi TM3000, and FEI Quanta 200 3D scanning electron microscopes. All equipment was provided by the Resource Centers of St. Petersburg State University: “Development of Molecular and Cellular Technologies” and “Resource Center for Microscopy and Microanalysis.” Counting and measurements of the sensilla on the photographs were made with the freely distributed ImageJ 1.52r program (ImageJ, 2023). The light microscopy was made with a Leica DM 1000 microscope using a Leica EC3 camera and additional microphotographs were obtained with a Nicon D5300 camera with Tamron SP 90 macro lens. More information on the methods and material can be found in our publications cited above.

Results

Maxillary palps of all examined caddisflies are longer than labial palps. Primitive Lepidoptera have also the same palp proportions as in the Trichoptera, although in more advanced families of this latter order the maxillary palps are known to be highly reduced and labial palps developed. The first and second segments of five-segmented maxillary palps in most studied families are the shortest and usually equal in length, with the first segment cylindrical and the second more nearly globular (Fig. 1A). In a few instances, e.g., in Hydrobiosidae and Philopotamidae the second segment is up to 3 times longer than the first one and has a cylindrical shape. Third, fourth, and fifth segments of maxillary palps are elongate and cylindrical. In most examined species, the third and fifth segments in the suborder Integripalpia are almost equal in length, whereas the fifth segment in the suborder Annulipalpia is more than 2 times longer than the third segment. The fourth segment is usually 1.5–3.0 times shorter than the third and fifth except for a few species of Hydrobiosidae, Hydroptilidae, Ptilocolepidae, and Rhyacophilidae. The labial palps always have 3 segments with the shorter first and second segments approximately equal in length and the last one repeating the elongation of that of the maxillary palp.

We have observed seven types of sensilla on the maxillary and labial palps of studied species described below. Besides the sensilla, the mouthpart palps and other body parts are covered by long easily detachable hair-like scales very similar to the long trichoid sensilla except that they have no haemolymph-filled internal lumen and neurons inside. This similarity prevents the discrimination of trichoid sensilla and hair-like scales by their shape. Apparently the scales and the trichoid sensilla have the same structural basis and trichogenous cells are operating in the same way forming the cuticular outgrowths. We consider these trichoid structures as sensilla until it would be proven otherwise; we also consider moth scales as structural serial homologs of long trichoid sensilla.

Long trichoid sensilla (*lts*: Figs 1, 2A, 3A) and trichoid scales similar to them are randomly (non-specifically) distributed over all segments of maxillary and labial palps of all specimens examined, usually on the dorsal surfaces. All studied caddisflies possess one subtype of this sensilla

