Diversity of the olfactory sensilla in caddisflies (Trichoptera)

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Abstract

Antennal segments in Trichoptera are provided with various sensilla showing the maximal diversity on the antennal flagellum. Comparative studies of cuticle parts of sensilla provide rich material on various sensory structures. Preliminary results of a comparative study of the antennal surface in 28 families of Trichoptera reveal more than 17 structural types of the cuticular microstructures. Some of them (microtrichia, scales, and 2 specialized types of trichia) are apparently not sensilla. The diversity of sensory structures is illustrated and discussed in connection with taxonomy and evolution.

Key words: Antenna, flagellum, micromorphology, scanning electron microscopy; transmission electron microscopy

Introduction

Sensilla are a major component of insect olfactory reception. The structure of insect sensilla were the subject of numerous studies during the 20th century. Different systems of terminology were used (*e.g.*, Schneider 1964; Slifer 1970; Zacharuk 1980; Hallberg & Hansson 1999; Vshivkova *et al.* 2007; Vshivkova & Makarkin 2010; Crespo 2011), but we continue to follow the most widely accepted old system by Snodgrass (1935), with some modifications. All these systems concern mostly the cuticular structures of the sensilla in relation to their shape, size, presumed function, and permeability to staining, with less attention to the neurons and their function which is deduced from a limited number of comparative physiological investigations.

In contrast, although larval antennae of caddisflies have attracted some interest as a subject of comparative studies of sensilla (Denis 1984) and selected data have been used in studies of phylogeny (Frania & Wiggins 1997), the comparative investigations of sensilla in adult Trichoptera are often inadequate because researchers studied only a single or few related species without taxonomical background (Tozer 1982; Slifer & Sekhon 1971). The comparative study of sensilla in a few species of adult Hydroptilidae by Wells (1984) revealed significant diversity of sensilla in members of a single family, making generalizations on the antennal sensory structures based on one or two species (*e.g.*, Hallberg & Hansson 1999; Crespo 2011) very superficial. Our comparative studies of Limnephilidae and Phryganeidae (Ivanov & Melnitsky 2011) and Molannidae (Melnitsky & Ivanov this volume) also showed significant diversity of the cuticular parts of the sensilla within the families and genera. Some preliminary data on this subject were published by us elsewhere (Melnitsky & Ivanov 2011). The diversity of sensilla in Trichoptera was also considered by Faucheaux (2004b) who found significant similarity of cuticular parts to antennal structures of Lepidoptera.

This publication is a progress report on the studies of sensory structures in Trichoptera carried out by us to understand the evolution of communicative systems in caddisflies. Some data have been published previously and showed significant diversity in the related families (Ivanov& Melnitsky 2011; Melnitsky & Ivanov 2011). In this paper, we review structural types of cuticular parts of sensilla as most appropriate for use in species descriptions, taxonomy, and phylogenetic studies. The main purpose of this publication is to illustrate certain distinct types of sensilla in various families of Trichoptera to provide future studies with morphologic references, and to discuss some inconsistencies and controversies in current publications on sensilla morphology. The internal structures and, especially, functions of sensilla in Trichoptera are poorly studied and their use in taxonomic studies, although welcome, is a very remote goal.

Material and methods

Ultrastructural studies of the antennal surface and sensilla were made with Scanning Electron Microscopy (SEM). Antennae were dried and mounted on microscope holders with subsequent metal coating; silver was used for Fei Quanta 200 3D, platinum for Hitachi TM-1000 and gold for Hitachi S-570 and Philips SEM 501 B microscopes. Films made by Hitachi S-570 and Philips SEM 501 B were digitized with Epson 4490 scanner. All graphic digital files have been edited, including cropping, moderate sharpening, and contrasting in the graphic computer programs. Additional light microscopy (LM) studies were made with the following microscopes: Biolam–I (at magnifications up to 600x and top illumination and Nikon D-70 camera as a photo device), Olympus BH–2 (transmitting light, with Canon EOS 1000D or Sony Cybershot DSC-F707 photo cameras), and dissecting microscope Mikmed 2 (coupled with Canon PowerShot A640 photo camera).

A total of 68 species from 27 families was used to obtain data on the sensilla diversity:

