PALP SENSORY STRUCTURES IN ADULT CADDISFLIES OF THE SUBORDER ANNULIPALPIA (TRICHOPTERA): A SCANNING ELECTRON MICROSCOPY STUDY

V. D. Ivanov[*], K. T. Abu Diiak, S. I. Melnitsky, M. Yu. Valuyskiy

*Department of Entomology, St. Petersburg State University, St. Petersburg, 199034, Russia. *Corresponding author, E-mail: v--ivanov@yandex.ru*

Summary. Sensory structures and their patterns are investigated by scanning electron microscopy in 38 species representing ten families of the suborder Annulipalpia (Trichoptera). Palp sensilla comprise seven types: long trichoid, chaetoid, campaniform, mushroom-like pseudoplacoid, petaloid, thick basiconic, and thin basiconic sensilla. Comparative analysis suggests the presence of family-specific patterns of the palp sensory surfaces. Palp sensilla and their sensory patterns persist in the instances of partial palp reduction. Considerations on the evolution trends, functionality, and taxonomic importance of palp sensory structures are provided.

Key words: Trichoptera, reception, morphology, sensilla, mouthparts, palps, evolution.

1

Резюме. Методом сканирующей электронной микроскопии исследованы сенсорные структуры и закономерности их распределения у 38 видов, представляющих 10 семейств подотряда Annulipalpia (Trichoptera). Сенсиллы щупиков делятся на 7 типов: длинные трихоидные, хетоидные, кампаниформные, грибовидные псевдоплакоидные, лепестковидные, толстые базиконические и тонкие базиконческие сенсиллы. Сравнительный анализ позволяет предположить наличие особенностей сенсорных поверхностей щупиков, специфичных для семейств. Сенсиллы придатков ротового аппарата и закономерности их распределения сохраняются в случаях частичной редукции щупиков. Приведены соображения о тенденциях эволюции, функциональности и таксономической важности сенсорных структур щупиков.

INTRODUCTION

The suborder Annulipalpia is one of the principal phylogenetic branches of caddisflies (Trichoptera). The name of this suborder refers to the elongated and flexible terminal segments of the adult maxillary and labial palps, which often have many tiny rings. Discussing the key characters of the newly erected suborder Annulipalpia, A.V. Martynov (1924) recognized the mouthpart palp structure as a principal character outlined this suborder, although made several reservations including a few families with non-specialized structure of the mouthpart palps. Such families as Rhyacophilidae s. l. with inclusion of Glossosomatidae and Hydrobiosidae, as well as Hydroptilidae s. l. with Ptilocolepidae inside were also members of Annulipalpia in the Martynov's system since they have another palp peculiarity, the large sensory complex looking like a small needle on the tip of the palp. Other important arguments for recognition of the suborder Annulipalpia were larval adaptations as the campodeiform larval body shape and the fixed net- or tube-like retreat structure. The sister suborder, Integripalpia, have neither long flexible annulated terminal segments of the mouthpart palps, nor terminal palp needle, not campodeiform larvae with fixed retreats. Subsequent changes of the major Trichoptera phylogeny (Ross, 1967; Weaver, 1984; Ivanov & Sukatcheva, 2002) retained the family pattern proposed by Martynov (1924, 1934) but narrowed the limits of Annulipalpia devoid of the families with short non-annulated terminal palp segments.

There are three well-defined and distinct evolutionary branches within the suborder Annulipalpia, which are often (e.g., Ivanov & Sukatsheva, 2002; Thomas *et al.*, 2020) considered as superfamilies: Hydropsychoidea, Psychomyioidea, Philopotamoidea. Phylogenetic relationships between these groups continue to be discussed in the literature. A number of authors considered the superfamily Philopotamoidea as the most archaic and contrasted it with two other superfamilies (Ross 1967; Weaver 1984; Frania & Wiggins, 1997). On the other hand, recent studies, including those involving molecular data, set the superfamily Hydropsychoidea aagainst the rest of Annulipalpia (Kjer *et al.*, 2001; Malm *et al.*, 2013; Thomas *et al.*, 2020). It is supposed that the division of all three branches of the annulipalpian caddisflies occurred in the Early Triassic (Thomas *et al.*, 2020); Necrotauliidae, the primitive ancestral family in the Trichoptera phylogenetic branch, existed as early as middle Triassic (Ivanov & Sukatsheva, 2002).

2

We consider here the family Philopotamidae as the most primitive among the annulipalpian Trichoptera with the fossil record extended to Middle Jurassic (Ivanov & Sukatsheva, 2002). The superfamily Hydropsychoidea with the solitary family Hydropsychidae s. l. including Arctopsychidae (Thomas *et al*., 2020) is apparently more advanced and younger, with reliable fossil remnants only in the Cenozoic resins. Its affinities should be clarified on larger datasets. We expect that our data on sensilla might be a step towards better understanding of the Hydropsychidae relationships.

According to the latest molecular data and numerical analysis (Kjer *et al*., 2016; Thomas *et al*., 2020), two evolutionary groups can be distinguished within the superfamily Psychomyioidea. The first group includes families Dipseudopsidae, Psychomyiidae, Xiphocentronidae; the family Hyalopychidae is included into Dipseudopsidae according to the larval structures, although the mouthpart morphology of the type genus, *Hyalopsyche* stresses its peculiar status and indicates deep divergence from the rest of Dipseudopsidae. The second group includes the families Pseudoneureclipsidae, Ecnomidae and Polycentropodidae; Pseudoneureclipsidae shared more resemblance with Ecnomidae on the recent cladograms.

Persistent structure of the terminal palp segments in Annulipalpia became a standard character for the determination keys in textbooks and manuals. Only few exceptions are known for species from families belonging to this phylogenetic branch. The species of genus *Paduniella* (Psychomyiidae) were reported to have no annulation and flexibility of mouthpart palp segments (Martynov, 1934); instead, their maxillary palps have six segments instead of five typical for the Trichoptera. The additional segment seems to be produced by a secondary subdivision of the terminal segment. A few species of the family Hydropsychidae have diminished palps; in this instance, the short palp segments have no annulation and flexibility (Ivanov *et al*., 2023). One more example is the genus *Hyalopsyche* from Hyalopsychidae often recognized as a subfamily within Dipseudopsidae; the terminal segments of the maxillary palps are neither elongated nor flexible, and the labial palps are absent (Martynov, 1934).