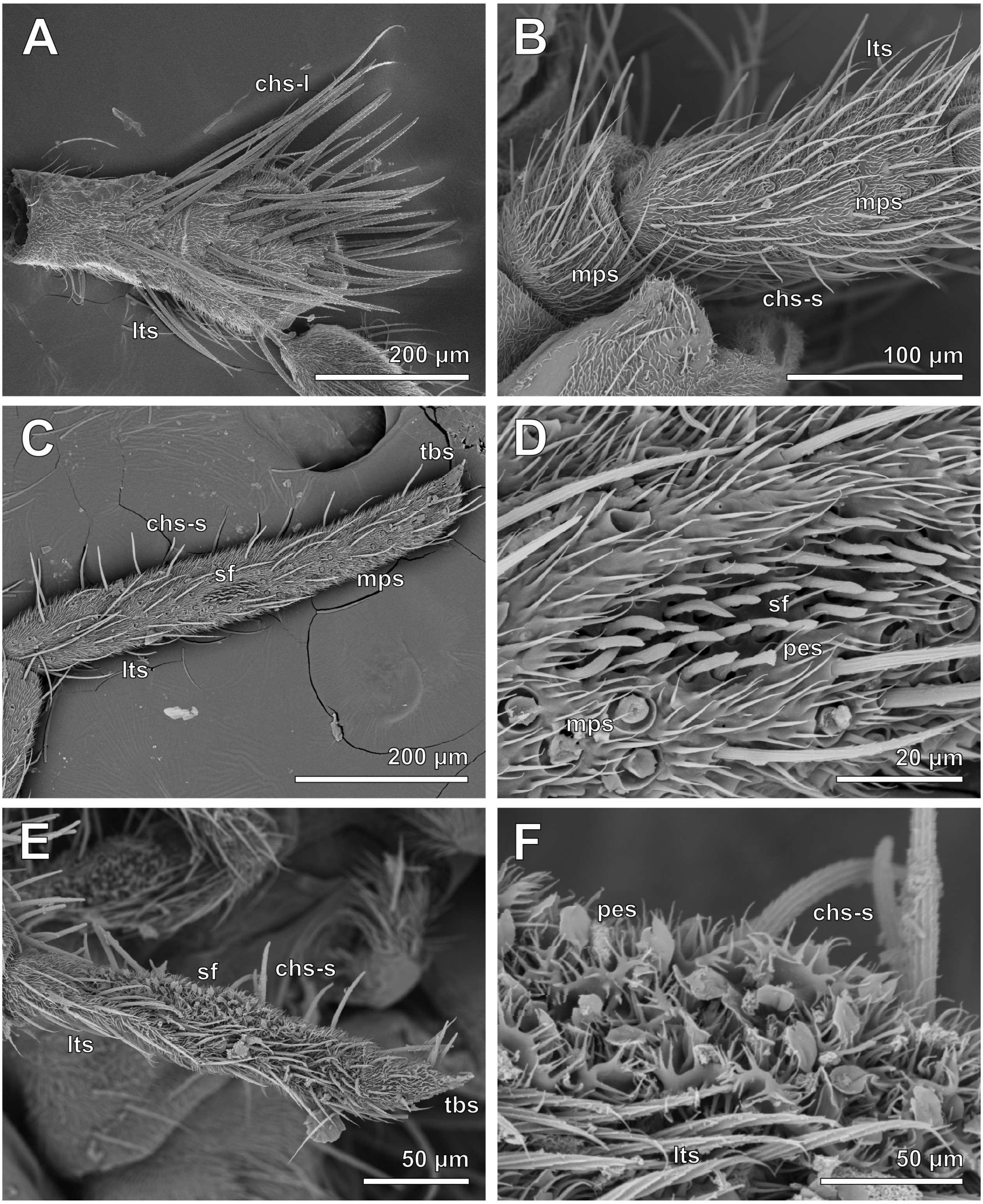

Figure 1. Palp segments of basal Trichoptera and their features. **A.** First and second segments of a maxillary palp of *Rhyacophila munda* male; **B.** First and second segments of a maxillary palp of *Dolophilodes ornata* female; **C.** Fifth segment of a maxillary palp of *Rhyacophila nubila* male; **D.** The same, sensory field of petaloid sensilla; **E.** Third segment of labial palp of *Dolophilodes ornata* female; **F.** The same, sensory field of petaloid sensilla. Abbreviations: chs-l = long blunt chaetoid sensilla; chs-s = short blunt chaetoid sensilla; lts = pointed long trichoid sensilla; mps = mushroom-like pseudoplacoid sensilla; pes = petaloid sensilla; sf = sensory field; tbs = thick basiconic sensilla.

type, the pointed trichoid sensilla. They have flattened elongate shape, acute tips, and longitudinal ridges with dorsal serration. ***Blunt chaetoid sensilla*** (*chs*: Figs 1, 2A, B, 3C, D) were found on all segments of both pairs of palps in all studied species. These sensilla are hair-shaped, each with a round cross section, longitudinal striations, and a blunt tip. Palps of Trichoptera have two subtypes of these sensilla, long and short. Long and sclerotized blunt chaetoid sensilla with rounded or bean-shaped sockets occur in dense groups on medial surfaces of first and second segments of maxillary palps of more basal families like Rhyacophilidae, Glossosomatidae, most Hydroptilidae and Philopotamidae (Figs 1A, 2B). They are upright and, if touched, can incline toward the surface of a segment directed by their socket walls. Sensilla of this type do not form such groups in Hydrobiosidae, *P. adelungi* (Glossosomatidae) and *A. sexmaculata* (Hydroptilidae). More advanced species of the higher Annulipalpia and of the genus *Chimarra* (Philopotamidae) have these sensilla only on distal parts of second segments of maxillary palps.