Himalopsyche todma Schmid, *Rhyacophila nubila* Zetterstedt, *Rhyacophila kaltatica* Levanidova (Rhyacophilidae); *Apsilochorema annandalei* Martynov, *Ulmerochorema stigmum* (Ulmer) (Hydrobiosidae); *Glossosoma nylanderi* McLachlan (Glossosomatidae); *Hydropsyche* (*Ceratopsyche*) *newae* Kolenati, *Hydropsyche* (*Hydropsyche*) *contubernalis* McLachlan (Hydropsychidae); *Stenopsyche similis* Ulmer (Stenopsychidae); *Chimarra batukaua* Malicky, *Dolophilodes ornata* Ulmer, *Gunungiella gundergonia* Melnitsky & Ivanov, *Philopotamus ludificatus* McLachlan, *Wormaldia simplicissima* Melnitsky & Ivanov (Philopotamidae); *Phryganea bipunctata* Retzius, *Phryganea grandis* L., *Agrypnia pagetana* Curtis (Phryganeidae); *Plectrotarsus tasmanicus* Mosely (Plectrotarsidae); *Silvatares collyrifer* (Barnard) (Pisuliidae); *Anabolia laevis* (Zetterstedt), *Monocosmoecus pulcher* Ulmer, *Dicosmoecus palatus* (McLachlan), *Ecclisomyia kamtshatica* (Martynov), *Potamophylax latipennis* (Curtis), *Potamophylax cingulatus* (Stephens), *Halesus tessellatus* (Rambur), *Chaetopteryx villosa* (Fabricius), *Pycnopsyche scabripennis* (Rambur), *Frenesia missa* (Milne), *Pseudostenophylax amurensis* (McLachlan), *Grensia praeterita* (Walker) (Limnephilidae); *Allomyia sajanensis* Levanidova, *Apatania complexa* (Martynov), *Baicalina bellicosa* Martynov, *Baicalina reducta* Martynov, *Thamastes dipterus* Hagen (Apataniidae); *Neophylax splendens* Denning, *Oligophlebodes minutus* (Banks), *Thremma anomalum* McL., (Thremmatidae); *Archithremma ulachensis* Martynov, *Farula malkini* Ross, *Uenoa hiberna* Kimmins (Uenoidae); *Brachycentrus americanus* (Banks), *Micrasema gelidum* McL. (Brachycentridae); *Crunoecia irrorata* (Curtis), *Lepidostoma elongatum* (Martynov), *Lepidostoma coreanum* Kumanski & Weaver, *Lepidostoma hirtum* (Fabricius) (Lepidostomatidae); *Oeconesus maori* McLachlan (Oeconesidae); *Goera pilosa* (Fabricius), *Goera tungusensis* Martynov (Goeridae); *Sericostoma personatum* (Spence) (Sericostomatidae); *Beraea pullata* (Curtis) (Beraeidae); *Odontocerum albicorne* (Scopoli), *Psilotreta falcula* Botosaneanu (Odontoceridae); *Philorheithrus lacustris* Tillyard (Philorheithridae); *Limnocentropus inthanonensis* Malicky & Chantaramongkol (Limnocentropodidae); *Tasimia palpata* Mosely (Tasimiidae); *Taskiria austera* Neboiss (Kokiriidae), *Zelolessica cheira* McFarlane, (Helicophidae); *Olinga feredayi* (McLachlan) (Conoesucidae); *Molanna albicans* (Zetterstedt), *Molanna nigra* (Zetterstedt), *Molanna submarginalis* McLachlan, *Molanna uniophila* Vorhies, *Molanna moesta* Banks, *Molanna angustata* Curtis, *Molannodes tinctus* (Zetterstedt) (Molannidae).

Results

The nomenclature of sensilla is not well established, despite of decades of studies. Creation of a universal classification is impeded by numerous intermediate forms in relation to their size and small structural features between different types of sensilla, and their diversity. Lack of physiological information for various types of sensilla is also notable.