Apparent specialization of the long annulated terminal palp segments attracted rather small attention of researchers to fine structure of these segments and probable functional reasons of such adaptation. Frania and Wiggins (1997) discussed the usability of segment annulation as a character in the Trichoptera phylogeny. They have shown that the palp annulation in the species *Arctopsyche grandis* (Hydropsychidae s. l.: Arctopsychinae) does not make regular rings; instead, the flexible structure is produced by numerous sclerotized islands each bearing a bristle, and desclerotized areas between them make a mesh-like pattern so the annulation is imaginary. They also noticed the flexible mouthpart palps of some Leptoceridae (suborder Integripalpia) as possible homoplasia, although the studied species of the latter family had no apparent annulations and the similarity of this family to the Annulipalpia in their character set finally have been rejected. Important information on the fine structure of palps vas published by M. Kubiak and his co-workers (2015) in the recent morphological study of the annulipalpian species, *Philopotamus ludificatus*

McLachlan, 1878 (Philopotamidae). They described overall morphology, sensilla types and patterns of mouthpart palps in this species. The apical sensory complexes of palps were comparatively studied by Ivanov *et al*. (2018). More information was recently published by our team: the paper on the ground plan of the mouthpart sensilla in Trichoptera (Abu Diiak *et al*., 2023a) includes the comparative analysis of palp structures in the most phylogenetically basal Trichoptera families, and the diversity of sensory surfaces in the basal family Rhyacophilidae is considered in other publication (Abu Diiak *et al*., 2023b). One more paper (Ivanov *et al*., 2023) describes the structure and sensilla patterns in the advanced family Hydropsychidae. The sensilla nomenclature is not fully established; we follow the morphological typology used in our recent publications listed above.

The reasons of development of the peculiar adaptation like an elongate, flexible, annulated last segment on both pairs of the mouthpart palps is still unknown. Until recently, the fine structure of palps is studied very fragmentary to provide a solid ground for comparisons. The primary function of palps is the sensory support of feeding and other forms of behavior. Thus, more studies of sensory surfaces are necessary to disclose the significance of palp adaptations. We present in this publication the first thorough comparative morphological assessment of the palp sensory structures of the Annulipalpia based on 14 newly studied species of the previously disregarded superfamily Psychomyiodea and consider other data representing all traditionally recognized Annulipalpia families; totally 38 species are considered. The main goals are to provide the overview of the palp structural diversity within Annulipalpia, to consider the major differences of families in this respect, the principal trends of evolution in the suborder, and the interpretation of the annulipalpian structures from the functional point of view. This study will facilitate future studies of sensilla physiology, taxa relationships, behavioral patterns, and associated topics in relation to caddisflies and will provide reliable data and a starting point for the further comparisons to another phylogenetic branch of Trichoptera, the suborder Integripalpia.

MATERIAL AND METHODS

The material for this study was obtained from the collections of the Department of Entomology of St. Petersburg State University and Zoological Institute of Russian Academy of Sciences. The palp sensory surface was studied in 38 species from 10 families of the suborder Annulipalpia (species with both sexes studied are marked with *): *Philopotamus montanus* (Donovan, 1813); *Dolophilodes ornata* Ulmer, 1909; *Wormaldia khourmai* Schmid, 1959; *Chimarra marginata* (Linnaeus, 1767); *Ch. thienemanni* Ulmer, 1951; *Ch. okuihorum* Mey, 1998 (Philopotamidae); *Stenopsyche marmorata* Navas, 1920 (Stenopsychidae); *Arctopsyche palpata* Martynov, 1934; *Parapsyche apicalis* (Banks, 1908) (Hydropsychidae: Arctopsychinae); *Hydropsyche newae* Kolenati, 1858; *H. pellucidula* (Curtis, 1834); *H. stimulans* Ross, 1938; *H. angustipennis* (Curtis, 1834); *Hydronema persica* Martynov, 1914; *Cheumatopsyche infascia* Martynov, 1934 (Hydropsychidae: Hydropsychinae);

4

Diplectrona robusta Martynov, 1934; *D. dulitensis* Kimmins, 1955; (Hydropsychidae: Diplectroninae); *Smicridea murina* McLachlan, 1871 (Hydropsychidae: Smicrideinae); *Leptonema viridianum* Navas, 1916; *Aethaloptera evanescens* (McLachlan, 1880); *Amphipsyche gratiosa* Navas, 1922; *Macrostemum radiatum* (McLachlan, 1872); *M. midas* Malicky, Chantaramongkol, 1998; *Polymorphanisus nigricornis* Walker, 1952 (females) (Hydropsychidae: Macronematinae); *Neureclipsis bimaculata* (Linnaeus, 1758); *Polycentropus flavomaculatus* (Pictet, 1834); *Plectrocnemia conspersa* (Curtis, 1834); *Cyrnus fennicus* Klingstedt, 1937; *C. flavidus* McLachlan, 1864 (Polycentropodidae); *Psychomyia flavida* Hagen, 1861; *P. pusilla* (Fabricius, 1781); *Lype phaeopa* (Stephens, 1836) (Psychomyiidae); *Ecnomus tenellus* (Rambur, 1842) (Ecnomidae); *Xiphocentron mnesteus* Schmid, 1982 (Xiphocentronidae); *Dipseudopsis indica* McLachlan, 1875; *D. varians* Ulmer, 1929; *Hyalopsyche sachalinica* Martynov, 1910 (Dipseudopsidae); *Pseudoneureclipsis chrysippus* Malicky et Sompong, 2000 (Pseudoneureclipsidae).

The palps were examined by using scanning electron microscopy. In the material stored in ethanol, the removed insect palps were air-dried, mounted on specimen holders using conductive tape and coated with a 20-nm layer of monomolecular gold using a Leica EM SCD500. The dry material from other samples was soaked in a desiccator to prevent damaging the specimens while mounting them on the holders, and then it was treated similarly. Photographs of the sensory surfaces of the palps and sensilla were obtained by scanning electron microscopes Tescan MIRA3, Hitachi TM3000 and FEI Quanta 200 3D. This technique is widely used and was previously applied to study caddisfly antennae (Ivanov & Melnitsky, 2011, 2016; Melnitsky & Ivanov, 2011, 2016; Melnitsky *et al.*, 2018, 2019; Valuyskiy *et al.*, 2017, 2019, 2020; Abu Diiak *et al.*, 2021, 2022). The necessary equipment was provided by the resource centers of St. Petersburg State University "Development of Molecular and Cell Technologies" and "Resource Center of Microscopy and Microanalysis".

Counting and measurements were carried out in series photographs using the ImageJ 1.52a program. The sensilla on the segment surfaces were counted manually by using the "Multi-point tool". Scale calibration was performed using "Set scale" command before all sensilla measurements. The sizes of the sensilla were measured using the "Straight line" or "Segmented line" tools, as well as the "Measure" command. The diameter was measured for mushroom-like pseudoplacoid and campaniform sensilla. The length was measured for all other sensilla types. The ranges of variation in sensilla dimensions are provided for each sensilla type.