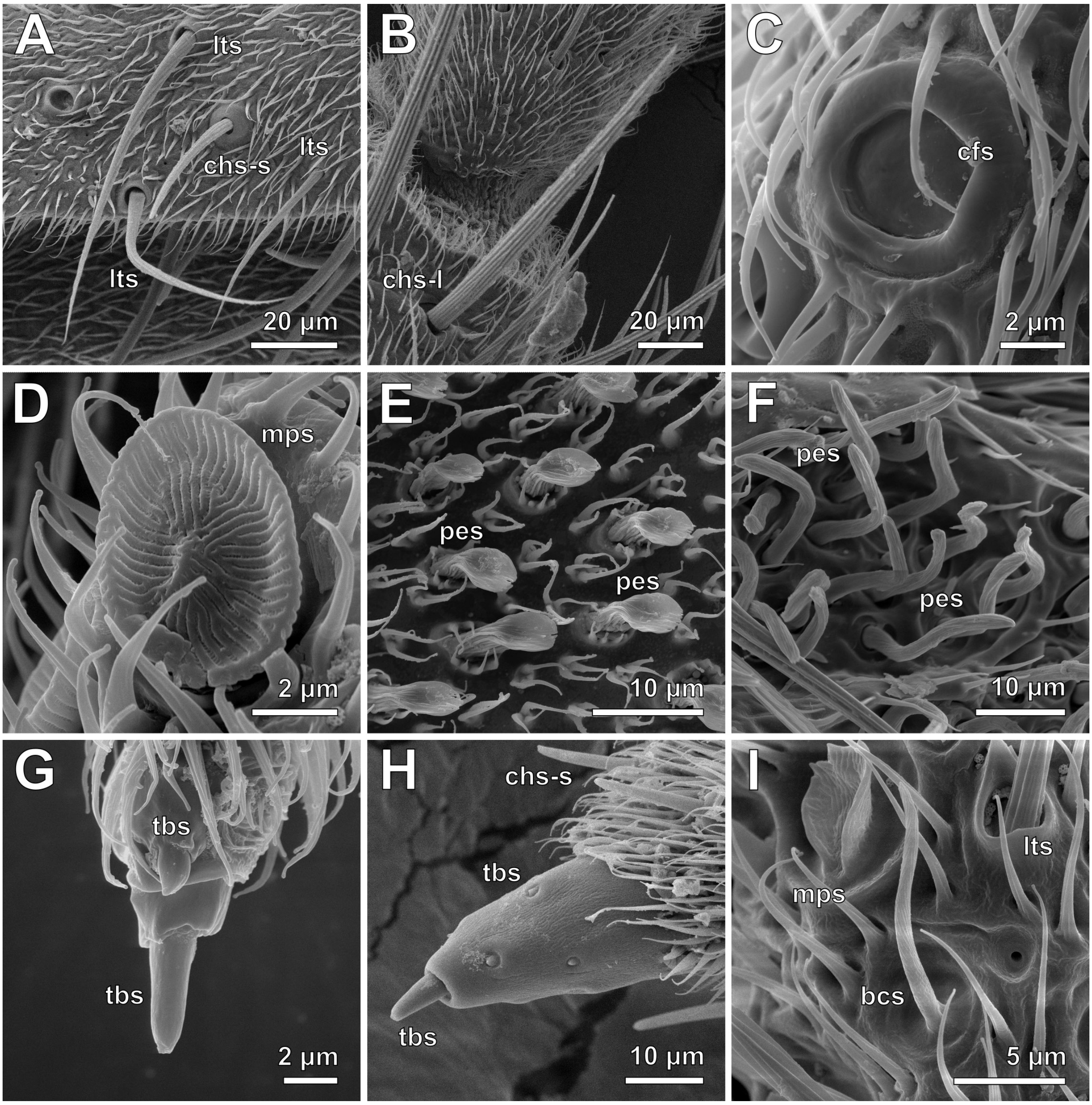

Figure 2. Sensilla types on the palps of Trichoptera. **A.** Long trichoid and chaetoid sensilla on the third segment of a maxillary palp of a *Rhyacophila fasciata aliena* female; **B.** Long chaetoid sensillum on the second segment of a maxillary palp of a *Rhyacophila fasciata aliena* male; **C.** Campaniform sensillum on the first segment of a labial palp of a *Chimarra marginata* male; **D.** mushroom-like pseudoplacoid sensillum on the fourth segment of a maxillary palp of a *Chimarra thienemanni* male; **E.** Flattened petaloid sensilla on the third segment of a labial palp of a *Oligotricha lapponica* male; **F.** Curved petaloid sensilla on the third segment of a maxillary palp of a *Oligotricha lapponica* male; **G.** Apical sensory complex of a maxillary palp of a *Dolophilodes ornata* male; **H.** Apical sensory complex of a maxillary palp of a *Rhyacophila nubila* female; **I.** Thin basiconic sensillum on the fifth segment of a maxillary palp of a *G. altaicum* male. Abbreviations: bcs = thin basiconic sensilla; cfs = campaniform sensilla; chs-l = long blunt chaetoid sensilla; chs-s = short blunt chaetoid sensilla; lts = pointed long trichoid sensilla; mps = mushroom-like pseudoplacoid sensilla; pes = petaloid sensilla; sf = sensory field; tbs = thick basiconic sensilla.

Short and weakly sclerotized blunt chaetoid sensilla (Fig. 2A) are present on all segments of maxillary and labial palps. The highest density of these thin chaetoid sensilla is observed on medial and ventral surfaces of third–fifth segments of maxillary and labial palp segments. In a number of instances these sensilla make parallel lines on ventral surfaces of palp segments. In these instances the chaetoid sensilla are easily distinguishable from the trichoid sensilla by their orientation. The trichoid sensilla are directed to the apices of the palp, and the chaetoid ones are either in upright position or directed slightly toward the base of the palp. ***Campaniform sensilla*** (*cfs*: Fig. 2C) each have a small (2.5 to 5 µm) thin flat or dome-shaped cuticular area surrounded by an elevated cuticular ring. They occur sporadically on the 1st segment of labial palps and the 2nd segment of maxillary palps (singly or in groups of up to 5 sensilla). Sometimes solitary campaniform sensilla can be found on other segments. ***Mushroom-like pseudoplacoid sensilla*** (*mps*: Figs 1D, 2D, I, 3C) occur widely among more basal families like Philopotamidae, Rhyacophilidae, Glossosomatidae, as well as in some more advanced families like Phryganeidae, on both maxillary and labial palps, with a tendency to be more numerous on dorsal surfaces. They have a thick and short, unmovable stem originating in their socket cavity and ending in a rounded or flattened and wider apical part forming a cap as in a mushroom, with pore-bearing grooves on the cap. These sensilla in the family Phryganeidae have modified caps as 2 horn-like projections and are called bilobed sensilla. These sensilla are slightly elongate distally in a few species of Philopotamidae and in most Glossosomatidae except some *Agapetus* and *Synagapetus* species (Fig. 2I). Mushroom-like pseudoplacoid sensilla are most abundant and non-specifically distributed over all palp segments in Philopotamidae. The Glossosomatidae species have these sensilla on third–fifth segments of maxillary palps in the majority of studied species of *Glossosoma*, although the advanced genera have reduced numbers of these sensilla either on each fifth