Microstructures found on the antennal surface can be divided into two main groups based on the structure of their cuticular parts: Long and short sensilla forming the upper and lower levels of coverage on the antenna, respectively. Long cuticular microstructures on the antennae of the species studied are presented as receptor trichoid sensilla of several different subtypes. Characteristics of representatives are shown in Figures 1–3.
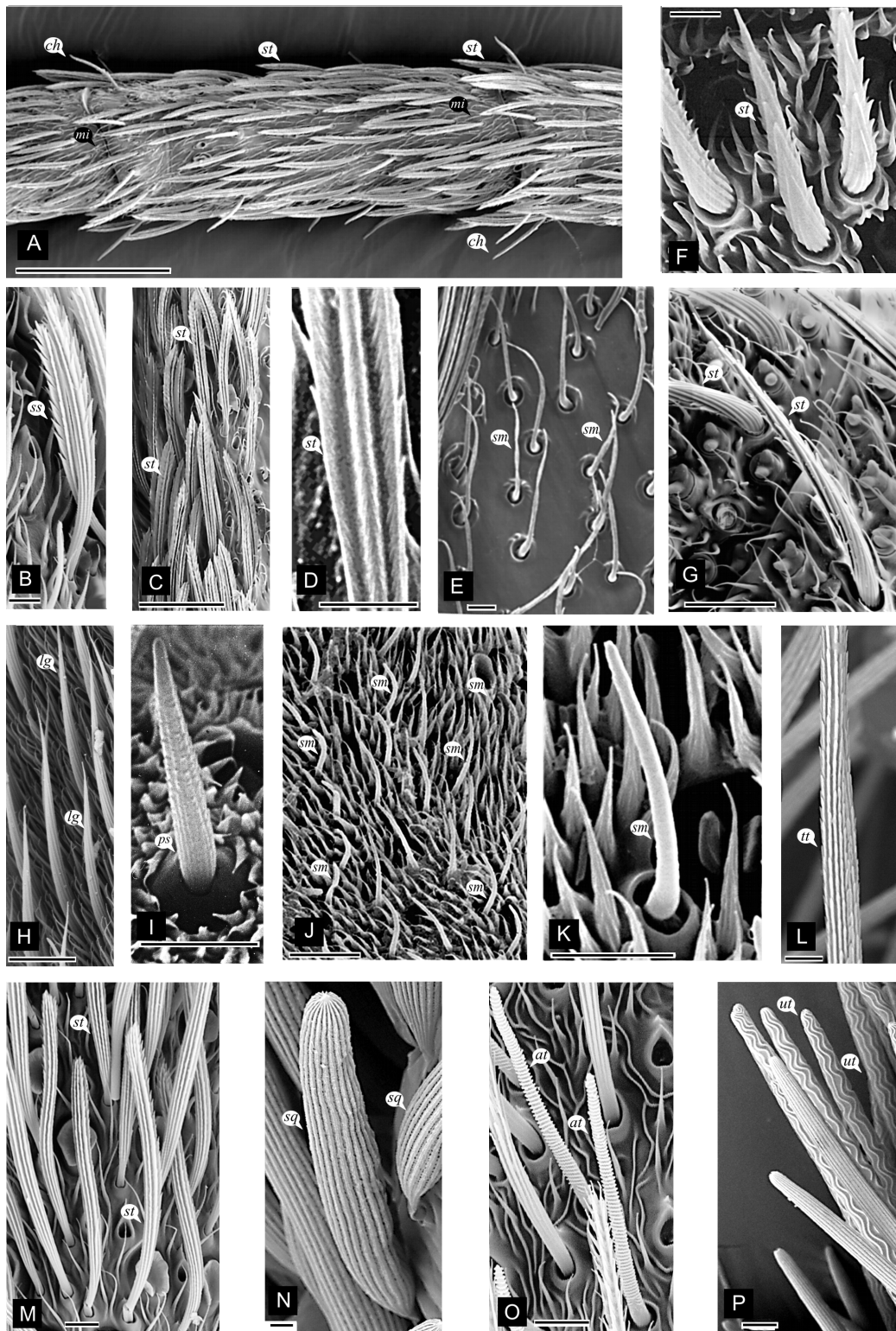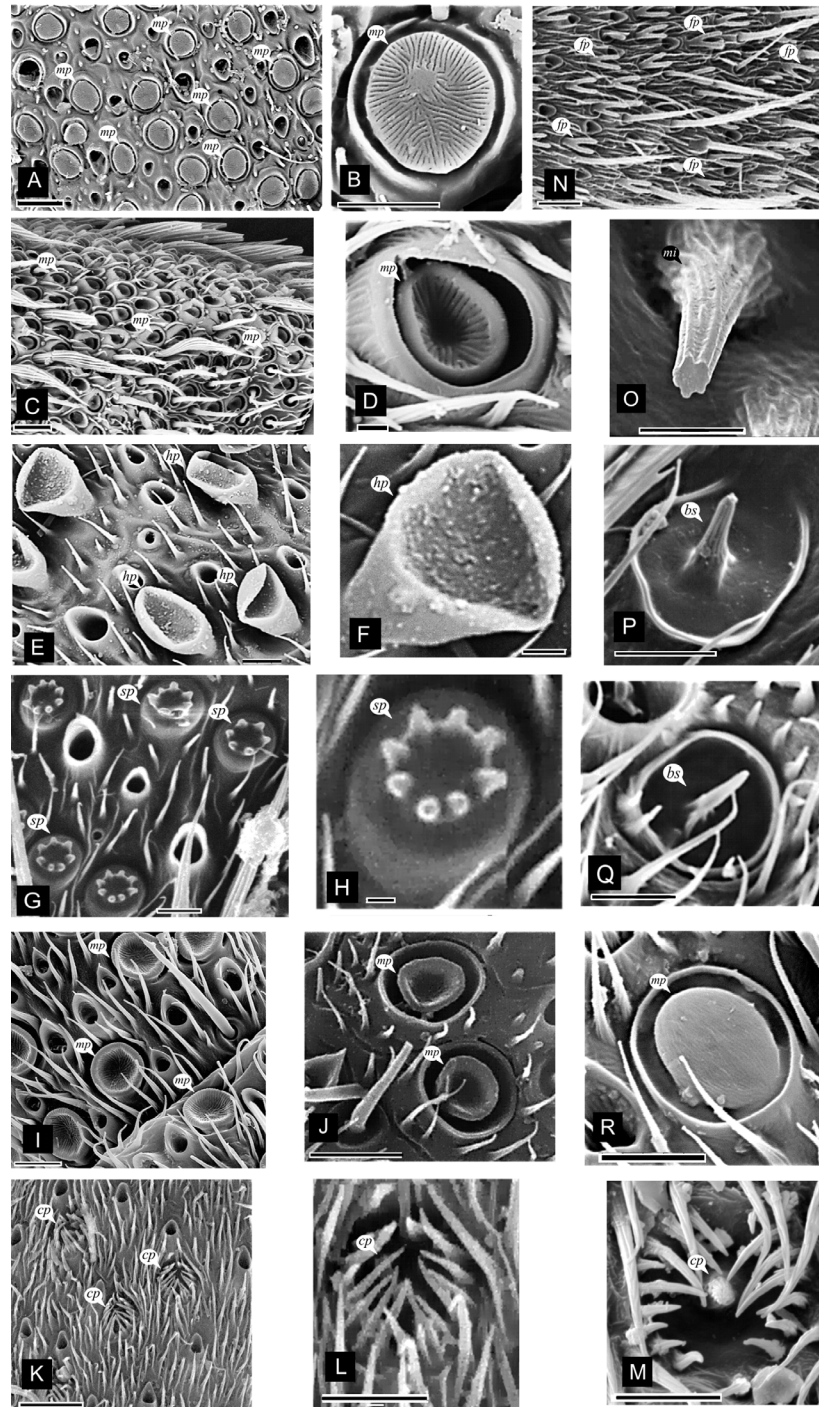
FIGURE 1. Antennal structures of Trichoptera. A–E. *Molanna angustata* Curtis. A—flagellomeres with chaetoid sensilla (*ch*) and serrate trichoid sensilla (*st*) with microtrichia (*mi*), scale 100 µm; B—small serrate trichoid sensilla (*ss*), scale 5 µm, scale 10 µm; C—cover of serrate trichoid sensilla (*st*) on dorsal surface of antenna; D—fragment of medial part of sensillum, scale 5 µm; E—smooth trichoid sensilla (*sm*), scale 10 µm; F—*Potamophylax cingulatus* (Stephens), serrate trichoid sensilla (*st*), scale 5 µm; G—*Phryganea grandis* L., serrate trichoid sensilla (*st*), scale 40 µm; H—*Grensia praeterita* (Walker), long grooved trichoid sensilla (*lg*), scale 10 µm; I—*P. cingulatus*, pseudotrichoid sensillum (*ps*), scale 10 µm; J—*Halesus tessellatus* (Rambur), smooth trichoid sensilla (*sm*), scale 10 µm; K—*H. tessellatus*, smooth trichoid sensillum (*sm*), scale 5 µm; L—*Lepidostoma elongatum* (Martynov), thin trichia (*tt*), scale 5 µm; M—*Beraea pullata* (Curtis), serrate trichoid sensilla (*st*), scale 5 µm; N—*L. elongatum*, "squashes" (*sq*), scale 5 µm; O—*Crunoecia irrorata* (Curtis), annulated trichoid sensilla (*at*), scale 5 µm; P—*L. elongatum*, undulated trichoid sensilla (*ut*), scale 10 µm.