RESULTS

General structure of palp segments

Maxillary palps are five-segmented in most species of Annulipalpia (Figs 1–6). First–fourth segments have cylindrical shape. The first segment is the shortest. The second is usually 1.5–3 times longer than the first one. Sometimes first and second segments have approximately equal length (Stenopsychidae, Polycentropodidae,
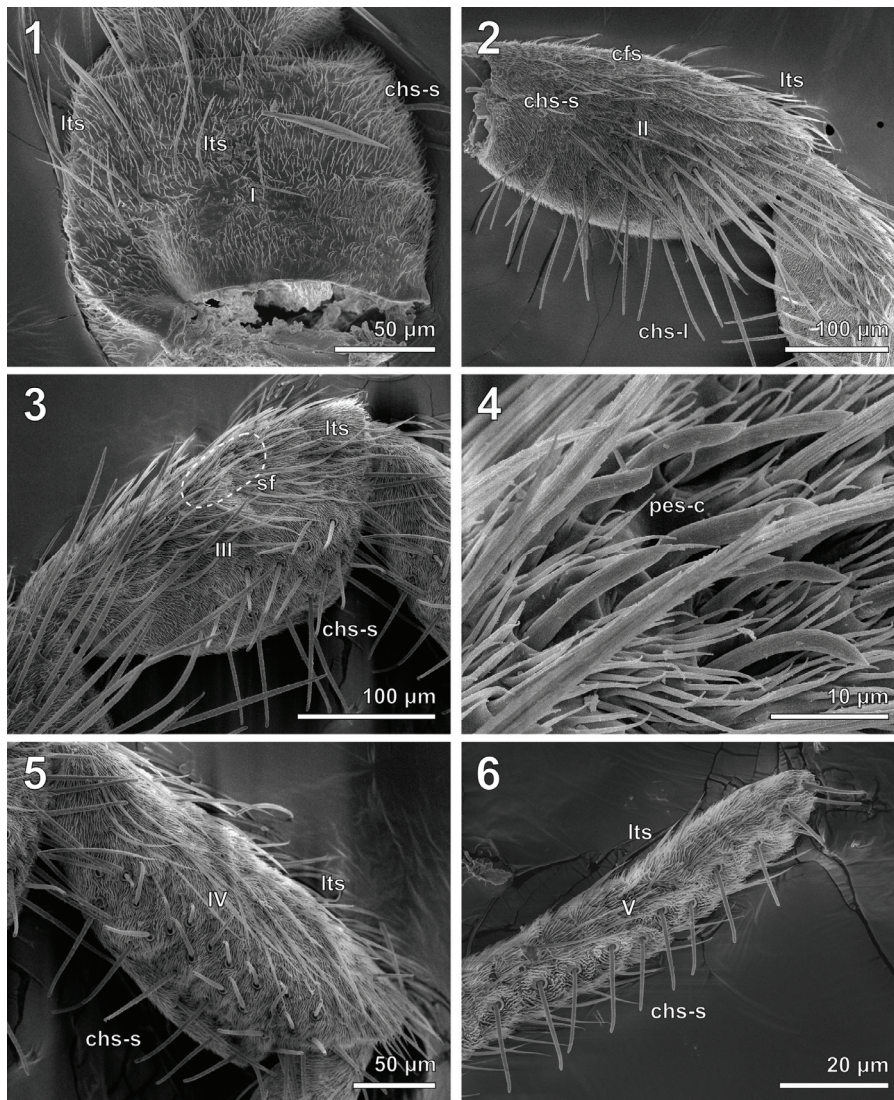
Figs 1–6. Medial (1–5) and ventrolateral (6) surfaces of maxillary palp of *D. robusta* male (Hydropsychidae). 1 – first segment; 2 – second segment; 3 – third segment; 4 – sensory field of petaloid sensilla on the first segment; 5 – fourth segment; 6 – tip of the fifth segment. Abbreviations: cfs – campaniform sensilla; chs-l – long chaetoid sensilla; chs-s – short chaetoid sensilla; lts – long trichoid sensilla; pes-c – curved petaloid sensilla; sf – sensory field. Roman numerals represent segment numbers.

Pseudoneureclipsidae, and *H. sachalinica*). The second segment has a distal out-growth on its medial surface in Polycentropodidae, Dipseudopsidae, and females of *L. phaeopa* (Psychomyiidae). Third segment is usually 1.5–2 times longer than the second. Fourth segment may have the same length as third one (Hydropsychidae, Ecnomidae, *C. fennicus*, *H. sachalinica*, *P. flavida* and *X. mnesteus*) or be 1.5–3 times shorter (other studied species). The fifth segment is usually 2–4 times longer than the fourth one. Sometimes its length exceeds total length of all previous segments (Hydropsychidae, Stenopsychidae and *P. montanus*). Fifth segment of maxillary palps in *H. sachalinica* (Dipseudopsidae) has approximately the same length as the third segment. In some representatives of Hydropsychidae, the maxillary palps are reduced to two shortened segments.

Labial palps consist of three segments (Figs 7–8). First and second segments are usually cylindrical and equal in length. These segments have a narrow proximal part in species of the genus *Dipseudopsis*. The third segment is 1.5–3 times as long as the first or second one. Labial palps are completely absent in *H. sachalinica* (Dipseudopsidae) and some representatives of Hydropsychidae: Macronematinae (*Aethaloptera evanescens* and *Polymorphanisus nigricornis*).
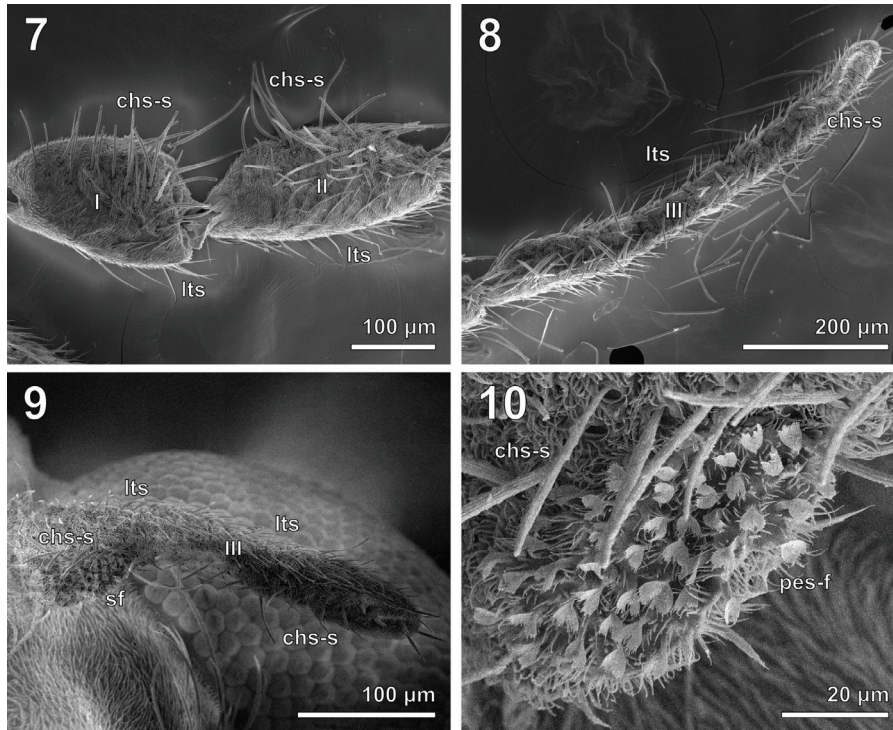
Figs 7–10. Labial palps of *P. apicalis* (7–8) and *N. bimaculata* (9–10) females. 7 – first and second segments; 8, 9 – third segment; 10 – sensory field on the third segment. Abbreviations: chs-s – short chaetoid sensilla; lts – long trichoid sensilla; pes-f – flattened petaloid sensilla; sf – sensory field. Roman numerals represent segment numbers.