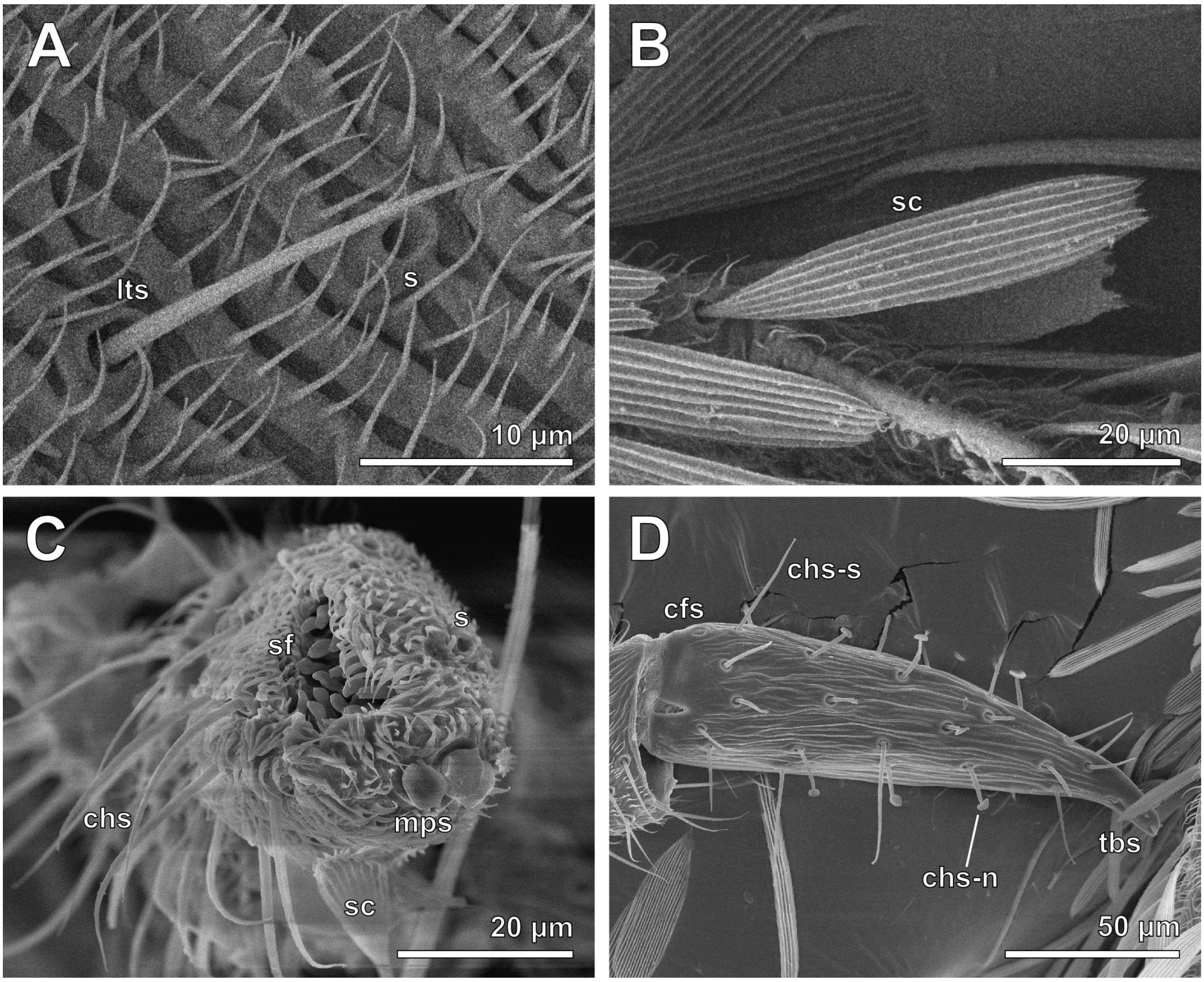

Figure 3. Palp sensory surface of basal Lepidoptera. **A.** Pointed long trichoid sensillum on the fourth segment of a maxillary palp of a *Micropterix maschukella* female; **B.** Scale on the fourth segment of a maxillary palp of a *Eriocrania cicatricella* male; **C.** Apical part of the third labial palp segment of a *M. maschukella* male; **D.** Fifth maxillary palp segment of a *M. maschukella* female. Abbreviations: cfs = campaniform sensilla; chs-s = short blunt chaetoid sensilla; chs-n = nail-shaped chaetoid sensilla; lts = pointed long trichoid sensilla; mps = mushroom-like pseudoplacoid sensilla; s = empty socket of pointed long trichoid sensilla; sc = scales; sf = sensory field; tbs = thick basiconic sensilla.

maxillary palp segment (*Padunia adelungi*, *Agapetus sindis*, *Agapetus fuscipes* and *Synagapetus oblongatus*), or on third segments of labial palps (*P. adelungi* and *G. altaica*). The abundance of these sensilla in the Rhyacophilidae varies from species to species, and in one species, *Rh. angulata*, they cover the entire palp surface as in Philopotamidae. ***Petaloid sensilla*** (*pes*: Figs 1C–F, 2E, F, 3C) were found in all studied species except *Padunia adelungi*, *Agapetus sindis* (Glossosomatidae), *Wormaldia khourmai*, and *Chimarra marginata* (Philopotamidae), visible as finger-like or flag-like structures without individual sockets placed in soft-bottom cavities with their tips protruding above the surface of the palp segment. There are two subtypes of these sensilla: flattened petaloid sensilla (Fig. 2E) and curved petaloid sensilla (Fig. 2F). Most studied species, except Rhyacophilidae, Hydrobiosidae, and the genus *Chimarra* (Philopotamidae), possess flattened petaloid sensilla. The latter have a wide flat apical plate attached almost at a right angle to a slender stem. Curved petaloid sensilla were noted for Rhyacophilidae, Hydrobiosidae, and species of the genus *Chimarra*. These are elongate, curved, and pointed structures with slight spiral grooves. ***Thick basiconic sensilla*** (*tbs*: Figs 1C, E, 2G, H, 3D) were found to occur on smooth surfaces, devoid of microtrichia outgrowths of tips of maxillary and labial palps (apical sensory complexes). These sensilla are small, dome- or cone-shaped poreless structures, each surrounded by a circular groove. The terminal sensillum of the apical sensory complex is usually longer and thicker than others and in a few instances with fine longitudinal grooves (e.g., in *Rhyacophila impar*, *Glossosoma unguiculatum*, *G. altaicum*, and *Ptilocolepus colchicus*). Sensilla of this type are present in the less advanced families like Rhyacophilidae, Hydrobiosidae, Glossosomatidae, Ptilocolepidae, Philopotamidae, and Stenopsychidae. ***Thin basiconic sensilla*** (*bcs*: Fig. 2I) are short (6–12 µm) and slender peg-like structures with slight spiral striation and bases fused with surrounding cuticle found only on fourth and fifth segments of maxillary palps in *G. altaicum*.