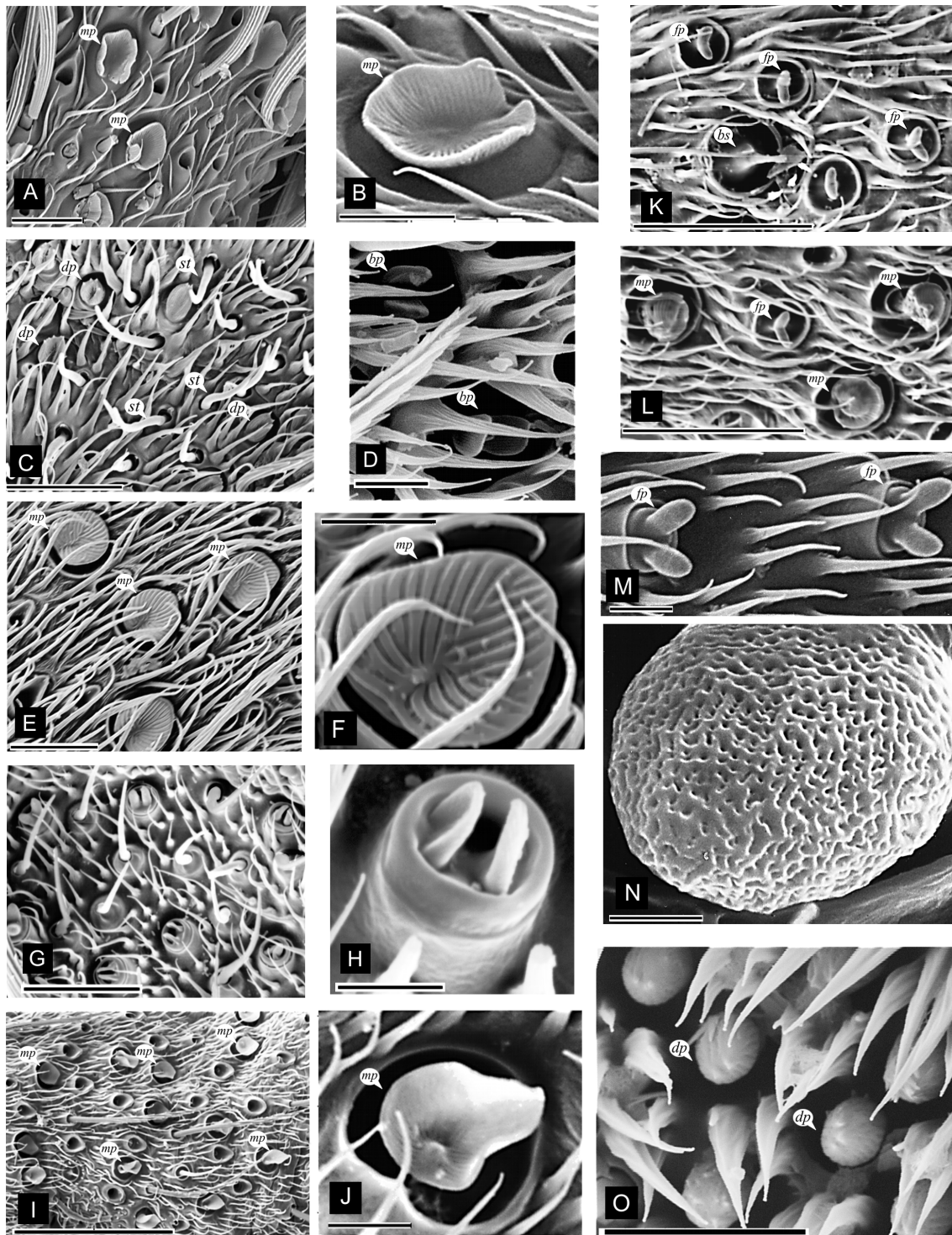
FIGURE 2. Antennal structures of Trichoptera. A—*Beraea pullata* (Curtis), mushroom-like pseudoplacoid sensilla (*mp*), scale 10 μm; B—*B. pullata*, mushroom-like pseudoplacoid sensilla (*mp*), scale 5 μm; C—*Anabolia laevis* (Zetterstedt), dentate pseudoplacoid sensilla (*dp*) and smooth trichoid sensilla (*st*), scale 20 μm; D—*Halesus tessellatus* (Rambur), bilobed pseudoplacoid sensilla (*bp*), scale 5 μm; E—*Dolophilodes ornata* Ulmer, mushroom-like pseudoplacoid sensilla (*mp*), scale 10 μm; F—*D. ornata*, mushroom-like pseudoplacoid sensilla (*mp*), scale 4 μm; G—*Phryganea grandis* L., forked pseudoplacoid sensilla (*fp*) and smooth trichoid sensilla (*st*), scale 30 μm; H—*P. grandis*, forked pseudoplacoid sensilla (*fp*), scale 10 μm; I—*Rhyacophila kaltatica* Levanidova & Schmid, mushroom-like pseudoplacoid sensilla (*mp*), scale 50 μm; J—*R. kaltatica*, mushroom-like pseudoplacoid sensilla (*mp*), scale 5 μm; K—*Rhyacophila nubila* Zetterstedt, forked pseudoplacoid sensilla (*fp*) and basiconic sensillum (*bs*), scale 20 μm; L—*R. nubila*, mushroom-like (*mp*) and forked (*fp*) pseudoplacoid sensilla, scale 20 μm; M—*Phryganea bipunctata* Retzius, forked pseudoplacoid sensilla (*fp*), scale 5 μm; N—*P. bipunctata*, one fork of forked pseudoplacoid sensillum, scale 1 μm; O—*Pseudostenophylax amurensis* McLachlan, dentate pseudoplacoid sensilla (*dp*), scale 10 μm.