The surface of all segments of both pairs of palps except articulations and apical sensory complexes is densely covered with microtrichia – small non-innervated processes (Figs 1–10). Terminal segments of both pairs of palps have numerous transverse and oblique folds that allow them to bend easily (Fig. 6). In one species, *H. sachalinica*, this annulation is completely reduced.

Types of sensilla

Seven types of sensilla were found on the maxillary and labial palps of studied species:

Long trichoid sensilla (Fig. 11, lts) are elongated hair-like structures with longitudinal grooves, pointed tips, serrated ribs, and drop-shaped sockets. In cross section, these structures may be flattened (Hydropsychidae: genera *Hydropsyche*, *Cheumatopsyche* and *Smicridea*; Philopotamidae: *W. khourmai*; Dipseudopsidae: genus *Hyalopsyche*; Ecnomidae; Psychomyiidae; Pseudoneureclipsidae) or rounded (Hydropsychidae, except genera *Hydropsyche*, *Cheumatopsyche* and *Smicridea*; Dipseudopsidae: genus *Dipseudopsis*; Polycentropodidae; Xiphocentronidae; Stenopsychidae; Philopotamidae, except *W. khourmai*). They are always inclined in the distal direction overlaying the narrower part of the socket. Long trichoid sensilla are distributed more or less randomly (non-specifically) over the surface of all maxillary and labial palp segments except for dense assemblages of other sensilla. These structures often drop down leaving the empty sockets. This may indicate the lack of innervation and thus absence of sensory functions in some or most of them. We consider all these structures to have sensory functions until future histological studies provide more data on their internal structure. The size of long trichoid sensilla is highly variable from 25 to 185 µm in different studied species and even on the palps of the same individual.

Chaetoid sensilla (Figs 12–16) are hair-shaped structures with round cross section and longitudinal striation. They have convex sockets setting them almost at a right angle to the segment surface. Chaetoid sensilla were found on all palp segments in all studied species. These sensilla are more numerous on ventral and medial segment surfaces. The length of these sensilla tends to decline on more distal palp segments. Chaetoid sensilla have five subtypes within studied Annulipalpia species.

Short chaetoid sensilla (Fig. 12, chs-s) (15 – 70 µm in length) are the most common subtype of chaetoid sensilla. They were found on all segments of both pairs of palps mainly on medial and ventral surfaces. These are slightly sclerotized structures with blunt tips and hemispherical sockets. Sometimes they have terminal pore.

Long chaetoid sensilla (Fig. 13, chs-l) (95 – 170 µm in length) are strongly sclerotized and thickened subtype found on medial surfaces of the first and second maxillary palp segments. Each sensillum has a bean-shaped socket with raised socket walls allowing the sensillum to move only in one direction, and dome-shaped convex tip.

Truncated chaetoid sensilla (Fig. 14, chs-t) are similar to other subtypes of chaetoid sensilla but they have truncated concave tips, sometimes with a single pore. Their sockets have bean-like shape similar to long chaetoid sensilla. These sensilla are shorter

8

and thicker in Dipseudopsidae and Polycentropodidae. They occur on the second maxillary palp segment like long chaetoid sensilla, partly (*P. flavomaculatus* and genus *Smicridea*) or completely (Dipseudopsidae, Pseudoneureclipsidae), Xiphocentronidae and Polycentropodidae, except *P. flavomaculatus*) replacing them. Sensilla of this subtype were found in representatives of five studied families: Hydropsychidae (genus *Smicridea*), Xiphocentronidae, Pseudoneureclipsidae, Polycentropodidae and Dipseudopsidae. The males of *Dipseudopsis varians* have up to 25 sensilla of this subtype. In Polycentropodidae, aggregations of these sensilla include from 9 (*Neureclipsis bimaculata*) to 18 (*Plectrocnemia conspersa*) sensilla. Size comparison of these sensilla is shown in the Table 1.

Table 1. Size comparison of truncated chaetoid sensilla in Annulipalpia.

Size in µm	*Dipseudopsis varians*	*Dipseudopsis indica*	*Neureclipsis bimaculata*	*Plectrocnemia conspersa*	*Pseudoneureclipsis chrysippus*	*Xiphocentron mnesteus*	*Smicridea murina*
Male	30–36	40–44	69–77	100–111	83–111	116–159	105–112
Female	35–38	n/a	50–57	n/a	n/a	n/a	103–157

Conical chaetoid sensilla (Fig. 15, chs-c) were found only in species of the genus *Macrostemum*. Sensilla of this subtype are thicker (up to 10 µm) and shorter (47–52 µm) comparing to long chaetoid sensilla; their sockets are slightly flattened instead of hemispherical as in other chaetoid sensilla.

Thorn-shaped chaetoid sensilla (Fig. 16, chs-ts) were found on maxillary and labial palps of *Ch. thienemanni*. These are extremely shortened (3-10 µm) chaetoid sensilla with pointed tips and serrated surface forming large groups on medial surfaces of all labial palp segments and 3rd–5th segments of maxillary palps.

Campaniform sensilla (Figs 12, 17, cfs) have a thin cuticular region surrounded by a sclerotized cuticular ringless than 5 µm in diameter. These sensilla are usually located on the first segment of labial palps and the second segment of maxillary palps where they form groups or rows of 3–9 sensilla. Sometimes these sensilla occur solitary on other segments.