Specific areas on palps covered exclusively with petaloid sensilla are recognized as sensory fields (Figs 1C–F, 3C). These structures are mostly oval-shaped or strip-shaped, although some species have extremely long and wide sensory fields spreading across half of the segmental surface as on labial palps of *Agraylea sexmaculata*. The position of these fields on the segment is very variable within the studied families: they may occur ventrally in Glossosomatidae, Hydroptilidae, Ptilocolepidae, some Philopotamidae like *Dolophilodes ornata* and *Philopotamus montanus*, medially in *Ch. thienemanni* and *S. marmorata*, laterally in *Ch. okuihorum*, and dorsally in Rhyacophilidae and Hydrobiosidae. Numbers of the petaloid sensilla in each field vary within the family and even the genus. Counting of these sensilla on the labial palps shows the same great variations. The sensory fields are present in most studied species of the lower Trichoptera families except for labial palps of *Padunia adelungi*, *Agapetus sindis*, *Ulmerochorema stigma*, *Wormaldia khourmai*, *Chimarra marginata*, and *Ch. okuihorum*, and maxillary palps in *Rhyacophila impar*, *Rh. Munda*, *Himalopsyche acharai*, *U. stigma*, *Taschorema apobamum*, *Chimarra thienemanni*, and *Ch. okuihorum*.

The maxillary and labial palps in the lower families also have the apical sensory complexes looking like slightly elongate outgrowths with smooth surfaces lacking microtrichia and provided with thick basiconic sensilla (Figs 1C, E, 2G, H). Typically, the larger apical thick basiconic sensillum exceeds 3 µm; 2–5 lateral sensilla are shorter, less than 2 µm in length. Two species, *P. colchicus* and *T. apobamum*, have larger lateral sensilla compatible with the apical one.

The mouthpart palps in lower Lepidoptera (Fig. 3) are found to have the same number of segments as in Trichoptera and are similar in structure. They have sensilla of the same types as in Trichoptera. Both pairs of palps of Lepidoptera are covered with scales replacing most long trichoid sensilla (Fig. 3B), but a small number of long trichoid sensilla is still present on their palps (Fig. 3B). A unique subtype of chaetoid sensilla, nail-shaped, was found on the fifth segment of maxillary palps in *Micropterix maschukella*. This subtype is characterized by small rounded plates attached to their tips (Fig. 3D). Sensory fields observed in Lepidoptera are visible as depressions on the third segment of labial palps provided with 15–20 petaloid sensilla nested inside the depression (Fig. 3C). These depressions each have a subapical morphologically dorsal position. Two studied species of Lepidoptera have apical sensory complexes of thick basiconic sensilla on fifth segments of maxillary palps. This complex in Micropterigidae has the same pattern of sensilla with larger terminal and smaller lateral basiconic sensilla as in the majority of Trichoptera (Fig. 3D); in contrast, the apical sensory complex in Eriocraniidae has 4–5 almost-equal apical sensilla. The 5th maxillary palp segments in Micropterigidae and Eriocraniidae have a smooth transition to these complexes recognizable only by a peculiar smooth or ribbed cuticle, whereas in Trichoptera the apical sensory complex is apparently narrower than the rest of the segment with an apparent step at the base of the complex. The labial palps of Lepidoptera have their sensory pits in a subapical position; we consider them as homologs of the sensory fields of petaloid sensilla on the labial palps of Trichoptera, so the straight poreless basiconic sensilla in Lepidoptera are presumably the homologs of the petaloid sensilla.

Discussion

The set of palp sensilla characterized by six main types is uniform throughout the families of the lower Trichoptera and is similar to structures of the lower Lepidoptera. We consider these principal types of sensilla as a part of the ground plan for Trichoptera and, probably, also as a part of the Amphiesmenoptera ground plan. All these types and subtypes are universal in Trichoptera palps, widespread, and indicate the similarity of palp functions in different species. We also suppose the palp segment structure found in modern Rhyacophilidae and Glossosomatidae is similar to that of the Trichoptera ancestor. The palp segment proportions are similar in Trichoptera and Lepidoptera, so they can be taken as a ground plan feature for both orders.

A few subtypes should be noted for certain sensilla types. The 2 subtypes described above for the blunt chaetoid sensilla are unlike in size and sclerotization: the long dark chaetoid sensilla and the short, light, thin-walled sensilla, are readily distinguishable in a given specimen, but sometimes are difficult to discriminate in a series of species with different insect size and cuticle thickness. Thus, we don’t give here any quantitative differences of these subtypes applicable to all Trichoptera species. Similarly, the subtypes of petaloid sensilla, curved and flattened petaloid, have some transitions from one type to another in the shape changes from a small almost straight upright sharp-pointed peg to a peg with prominent s-shaped curvature and, finally, to the curved sensilla with flattened plate- or flag-like terminal area. We consider simpler curved sensilla as more primitive and flattened as an advanced subtype. This hypothesis is supported by occurrence of the curved subtype in the least advanced families Rhyacophilidae, Hydrobiosidae, and Philopotamidae.