FIGURE 3. Antennal structures of Trichoptera. A—*Limnocentropus inthanonensis* Malicky & Chantaramongkol, mushroom-like pseudoplacoid sensilla (*mp*) , scale 5 µm; B—*L. inthanonensis,* mushroom-like pseudoplacoid sensillum, scale 5 µm; C—*Taskiria austera* Neboiss*,* mushroom-like pseudoplacoid sensilla (*mp*), scale 10 µm; D—*T. austera,* mushroom-like pseudoplacoid sensillum, scale 5 µm; E—*Sericostoma personatum* Spence, horn-like pseudoplacoid sensilla (*hp*), scale 5 µm; F—*S. personatum*, horn-like pseudoplacoid sensillum (*hp*), scale 1 µm; G—*Oeconesus maori* McLachlan, stellate pseudoplacoid sensilla (*sp*), scale 5 µm; H—*O. maori*, stellate pseudoplacoid sensillum, scale 1 µm; I—*Chimarra batukaua* Malicky, mushroom-like pseudoplacoid sensilla (*mp*), scale 5 µm; J—*Glossosoma nylanderi* McLachlan, mushroom-like pseudoplacoid sensilla (*mp*), scale 10 µm; K—*Hydropsyche newae* Kolenati*,* coronal pseudoplacoid sensilla (*cp*), scale 30 µm; L—*H. newae,* coronal pseudoplacoid sensillum (*cp*), scale 5 µm; M—*Dolophilodes ornata* Ulmer, coronal pseudoplacoid sensillum (*cp*), scale 5 µm; N—*Goera tungusensis* Martynov, forked pseudoplacoid sensilla (*fp*), scale 5 µm; O—*Phryganea grandis* L., broken microtrichia, scale 2 µm; P—*Molanna angustata* Curtis, basiconic sensillum (*bs*), scale 10 µm; Q—*Rhyacophila kaltatica* Levanidova & Schmid, basiconic sensillum (*bs*), scale 5 µm; R—*Apsilochorema annandalei* Martynov, mushroom-like pseudoplacoid sensilla (*mp*), scale 5 µm.