Mushroom-like pseudoplacoid sensilla (Fig. 18, mps) have flat or concave rounded caps attached to a short unmovable stem in a shallow socket. The caps of these sensilla are covered with numerous pore-bearing grooves diverging from the center. The diameter of caps of these sensilla varies from 4 to 8 µm. Mushroom-like pseudoplacoid sensilla in Philopotamidae and Psychomyiidae cover almost entire surface of both pairs of palps except for sensory fields of petaloid sensilla, dense
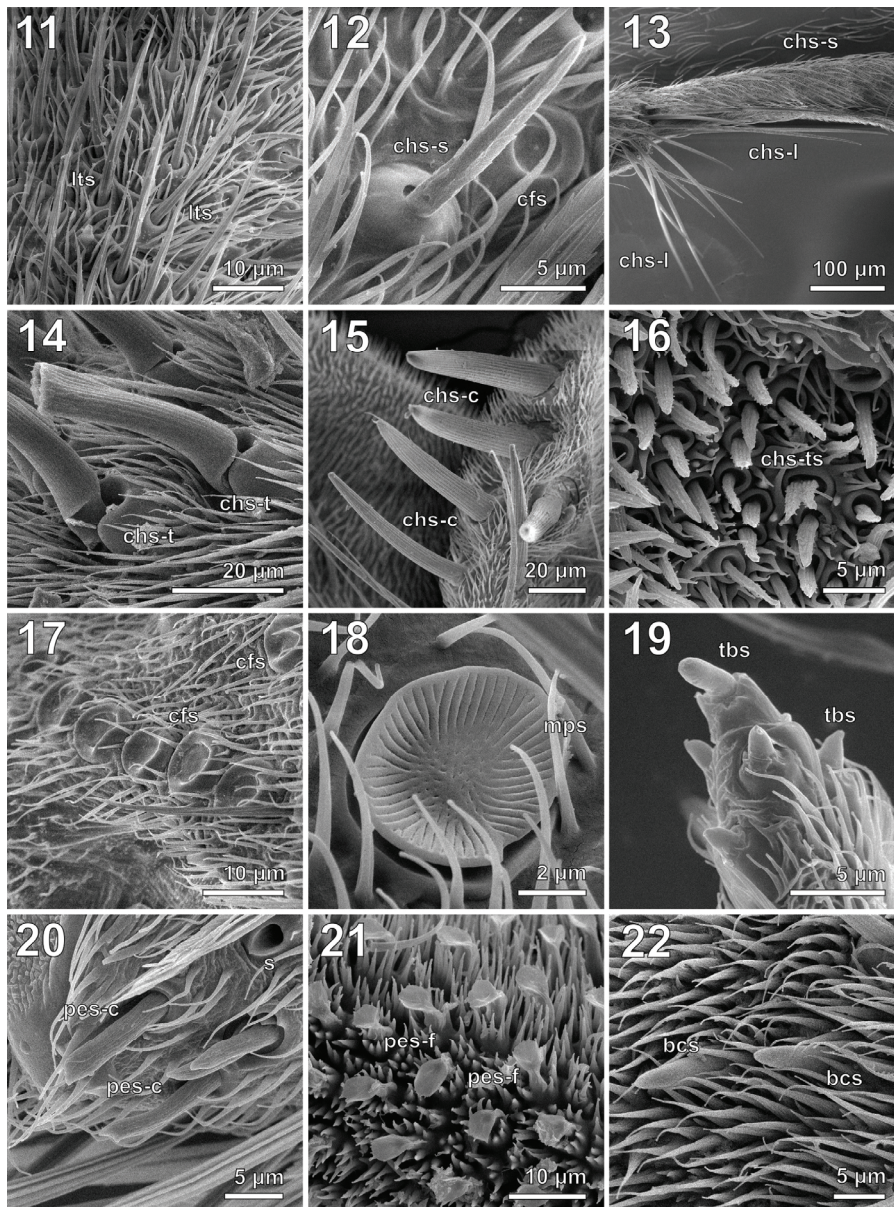
Figs 11–22. Palp sensilla of caddisflies of the suborder Annulipalpia: 11 – *N. bimaculata* female, long trichoid sensilla on lateral surface of the fifth maxillary palp segment; 12 – *N. bimaculata* female, short chaetoid sensillum on ventral surface of the fourth maxillary palp segment; 13 – *Ch. marginata* male, a group of long chaetoid sensilla on medial surface of the second maxillary palp segment; 14 – *D. varians* male, truncated chaetoid sensillum on

medial surface of the second maxillary palp segment; 15 – *M. midas* male, conical chaetoid sensilla on medial surface of the second maxillary palp segment; 16 – *Ch. thienemanni* male, thorn-shaped chaetoid sensilla on medial surface of the fourth maxillary palp segment; 17 – *P. flavomaculatus* male, a row of campaniform sensilla on the second maxillary palp segment; 18 – *L. phaeopa* male, mushroom-like pseudoplacoid sensillum on the fourth maxillary palp segment; 19 – *D. ornata* male, apical sensory complex on the third segment of labial palp; 20 – *H. sachalinica* male, curved petaloid sensilla on the fourth maxillary palp segment; 21 – *S. bergeri* female, flattened petaloid sensilla on the third labial palp segment; 22 – *D. varians* male, thin basiconic sensilla on the third labial palp segment. Abbreviations: bcs – thin basiconic sensilla; cfs – campaniform sensilla; chs-c – conical chaetoid sensilla; chs-l – long chaetoid sensilla; chs-s – short chaetoid sensilla; chs-t – truncated chaetoid sensilla; chs-ts – thorn-shaped chaetoid sensilla; lts – long trichoid sensilla; mps – mushroom-like pseudoplacoid sensilla; pes-c – curved petaloid sensilla; pes-f – flattened petaloid sensilla; s – empty sockets of long trichoid sensilla; tbs – thick basiconic sensilla.

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clusters of chaetoid sensilla and apical sensory complexes. They are also present on the fifth segment of maxillary palps in *X. mnesteus* (Xiphocentronidae). These sensilla are absent on palps in the majority of studied families.

Thick basiconic sensilla (Fig. 19, tbs) are small aporous peg-like structures, which occur only in the apical sensory complexes located on the palp tips. Each apical sensory complex bears one terminal thick basiconic sensillum (4–7 μm) on its tip; the sides of these complexes have 2–5 shorter (< 2 μm) lateral thick basiconic sensilla. No microtrichia occur on apical sensory complexes.

Petaloid sensilla (Fig. 20–21, pes-c, pes-f) are small, often curled structures with soft cuticle usually grouped in specialized sensory fields placed within pit-like surface depressions of the palp integument. They have two morphological subtypes: curved (Fig. 20, pes-c) and flattened ones (Fig. 21, pes-f). The curved petaloid sensilla have sharp tips and round cross section; they are covered with slight spiral grooves. This subtype of petaloid sensilla occurs only on the maxillary palps, usually on third and/or fourth segments. In one species, *Hyalopsyche sachalinica* (Dipseudopsidae), sensory fields of these sensilla are located on the fourth and fifth segments of maxillary palps. The flattened petaloid sensilla form sensory fields on the third segments of labial palps. This subtype is characterized by a flat apical part resembling a leaf attached to a short stem. The apical part is usually divided into two lobes. Size 5–20 μm.

Sensory fields of petaloid sensilla occur both on maxillary (Fig. 4) and labial palps (Fig. 10). These are more or less dense and compact groups of petaloid sensilla, which can have rounded or elliptical shape. They may be slightly submerged or positioned on the same level as surrounding cuticle.

Basiconic sensilla (Fig. 22, bcs) were found in both sexes of *D. varians*. These are short (10–15 μm) blunt-tipped structures of typical shape with wide base gradually narrowing towards the tip. These sensilla have slight spiral grooves. They occur only on the ventral surface of the third segment of labial palps among short chaetoid sensilla.

11

Family-specific patterns of the palp sensory surfaces

Philopotamidae. The second segment of maxillary palps in Philopotamidae is elongated and cylindrical; the group of large medial chaetoid sensilla shifted to its distal part comprises 4–15 sensilla. Both pairs of palps possess many non-specifically distributed mushroom-like pseudoplacoid sensilla, which cover the whole surface of palps, except clusters of chaetoid sensilla, sensory fields of petaloid sensilla and apical sensory complexes. The apical sensory complexes with 0–5 lateral thick basiconic sensilla are present on tips of both maxillary and labial palps in the Philopotaminae subfamily (Fig. 19). Representatives of Chimarrinae subfamily lack apical sensory complexes and thick basiconic sensilla. Sensory fields of petaloid sensilla, if present, are located on the third (*Ch. thienemanni* and *Ch. okuihorum*) or fourth (*H. tasmanica*) segment of maxillary palps and on the third segment of labial palps (except *H. tasmanica*, *W. khourmai*, *Ch. marginata* and *Ch. okuihorum*). The fourth segment of maxillary palps in *D. ornata* has single petaloid sensilla on its distal part. Two species have notable peculiarities of their palp sensilla coverage. One of the species, *Ch. thienemanni*, has large strips of shortened thorn-shaped chaetoid sensilla (Fig. 16) on medial surfaces of its first–third labial palp segments and third–fifth maxillary palp segments. The borders of these strips have normal-sized chaetoid sensilla. The first segment of maxillary palp in *H. tasmanica* has a small group (up to 5) of long chaetoid sensilla on its dorsomedial surface. This group is absent in other Philopotamidae species or contains only short chaetoid sensilla.