The palp sensilla have some similarity to the sensilla on the antennae. The antennal sensilla were studied in a series of publications (Ivanov and Melnitsky 2011, 2016; Valuyskiy et al. 2017, 2020; Melnitsky et al. 2018). Comparisons of palp sensilla with sensilla on the antennae of the same species show a reduced and altered variety of sensilla on palps. For instance, the antenna of Rhyacophilidae species have several subtypes of pseudoplacoid sensilla (Valuyskiy et al. 2017), including mushroom-like, bilobed, and leaf-like sensilla, but the occurrence of multiple subtypes of pseudoplacoid sensilla was never found on palps (Abu Diiak et al. 2023a, b). The most widespread subtype of the pseudoplacoid sensilla on antennae, mushroom-like ones, is the only variety found on palps. This similarity of palp and antennal sensory surfaces suggests the mushroom-like pseudoplacoid sensilla as the most primitive and most universal structure, providing the starting point for the more advanced subtypes of pseudoplacoid sensilla. Another character stressing the simplicity of the palp sensory surface is the absence of the thin curved trichoid sensilla and Böhm’s bristles persisting on the antennae and lacking on palps.

The notable feature of the palp sensilla is their larger abundance towards the apical segments of the palps. We have poor statistic data on this subject so far because of the apparent limitation of the SEM method with respect to the quantity of specimens, but the counting on photographs suggests the least number of sensilla on the first segment of a palp. Similarly, the second segments are smaller and those of maxillary palps are covered by larger chaetoid sensilla leaving small space for the other types. The thinner pale chaetoid sensilla on the ventral surface positioned almost at right angles are more abundant at the terminal segments, especially on the ventral surface of the fifth maxillary segment in Annulipalpia. The presence of pseudoplacoid sensilla on terminal segments of the palps increases this disparity. In contrast, the antennal sensilla have a strong tendency to decrease in numbers towards the antennal apex (Valuyskiy et al. 2017, 2020).

Martynov (1924, 1934) suggested that the presence of pits with sensilla on palps is a characteristic feature of higher Integripalpia families. Our studies showed the pits to occur in all studied families including Annulipalpia. The pits are soft depressions, the sensory fields described above, with thin cuticle covered with the petaloid sensilla. These fields are smaller in lower families including the basal Philopotamidae and Stenopsychidae, where the developing annulation of terminal segments move them to the more proximal segments of palps. The advanced Integripalpia, especially Plenitentoria, have larger sensory fields. The desiccation of pinned specimens makes the cavities of fine cuticle deeper and larger, so the sensory fields appear visible at lower magnifications of optical microscope.

The types, numbers, and distribution patterns of sensilla in basal families are similar, therefore these parameters are mostly uninformative for diagnosis or phylogeny on the family level. Some characters might be useful, for example, the large number of pseudoplacoid sensilla on segments of palps in the Philopotamidae species is specific for this family. The family Stenopsychidae of the same superfamily Philopotamoidea lack these sensilla, so the exceptional proliferation of the pseudoplacoid sensilla seems to be a Philopotamidae autapomorphy. Other lower families like Rhyacophilidae can have numerous pseudoplacoid sensilla but, as a rule, only on the terminal segments of maxillary palps.

Pairwise comparison of related families suggests using palp sensilla for discrimination of families in taxonomic revisions and even in keys. The absence of pseudoplacoid sensilla in Stenopsychidae in contrast to the presumably related Philopotamidae is discussed above. The phylogenetically related families Rhyacophilidae and Hydrobiosidae are significantly different in the complete absence of pseudoplacoid sensilla on the palps of the latter. The family Ptilocolepidae, unlike its close relative Hydroptilidae, has typical trichoid sensilla while hydroptilids have modified heavy serration of the entire dorsal surface of the trichoid sensilla; hence, the serrated sensilla surface might appear to be an apomorph character of the latter family after examination of more material.

Comparison of sensilla patterns in the studied Trichoptera families suggests a hypothetical ground plan of the mouthpart palp sensilla. The mouthpart sensory structures initially comprise six types of sensilla: long trichoid, blunt chaetoid, campaniform, mushroom-like pseudoplacoid, petaloid, and thick basiconic sensilla. The two basal segments of the maxillary palps covered by a mixture of the trichoid and blunt chaetoid sensilla seem to be shorter than the rest of segments in the Trichoptera ancestor. The trichoid sensilla were more abundant dorsally on palps with their tips pointing to the palp tip, whereas the chaetoid sensilla were frequent on ventromedial surfaces in upright position. A few campaniform sensilla were developed on the basal segments. Some numbers of pseudoplacoid sensilla might be present on all segments, their number increased on the distal part of the maxillary palp. The chaetoid sensilla at the anterior edge of the first segment and on the ventromedial surface of the second segment were large and strong, others were smaller and softer. The terminal fifth segment had no annulation, and a well-developed apical sensory complex at its apex. The petaloid sensilla formed a sensory subapical field on the dorsolateral surface of the fifth maxillary segment. The apical sensory complex was probably shifted to a ventral position relative to the segment longitudinal axis. The ground plan of the three-segmented labial palp structure and sensilla distribution should be similar to those of the maxillary palp, without long basal chaetoid sensilla. Petaloid sensilla on the labial palps formed a sensory field on the dorsal surface of the third segment. The apical sensory complex has the same size and structure as on the maxillary palps. This hypothesis of the ancestral sensilla pattern includes also elements of the ground plan of Amphiesmenoptera, the common ancestor of the Trichoptera and Lepidoptera orders.