The dense coverage of microtrichia (Figs 1A, J; 3O) make a fur-like appearance of the antennal surface; these microstructures have no receptor function and are devoid of any internal cavity (Fig. 3O). Their distribution on segments of an antenna is uniform but does not extend to the segmental articulations, sensilla sockets, and belt-like cuticular rings on segments of the flagellum (flagellomeres). Sometimes (in Molannidae: *Molanna*) microtrichia are also absent on male specialized sensory zones of flagellomeres (Melnitsky & Ivanov this volume). The microtrichia might serve as a "fur" making a thin, stable layer of air close to the body surface. This layer serves as a barrier against the thermal and water exchange and thus protects the insect from the extremes of the environment.

Structures other than microtrichia are many times less abundant. They make two distinct layers on the body surface: The superior level looks like tall trees above the inferior level of forest grass. The layers are very conspicuous on the antennae and palpi because of the large numbers of sensilla. The upper layer of structures consists of two structural variants. The first is the apparent sensilla that will be extensively discussed below. These sensilla are firmly attached to the surface and can resist a significant amount of physical damage. The second variant is represented by various scales and similar structures; they usually have large size, narrow bases, and can be easily lost and leaving only sockets on the surface of cuticle. This second type is not generally innervated and is a homologue to scales of butterflies. They can be easily mixed with sensilla and their particular structure is beyond the scope of this paper.

The apparent mechanoreceptors on the antennae are of several types: Long trichoid sensilla nearly perpendicular (more than 60°) to the antennal surface (Fig. 1A), very short trichoid sensilla near the segmental articulations, and small campaniform sensilla. These mechanoreceptors are very uniform throughout insects. Their structure in Trichoptera is not different from those of other related orders. Although the distribution and number of these receptors can provide some insight into the taxonomy and perception in caddisflies, we believe that these topics deserve a separate publication.

The most numerous receptors on the surface of an antenna are olfactory sensilla. They belong to both the upper and lower levels of structures and are very diverse. In the upper layer of antennae there are six types of trichoid sensilla having different external structure. (1) **Chaetoid sensilla** (Fig. 1A) are located solitary on the lateral surface on each flagellomere and are likely to be mechanoreceptors. This type of sensilla is widely represented in various families. (2) **Long-grooved trichoid sensilla** are slightly curved with ribbed surfaces (Fig. 1H). These are the predominant trichoid sensilla on the antennae of caddisflies. These sensilla have large sockets and occur in several variants according to the development of spiral turn of the ribs. The actual number and distribution of these variants require special investigations. (3) **Serrate trichoid sensilla** (Figs. 1B−D, F, G, M) are included in the list provisionally; in many cases these structures are loosely attached and are lost in damaged specimens. Their general appearance resembles the scales often mentioned in various insect orders. Most scales are not sensory structures and perform other functions. In some instances, *e.g.*, in Hydropsychidae, the serrate trichoid sensilla make clusters near the sensory fields on the undersides of an antenna and might have sensory functions. Longitudinal grooves on the surfaces of the serrate trichoid sensilla are provided with numerous sharp blades or teeth. There is a large variety of intermediate forms of grooved and serrate trichoids, for example, in the families Beraeidae and Thremmatidae. Sometimes the teeth on the ridges are so long that the shape resembles a comb (Fig. 1B). (4) **Annulated trichoid sensilla** (Fig. 1O) are characterized by the presence of transverse ribs on the surfaces of sensilla. This type of sensilla has been found in *Crunoecia irrorata*, *Lepidostoma elongatum* (Lepidostomatidae); and *Tasimia palpata* (Tasimiidae). (5) **Undulated trichoid sensilla** (Fig. 1P) with rolling longitudinal ribs as sinusoidal curves on a surface are located only in Lepidostomatidae. (6) **Smooth trichoid sensilla** (Fig. 1E, J, K) are short structures, curved at the tip with smooth surfaces and acute apices. They were found in representatives of most of the studied families. These sensilla are arranged more or less evenly on the surfaces of the antennae, sometimes are clustered in groups on the sensory fields. The maximum number is found on the sensory fields of the antennae in Phryganeidae, Limnephilidae, Apataniidae, and Molannidae. This type of sensilla has not yet been found in Odontoceridae and Tasimiidae. (7) **Pseudotrichoid sensilla** (Fig. 1I) are similar to trichoid sensilla but have blunt apices, sometimes with small terminal structures. Generally these sensilla have ridges along their surfaces. They resemble the contact chemoreceptors found on other body parts in different insects and might have a gustatory function.

We are not certain about some peculiar larger structures of the antennae in Lepidostomatidae, including (a) "squashes" (Fig. 1N) each with a narrow petiole and a swollen main part, and (b) very long and thin trichia (Fig. 1L). Both are numerous; trichia are smooth, and "squashes" have perforated walls in grooves between

ridges. These two forms were observed also in abundance on other body parts, *e.g.,* wings, and their sensory function is highly questionable. They might be a specialized type of scales.

The variety of sensory structures of the lower layer is often much higher than that of the upper layer. They reach the greatest density per unit area in certain representatives of infraorder Plenitentoria (*e.g.,* in some Apataniidae: *Allomyia*). In some instances these small sensilla of the lower layer are hidden in the dense cover of microtrichia or submerged in sockets (Fig. 3D). The hiatus between some types of these structures is subtle and, in several cases, intermediates seem to provide smooth transitions between these types in related species. Various smaller sensilla are localized closer to the surface of the cuticle in the lower layer of an antenna. (8) **Basiconic sensilla** (Figs. 3P, Q) have wide flat sockets that are sometimes (Fig. 3Q) flanked at one side with specialized microtrichia as in the coronal sensilla; the body of a basiconic sensilla is represented by a conically tapered hair with sides and lobe-like microstructures in several blades on tip. This type of antennal sensilla probably is found in the majority of caddis families. Usually at least one basiconic sensillum is found on each flagellomere; they are not numerous. (9) **Coronal sensilla** (Fig. 3K–M) are similar to basiconic, but their sockets have numerous cuticular outgrowths around the circumference. This type has been found in Philopotamidae, Hydropsychidae, and Molannidae.