Stenopsychidae. The first segment of maxillary palps has a dorsomedial group of 5–8 long chaetoid sensilla on its distal part. Long chaetoid sensilla of the second maxillary palp segment form a group of 10–15 sensilla distally on the medial surface. Mushroom-like pseudoplacoid sensilla are completely absent on both pairs of palps. Apical sensory complexes are present on maxillary and labial palps and comprise 5–7 thick basiconic sensilla. Sensory fields of petaloid sensilla are located on the fourth segments of maxillary palps (*S. bergeri*) and third segments of labial palps (*S. bergeri* and *S. marmorata*).

Hydropsychidae. The second maxillary palp segment of *Smicridea murina* bears long truncated chaetoid sensilla. They are absent in all other species of the family which possess long chaetoid sensilla instead. Mushroom-like pseudoplacoid sensilla and apical sensory complexes are completely absent on both pairs of palps. Sensory fields of petaloid sensilla on maxillary palps (Figs 3–4, sf) are located on the third (*Ch. infascia*, *D. robusta*, *M. midas*), fourth (*A. palpata*, *P. apicalis*, *H. stimulans*) or third and fourth segments (*H. newae*, *H. pellucidula*, *H. angustipennis*, *L. viridianum*, *M. radiatum*). They are always absent on labial palps. In the case of reduction of mouthparts in some representatives of the subfamily Macronematinae, the labial palps are absent, and the maxillary palps either completely disappear (female *Aethaloptera evanescens*), or (male *Aethaloptera evanescens* and female *Polymorphanisus nigricornis*) consist of two segments. The long annulated fifth segment is absent, and the remaining segments are greatly shortened. The basal segment has a group of chaetoid sensilla and solitary long trichoid sensilla. The terminal one has a field of curved petaloid sensilla and a small number of chaetoid sensilla.

12

Polycentropodidae. The second segment of maxillary palps has a distal outgrowth on its medial surface. This outgrowth bears a group of truncated chaetoid sensilla. Mushroom-like pseudoplacoid sensilla and apical sensory complexes are completely absent on both pairs of palps. Sensory fields of maxillary palps are located on the third (genus *Cyrnus*) or fourth segments (*N. bimaculata*, *P. flavormaculatus*, *Pl. conspersa*). Sensory fields of labial palps (Figs 9–10, sf) are either located on the third segment (*C. fennicus*, *N. bimaculata*, *P. flavomaculatus*, *Pl. conspersa*) or absent (*C. flavidus*).

Ecnomidae. The first segment of maxillary palps bears a dorsomedial group of 3–5 long chaetoid sensilla on its distal part. Long chaetoid sensilla of the second maxillary palp segment also form a group with the same number of sensilla distally on the medial surface. Mushroom-like pseudoplacoid sensilla and apical sensory complexes are completely absent on both pairs of palps. Sensory fields of maxillary palps are located on both third and fourth segments. Petaloid sensilla are absent on labial palps.

Dipseudopsidae. The second segment of maxillary palps bears truncated chaetoid sensilla (Fig. 14) positioned on the medial outgrowth of the distal part of the segment (*D. indica* and *D. varians*). Mushroom-like pseudoplacoid sensilla and apical sensory complexes are completely absent on both pairs of palps. The distal part of the third segment of maxillary palps in *D. indica* and *D. varians* bears a diffuse assemblage of petaloid sensilla, which do not form a sensory field. Petaloid sensilla are always absent on labial palps. Third segments of labial palps possess basiconic sensilla on their ventral surfaces (Fig. 22). *D. indica* and *D. varians* have long annulated maxillary lobes with small peg-like sensilla on its distal part resembling basiconic sensilla of palps. One species, *Hyalopsyche sachalinica*, lacks labial palps. The number of chaetoid sensilla on maxillary palps of this species is greatly reduced: most palp segments bear single chaetoid sensilla. The apical segment has a group of up to 10 short chaetoid sensilla on its tip. Sensory fields in *H. sachalinica* are located on distal parts of the fourth and fifth maxillary palp segments. The fifth segment of maxillary palps in this species lacks annulation typical for the majority of Annulipalpia.

Pseudoneureclipsidae. The second segment of maxillary palps is short and has no distal outgrowth. It bears a medial group of 5–7 truncated chaetoid sensilla on its distal part. The first segment of maxillary palps also has 1–3 truncated chaetoid sensilla on its distal part. Mushroom-like pseudoplacoid sensilla and apical sensory complexes are completely absent on both pairs of palps. Sensory fields are absent on maxillary palps. The third segment of labial palps bears a sensory field of flattened petaloid sensilla.

Psychomyiidae. The second segment of maxillary palps is elongated and cylindrical. It has a medial outgrowth on its distal part in females of *L. phaeopa*. This outgrowth bears up to 10 short chaetoid sensilla. No truncated chaetoid sensilla were found. Apical sensory complexes are completely absent on both pairs of palps. All palp segments of males bear a large number of non-specifically distributed mushroom-like pseudoplacoid sensilla on both pairs of palps (Fig. 18). Females of *P. pusilla* and *L. phaeopa* have numerous mushroom-like pseudoplacoid

13

sensilla on lateral and dorsal surfaces of second and third segments of maxillary palps and single sensilla of this type on the fourth and fifth segments. No mushroom-like pseudoplacoid sensilla occur on labial palps and the first segments of maxillary palps in females of these species. Diffuse groups of curved petaloid sensilla are located on third (*P. pusilla*) or fourth (*P. pusilla* and *L. phaeopa*) maxillary palp segments. Petaloid sensilla are always absent on labial palps.

Xiphocentronidae. The second and third segments of maxillary palps bear a small distal group (2–4 sensilla) of truncated chaetoid sensilla on their medial surfaces. Mushroom-like pseudoplacoid sensilla are located only on the fifth segment of maxillary palps. Apical sensory complexes are completely absent on both pairs of palps. A diffuse group of curved petaloid sensilla is located on the fourth maxillary palp segment. Petaloid sensilla are absent on labial palps.