The major tendencies in the evolution of palp sensory surfaces in basal Trichoptera families can be outlined as shortening of the thick ventromedial chaetoid sensilla on second segments of maxillary palps (Fig. 4A), disappearance of the pseudoplacoid sensilla (Fig. 4B), reduction of petaloid sensilla mainly on the maxillary palps (Fig. 5A), and reduction and subsequent loss of the apical sensory complexes (Fig. 5B). These changes occur as parallel processes in non-related families of the two major phylogenetic branches, Integripalpia and Annulipalpia. We consider these transformations as a gradual modification of the ancestral sensilla pattern to serve new palp functions.

The apical sensory complexes decrease in size and sensilla numbers in both Annulipalpia families Philopotamidae and Stenopsychidae. They are absent in the rest of Annulipalpia (Fig. 5B). One of the most basal Integripalpia family, Rhyacophilidae, and the family Ptilocolepidae have these complexes in all studied species (Abu Diiak et al. 2023a, b). More advanced Integripalpia families show persistence of the apical sensory complexes in a few species of Hydrobiosidae and one modern subfamily, Glossosomatinae, of the family Glossosomatidae. The extinct subfamily

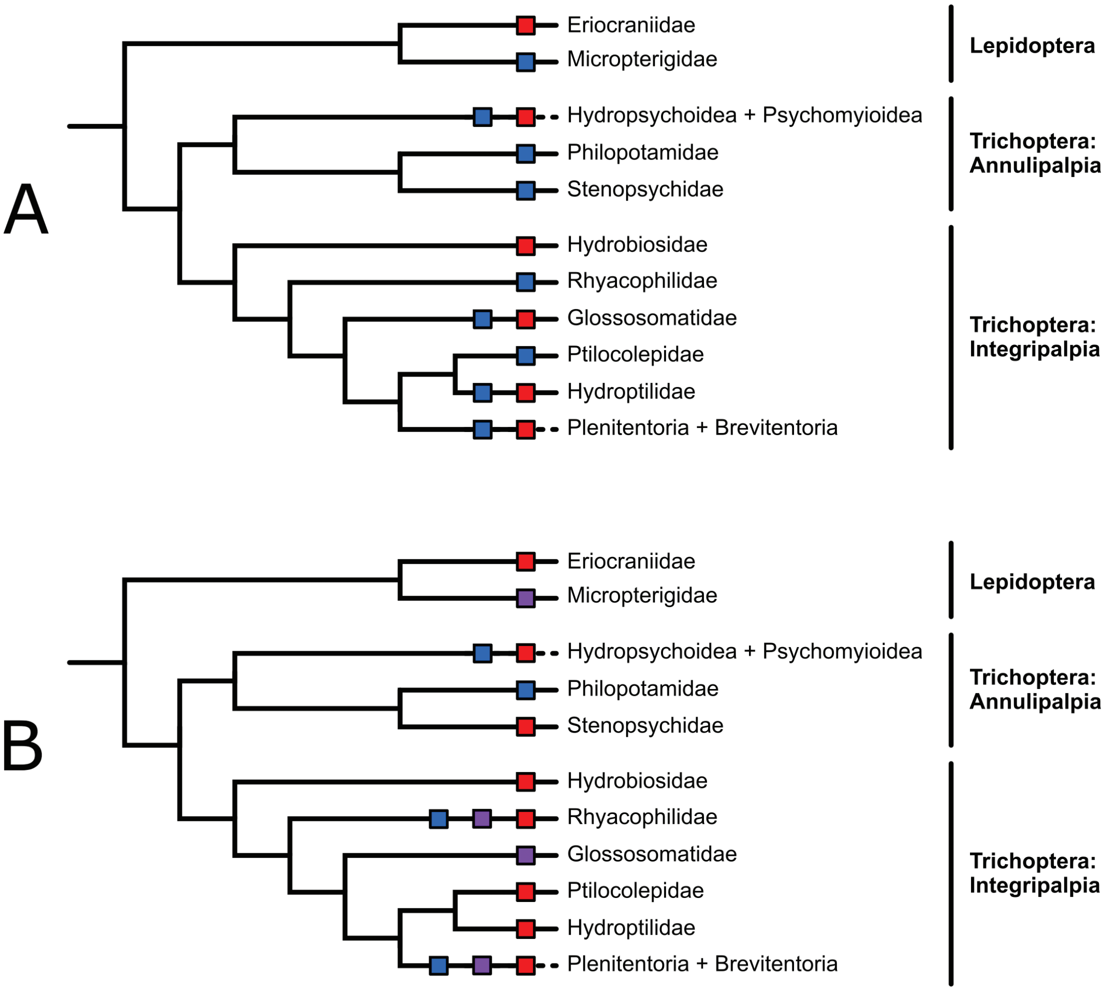

Figure 4. Distribution of palp sensory surface characters within Trichoptera. **A.** Presence (blue) or absence (red) of a group of long chaetoid sensilla on the first and second segments of maxillary palps; **B.** Degree of development of mushroom-like pseudoplacoid sensilla on the palps: on all labial and maxillary palp segments (blue), on distal segments of labial and maxillary palps (purple), or total reduction of pseudoplacoid sensilla (red). The phylogenetic tree is based on the data from Holzenthal et al. 2007a.