Several types of lower level sensilla, as far as we know, have been found only in caddisflies. Most of them are pseudoplacoid sensilla which are very specialized and diverse. They are found in all families except Philorheithridae, Odontoceridae, Tasimiidae, and some species of Goeridae and Lepidostomatidae. Comparative analysis allowed identification of seven types of pseudoplacoids on the antennae of Trichoptera. (10) **Mushroom-like pseudoplacoid sensilla** (Figs 2A, B, E, F, I, J, L; 3A–D, I, J, R) are the most prevalent pseudoplacoid sensilla in caddisflies. The form of the apical portion of a pseudoplacoid sensillum (similar to a plate or mushroom cap) can vary greatly in different taxonomic groups. As a rule, it looks like a horizontal or slightly concave, rounded, or oval mushroom or plate on a petiole with complicated microstructures on the top surface appearing as a net of small furrows and depressions. The shape and size of plate may vary. Mushroom-like pseudoplacoid sensilla are not found in Phryganeidae, Goeridae, Oeconesidae, Sericostomatidae and Kokiriidae. (11) **Bilobed pseudoplacoid sensilla** (Fig. 2D) are similar to the mushroom-like sensilla but have the apical plate dissected into two lobes. This type of sensilla is found in two subfamilies of the family Limnephilidae: Dicosmoecinae, and Limnephilinae (tribes Chilostigmini and Stenophylacini). They may be derived from the mushroom-like sensilla, but with excision: An initial stage of this transformation can be seen in Molannidae (*Molanna* spp: Melnitsky & Ivanov this volume) where the cap of sensilla is provided with a notch. These excisions vary among species; it can be assumed that in an extreme case, two such excisions meet at the petiole of a sensilla to form two terminal lobes. (12) **Forked pseudoplacoid sensilla** (Figs 2G, H, K–N; 3H) are highly variable in size, structure and form. They have been found on the antennae of Rhyacophilidae, Phryganeidae and Goeridae. Forked sensilla are present in all investigated species of Phryganeidae but, in our opinion, their persistence varies. For example, in Rhyacophilidae, small forked sensilla are found in *Rhyacophila nubila* along with typical mushroom-like sensilla (Ivanov & Melnitsky 2011). Long forked sensilla are present in *Goera tungusensis* and absent in *Goera pilosa*. It should be noted that the bilobed and forked sensilla are similar. The main difference is that the two terminal outgrowths of these sensilla are oriented more or less horizontally in bilobed types and turned upwards in forked types; the common stem of a bilobed sensillum is relatively long and narrow compared to its terminal lobes and in the stem of a forked sensillum is short and the same thickness as the terminal lobes or thicker. (13) **Dentate pseudoplacoid sensilla** (Figs 2C, O) have several pointed spines on the stalk of a sensillum that may be either flattened (*e.g.,* in *Anabolia laevis*) or saccular (*e.g.,* in *Halesus tessellatus*). This type of sensilla is found in Limnephilidae (Limnephilinae: Limnephilini, Stenophylacini; Pseudostenophylacinae), and Apataniidae (*Baicalina bellicosa*). (14) **Horn-like pseudoplacoid sensilla** (Fig. 3E, F) have a conical shape with a depressed apical part. They are found only in *Sericostoma personatum*—the only species in Sericostomatidae that we studied. The shape of the depression is highly variable, and the sizes and outlines of sensilla are also diverse. (15) **Stellate pseudoplacoid sensilla** (Figs 3G, H) were observed in *Oeconesus maori* (Oeconesidae) from New Zealand. The main part of this structure is a wide stalk provided with an elegant crown of several (6–8) short terminal projections.

The sensilla heads of lower level sensilla generally are elevated above the antennal surface but do not protrude far beyond the microtrichia; in some instances, the cap is level with the antennal surface or is even in the socket below the surface. Thus, formally one can recognize the "typical" pseudoplacoids if their terminal parts are above or on the same level with the socket border, and "coeloconic" pseudoplacoids (*e.g.,* in some

Limnephilidae) if they are entirely inside the socket. Similarly, the coronal and basiconic sensilla also can be submerged below the antennal surface in deep sockets. We do not separate the "coeloconic" sensilla from other structural types and expect to have more comparative data from future investigations to be certain if the coeloconic sensilla can be recognized as a distinct type in the general sensilla classifications.