DISCUSSION

The apical sensory complexes are present on palps only in the lower Annulipalpia belonging to Philopotamidae and Stenopsychidae (Philopotamoidea). A trend to disappearance of the apical complexes of the palps is common in more advanced Annulipalpia families and, in parallel, in some Philopotamidae as suggested previously on smaller dataset. These structures vanish in the more advanced Philopotamidae subfamily Chimarrinae and in the specialized genus *Gunungiella* (Philopotaminae) (Ivanov *et al*., 2018). The presence of apical sensory complexes in Philopotamoidea as a ground plan character (Abu Diiak *et al*., 2023a) suggests the basal position of this superfamily in relation to the two other superfamilies, although the phylogenetic weight of this character is low because of the numerous homoplasias in Annulipalpia and Integripalpia.

Sensory fields of the petaloid sensilla on labial palps retain the original position on the third segment in the majority of Philopotamoidea except *H. tasmanica*, *W. khourmai*, *Ch. marginata* and *Ch. okuihorum*. These fields lost in all Hydroipsy-choidea and most of Psychomyioidea except for Pseudoneureclipsidae and most species of Polycentropodidae (*C. fennicus, N. bimaculata, P. flavomaculatus, Pl. conspersa*). Absence of sensory fields probably indicates a more advanced state of the palp sensory surfaces in these families, contrary to modern considerations about the near basal position of these taxa. Evolution of these sensory fields on maxillary palps shows other tendencies in comparison with labial palps in relation to their ground plan position (Abu Diiak *et al*., 2023a) on the terminal maxillary palp segment. The petaloid sensory fields move in all Annulipalpia from the fifth segment to the fourth and third segments. Sensory fields on maxillary palps show four options in Annulipalpia. These sensory fields either are present on the third, or on fourth, else on both third and fourth, or else completely disappear. The basal shift of these fields from the terminal segments of the maxillary palps might be caused by transformation of the fifth palp segments developing annulation and flexibility that probably preven-ting the correct functions of petaloid sensilla. The only exception is *H. sachalinica* with the fields located on the fourth and fifth maxillary palp segments. Probably the

14

segment count in this instance should be altered: the non-annulated 5th segment is a homolog of previous subterminal 4th, and the visible 4th is in fact 3rd of the ancestor; the annulated fifth segment is lost, and an additional basal segment is inserted.

Previous comparative studies of the antennal sensilla in Trichoptera showed a significant diversity of structures (Melnitsky & Ivanov, 2011; Ivanov & Melnitsky, 2016; Valuyskiy *et al.*, 2017, 2019, 2020; Melnitsky *et al.*, 2018, 2019; Abu Diiak *et al.*, 2021, 2022). Insect antenna consists of three principal parts: the most basal scapus is a segment responsible for the movements of the rest of antenna with the cranial musculature turning it in relation to head and the intrinsic muscles moving distal part of antenna in relation to scapus. The second part is called pedicellus, a segment devoid of muscles and provided with internal receptors called the Johnston's organ for detection of the motion in the flagellum, the third part of the antenna, which consists of numerous segments covered with numerous sensilla for the chemoreception. These parts have no parallel in the palp segmentation, and function of palps is believed to be mostly the sensory support of feeding rather than olfactory reception and perception of the remote chemical signals. Hence, it is impossible to expect the close similarity in the sensilla coverage of these appendages.

The secondary subdivision of the terminal palp segments in Annulipalpia is an evolutionary parallel to secondary subdivision of flagellum, a solitary segment in the past, to the flagellomeres. The flagellomeres of antenna developed the regular sensilla patterns repetitive segment to segment. We did not observe similar regular sensilla patterns on the subdivided terminal palp segments with development of secondary subsegments. There is a well-developed coverage of upright short chaetoid sensilla set in two rows at regular intervals on ventral and trichoid sensilla on dorsal surfaces (Figs 6, 8, 9), but no regularity in respect to the annulation was found.

Certain sensilla types occur on the sensory surfaces of the antenna, the palp, and both sensory appendages. Trichoid, short chaetoid, pseudoplacoid, and campaniform sensilla were found on both the antenna and the palp sensory surfaces. Distribution patterns of these structures are similar for the trichoid, pseudoplacoid, and campaniform sensilla. These sensilla have non-specific distribution for the first two types and the specific distribution in position close to the mechanically loaded parts of the cuticle, generally at the segmental margins in proximal part of an appendage, for the latter type. The pseudoplacoid sensilla on both the antennal flagellum and palp segments were found only in Philopotamidae, and Psychomyiidae; other studied families have no pseudoplacoid sensilla on palps despite that all Psychomyioidea and Hydropsychidae have these sensilla on antenna.

Diversity of the antennal sensilla exceeds that of palps. In addition to the long trichoid sensilla, the antenna of Trichoptera possesses short curved trichoid sensilla probably responsible for the pheromone detection. These sensilla on antenna are usually grouped in sensory fields on ventrolateral surface of antenna for the precise targeting of the chemical signal. Other types are not present on palps are thick chaetoid, coronary, styloconic sensilla, and various subtypes of pseudoplacoid sensilla besides the most ubiquitous mushroom-like subtype initial for the evolution of pseudoplacoid sensilla. Contrary to thick basiconic sensilla of palps, the antennal sensilla always belong to the thin basiconic type. Specialized Boehm's bristles, a series of very short trichoid mechanoreceptor sensilla on basal antennal segments,

were not found on palps. No apical sensory complexes were found on antennae of Trichoptera.

Like antennae, the palps have sensory fields but, contrary to antennae, these fields have their own different specialized elements, the petaloid sensilla. The assemblages of petaloid sensilla on the terminal palp segments belong to the ground plan of the palp sensory surface of Trichoptera (Abu Diiak *et al.*, 2023a). The petaloid sensilla are present in all Annulipalpia families. Sometimes these fields vanish but the petaloid sensilla in these instances are still present forming diffuse groups on palps as in *Lype phaeopa* and *Dipseudopsis* spp.

Terminal segments of the maxillary and labial palps with their peculiar annulated surfaces are represented throughout the families of Annulipalpia with a few exceptions. One of these exceptions is the case of the advanced Hydropsychidae – Macronematinae. Some species of this subfamily have extremely reduced mouthparts with only shortened maxillary palps as the last remnants of maxillae; labial palps are always lacking in the studied instances in both sexes of *Aethaloptera evanescens* and females of *Polymorphanisus nigricornis* (Ivanov *et al.*, 2023). These reduced maxillary palps with two retained segments have smaller numbers of sensilla but no annulation. Males of *Hyalopsyche* have no labial palps, and their maxillary palps are transformed as discussed above. These examples of reduced annulation are probably caused by reduction of mouthparts and aphagous mode of life in adults. The third exception is represented by *Paduniella* (Martynov, 1934) actually shows 6-segmented maxillary palps, with only one flexible line dividing the terminal segments into 2 halves, thus the annulation is formally present as a single ring. The persistence of annulated mouthparts in Annulipalpia might be principal adaptation of the feeding apparatus caused by necessity to monitor the surface with horizontal sweep-like palp movements side to side while walking (Ivanov, 1993). The short chaetoid sensilla on the ventral surface of the terminal palp segments are on upright position ready to percept chemical stimuli of the substrate and the advanced flexibility of these segments provide ability to follow the roughness of the surfaces and to avoid small obstacles. The reduction of annulated structures on the terminal mouthpart segments occurs only with reduction of the palps. Smaller species of Psychomyiidae and Xiphocentronidae have shorter terminal palp segments; nevertheless, they retain annulation at least as a single joint in *Paduniella*.