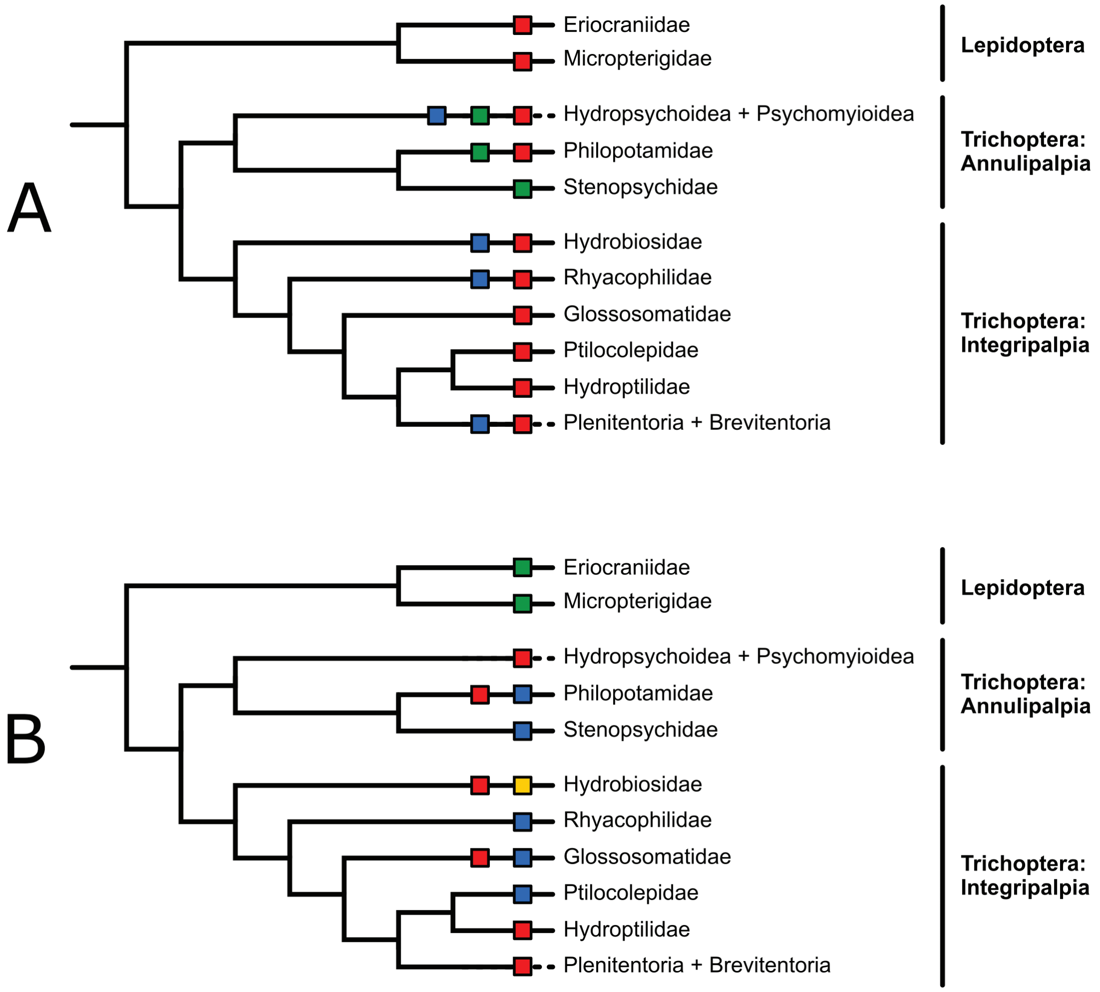

Figure 5. Distribution of palp sensory surface characters within Trichoptera. **A.** Localization of sensory fields on maxillary palp segments: on the fifth segment (blue), on the third and fourth segments (green), total reduction of sensory fields (red); **B.** Degree of development of apical sensory complex on the palps: on both pairs of palps (blue), only on maxillary palps (green), only on labial palps (yellow), total reduction of apical sensory complexes on both pairs of palps (red). The phylogenetic tree is based on the data from Holzenthal et al. 2007a.

Dajellinae of the family Glossosomatidae had the apical sensory complex at least on the maxillary palp (Ivanov and Melnitsky 2006). Two modern subfamilies of Glossosomatidae, Agapetinae and Protoptilinae, lack these complexes. The apical sensory complexes are absent in Hydroptilidae and all more phylogenetically advanced Integripalpia. Hence, the apical sensory complexes of the Trichoptera ancestor lost their significance and disappeared in advanced members of numerous phylogenetic branches, even within the families. In contrast, the petaloid sensilla are persistent on palps of Trichoptera except the advanced Annulipalpia and some Integripalpia (Fig. 5A), and on labial palps of Lepidoptera. They continue to perform their yet unknown functions and in some instances, as in Phryganeidae, are more developed than in basal families.

Conclusions

The results of our comparative investigation of palp sensory surfaces show significant similarity of the sensilla types and distribution patterns in the various families of lower Trichoptera. This similarity suggests that the ground plan for palps includes seven structural types of sensilla. The trends in subsequent evolution of the mouthpart sensilla in the basal Trichoptera families are the reductions of certain sensory structures at the apical and basal parts of palps. A comparison with Lepidoptera suggests the presence of patterns related to the ancestor of Amphiesmenoptera. We anticipate that the sensilla of palps might be useful for the taxonomy of caddisflies. Subsequent studies of Trichoptera sensory structures will uncover patterns of sensilla evolution in those taxa.

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