Comparison of the sensilla patterns in the studied families, despite various configuration, segment numbers, segment length, and degree of reduction shows the apparent similarity in sensory surfaces of various taxa. The trichoid sensilla tend to be dominant on the dorsal surfaces, the chaetoid are numerous ventrally, and the thick basiconic sensilla, if present, never move from the apical sensory complex. The ultimate instances of the palp reduction demonstrate the presence of typical palp sensilla on the retained segments. Thus, the sensilla are the structures of highest morphogenetic priority and retained even at the deep transformation and reduction of the mouthparts.

The sensilla patterns vary with the ramification of the phylogenetic tree. The basal families of both suborders, Annulipalpia and Integripalpia, have apparent similarity in the sensory surfaces (Abu Diiak *et al.*, 2023a, b). This resemblance might be caused by the functionality of palps in the common ancestor of Trichoptera

or even the ancestor of Amphiesmenoptera (superorder including Trichoptera and Lepidoptera). The sensilla distribution might support the modes of the palp functionality, with mechano- and chemoreception supported by chaetoid sensilla, local chemoreception by the basiconic sensilla of apical sensory complexes and the petaloid sensilla in sensory fields, and the mechanoreception by trichoid and campaniform sensilla. Functions of the pseudoplacoid sensilla are not yet fully understood; we supposed (Abu Diiak *et al.*, 2023a) that they might be hygro- or thermohygroreceptors useful for orientation towards the shoreline. Subsequent evolutionary changes resulted in the disappearance of pseudoplacoid and thick basiconic sensilla along with the apical sensory complexes, development of several subtypes of the chaetoid sensilla supporting chemoreception, and transformations of the petaloid sensilla and their sensory fields.

The taxonomic significance of the palp sensilla for the studied families is not yet apparent. We consider our study as a first step towards the application of fine structures of the palp sensory surfaces for taxonomy. Parallelism in losses of some ancient structures might obscure the phylogenetic relationships. For example, the apical sensory complexes on the terminal palp segments served as an argument for inclusion of Rhyacophilidae, Hydrobiosidae, Glossosomatidae, and Hydroptilidae into the infraorder Spicipalpia (Weaver, 1984). Subsequent studies showed the presence of these complexes in Annulipalpia (Ivanov, 1997; Ivanov *et al.*, 2018) hence Spicipalpia should be considered as a paraphyletic taxon; the molecular studies (Kjer *et al.*, 2001; Thomas *et al.*, 2020) agrees to this statement. The apical sensory complexes, in turn, as a part of Trichoptera/Amphiesmenoptera ground plan indicate the systematic position at higher taxonomy level and are useful for tracing the insect order relationships and understanding some fossils (Ivanov & Sukatsheva, 2002).

Another example of reduction is provided by the pseudoplacoid sensilla. These sensilla are non-specifically distributed across the palp surfaces except for dense groups of other sensilla in the ancestral condition (Abu Diiak *et al.*, 2023a). The family Philopotamidae well corresponds to this primitive pattern and the current understanding of the Trichoptera phylogeny as a basal family for the Annulipalpia. These sensilla are present also in Psychomyiidae demonstrating a sex-related poly-morphism in development: the females have lesser numbers of these sensilla than males with tendency to concentrate these sensilla on dorsal surfaces of more distal segments. The same transformation occurs in some species of Rhyacophilidae (Abu Diiak *et al.*, 2023 a, b) from Integripalpia stressing the parallelism in evolution. Hence, we cannot argue for the taxon uniting Psychomyiidae and Philopotamidae against all other Annulipalpia and must admit the parallel evolution. Some characters provided by palp sensilla look very persistent. For example, the sensory coverage of the terminal palp segments other than apical regions look uniform with dorsal inclined trichoid sensilla directed apically and ventral short chaetoid sensilla directed ventrally at right angles to the segment surface and sometimes even inclined towards the head, opposite to trichoid sensilla. Similar uniformity occurs on the 3rd and 4th segments with lesser numbers of sensilla.

Two character sets look the most promising for the taxonomic analysis. First of them is the position and development of the sensory fields of petaloid sensilla.

17

These fields are supposed to be the structural and functional homologs of the vom Rath's organs of Lepidoptera (Abu Diiak *et al*., 2023a); if so, their function should be the olfactory reception. These fields are persistent in most families although undergo various transformations: movements, shape and size changes, variations in sensilla structure. Maxillary palp transformation resulted in presence of these fields on the tip of the terminal maxillary palp segment of *H. sachalinica* together with unusual reduction of labial palps is noteworthy and argues for the family status of the subfamily Hyalopsychinae.

The second promising character set is the transformation of long chaetoid sensilla on maxillary palps and development of some associated structures. These sensilla are very characteristic for the first and second maxillary palp segments; their number on the first segment is much smaller than on the next one. These sensilla in the Annulipalpia have dorsal or dorsomedial position on the first and medial to ventromedial position on the second segment. The ground plan supposes the development of a number of these very large sensilla on medial surfaces of the two basal maxillary palp segments (Abu Diiak *et al*., 2023a). This plesiomorph character state is retained in the part of Psychomyioidea (Ecomidae, Psychomyiidae), whereas in other groups of Annulipalpia this character is altered. The Philopotamoidea have much shorter and thinner sensilla of this type in groups on the medial surface. The truncated chaetoid sensilla are least numerous but extremely long in Xiphocentronidae, a family of smallest Annulipalpia related to Psychomyiidae; apparently the sensilla continue to perform their functions although lack of space limits their number. Most Hydropsychoidea have no sensilla of this subtype, and the second maxillary palp segment is similar in shape with the subsequent third and fourth segments. The most striking transformation of these sensilla is found in Polycentropodidae, Pseudoneureclipsidae, and Dipseudopsidae indicating their putative close relationships. These families have ventromedial surfaces of the second maxillary segment provided with short and very stout truncated chaetoid sensilla with highly transformed basal areas (Fig. 14). The development of segment projection in Polycentropodidae and Dipseudopsidae might compensate the shortening of sensilla in these instances. The basal region of such a sensillum develops a support heel interacting with the socket outgrowth and provides a sort of detent. Function of these sensilla might involve a forced interaction with some rigid surface so the hardness of the ordinary long chaetoid sensilla is not sufficient. The transformation produced shorter but much stouter sensilla with segment outgrowth compensating the lack of its length. Some similarity to these sensilla is found in *Smicridea murina* with long truncated sensilla having similar transformation in the basal sensilla part.

The current studies of sensilla on the head appendages are concentrated on the shape of the cuticular part demonstrating a plenty of structural variants. Contrary, the histology and, especially, the functions of the sensilla in Trichoptera are insufficiently studied. The lack of information concerning the sensilla functions impedes the interpretation of the structural transformations and evolution of the sensilla. More data are necessary for the behavior supported by stimuli receiving with the aid of palp sensilla. We hope that the subsequent studies in these areas will help to uncover the evolution of the sensory surfaces in Trichoptera.

18

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