Discussion

Internal structures of the sensilla in Trichoptera were studied by Slifer and Sekhon (1971) on *Frenesia missa* (Milne). They found that the walls of "sensory pegs" (cuticular outgrowths of sensilla) can be entire or perforated by pores. Some sensilla are multineuronal (up to 5 sensory neurons). Data on the internal structure of pseudoplacoid sensilla have been preliminary reported by us at the ESITO conference (Zueva *et al.* 2011). Our data show that the internal parts of these sensilla consists of a cuticular part and soft tissue. The cuticular structures in cross-sections are represented by the depressed thin-wall socket surrounded by elevated cuticular ring of thick cuticle, and the body of the sensillum projecting from the bottom of the socket. The body typically has a well-developed wide stalk and an enlarged head that in the studied species (*Philopotamus montanus* (Donovan) is similar to the mushroom cap, with its concave dorsal surface with numerous radial grooves originating from a small central projection and elevated margins. These grooves have numerous perforations opening as tiny pits. Perforations were found also on the underside of cap margin. Each pseudoplacoid has a very thin cuticle compared to the normal antennal surface, including the outer parts of the socket. The perforations on the dorsal surface and partly on the ventral surface near the margins in *Ph. montanus* all lead to channels connected to the dendrites of the sensory neurons. These dendrites are visible on the TEM electron microphotographs as thin threads in the sensillum lymph which occupies the central part of the internal space in the head; they branch below the sensillum head surface, forming a dense plexus. The lateral parts of the stalk have several small cells that probably secrete the cuticle of the sensillum and the aqueous sensillum lymph. The dendrites enter the lymph in a narrow bundle. There are up to six neuron bodies with large nuclei visible below the sensilla. They are tightly packed, leaving almost no space for other structures except for a few smaller hypodermal cells. There is almost no space between the groups of neurons below the neighboring receptors in Philopotamidae—The distribution of these multicellular sensilla on their antennal surface is apparently limited by the space necessary for the neuron bodies.

The pores and ridges are visible mostly on the upper surface of the mushroom-like pseudoplacoids; the grooves have been noted also on the ventral surface of the head in *Wormaldia simplicissima* Melnitsky & Ivanov, and pores were found on the underside of mushroom caps in *Philopotamus montanus* (Zueva *et al.* 2011). More data are necessary to prove the occurrence of these microstructures on the ventral surfaces of mushroom caps of sensilla.

A review of past data on adult sensilla in Trichoptera by J.G. Crespo (2011) revealed a mixture of terminology concerning the cuticular parts of sensilla. While chaetica, campaniformia, squamiformia types by Tozer (1982) are based on Snodgrass' terminology, the thick-walled chemoreceptor pegs, thin-walled chemoreceptor pegs, thin-walled pegs in a depression, and a special type of thin-walled chemoreceptor called plate organs by Slifer & Sekhon (1971) are inherited from Slifer's (1970) nomenclature using the internal criterion (wall thickness) for the classification. Hallberg and Hansson (1999) recognized sensilla trichodea, placodea, bifida, coeloconica, and chaetica using the data by Slifer and Sekhon (1971), and consider the sensilla as mostly olfactory except for the last type, a probable mechanoreceptor or gustatory sensilla.

Comparing to our extended classification based on many more taxa, we can assume that our chaetoid and trichoid types of sensilla are an extended classification for chaetica (by Tozer) and trichodea (by Hallberg & Hansson) types. We prefer here the terminology unified with other sensilla types and see the gap between various types. Contrary to Tozer (1982), we do not pay much attention to the size of sensilla because the different size groups observed in a single species make a continuum when examining additional taxa. The "thick-walled chemoreceptor pegs" by Slifer and Sekhon (1971) are trichoids, "thin-walled chemoreceptor pegs" are mostly the smooth trichoid sensilla; their "thin-walled pegs in a depression" are comparable to basiconic sensilla (in its coeloconic form), and the "plate organs" stated as the unique sensillar type found only in Trichoptera are the mushroom-like pseudoplacoids (placoid sensilla by Hallberg & Hansson 1999).

Various types of sensilla outlined above were partly discussed previously (Ivanov & Melnitsky 2011; Melnitsky & Ivanov 2011). New data provided by additional taxa showed the persistence of major sensilla

types throughout the order Trichoptera. Additionally we have an improved understanding of sensilla types and their distribution in relation to the previously studied species (Melnitsky & Ivanov 2011). The original version have been published in the Russian version of the "Journal of Evolutionary Biochemistry and Physiology" dated the same year. The main efforts, in our opinion, should be concentrated on comparative studies within the families because we found significant variations on lower taxonomic levels and persistence of major structural types of sensilla throughout the order Trichoptera.

So far, structures of the cuticle have had very limited use in Trichoptera taxonomy and studies of phylogeny (Vshivkova *et al.* 2007). Major problem in such studies is the large diversity of cuticular derivatives and a lack of physiological data. Hence the present level of physiological knowledge provides very limited support for studies of morphology and taxonomy. Another problem is the variation and transitions in cuticular microstructures, making the typology unstable.

Functions of the sensilla are poorly studied and the material for Trichoptera is limited (Larsson & Hansson 1998). Previous GC-EAD studies of olfactory reception (*e.g.*, Löfstedt *et al.* 2008) show the total responses of whole antennae to volatiles and cannot help distinguish the functions of individual sensilla. Most of these sensilla are supposed to be olfactory, although some of them are probably mechanoreceptors, and some resemble gustatory sensilla. Reduction of antennal sensilla occurs in a few cases, *e.g.*, in Lepidostomatidae and in some Apataniidae where the pseudoplacoid sensilla have a tendency to reduction throughout a family (Lepidostomatidae) or less-inclusive taxon (in species of Apataniidae: Baicalinini). Similar reduction was found in *Mystacides longicornis* (Ivanov & Melnitsky 2011), a species with altered mating behavior and no pheromone communication (Solem & Petersson 1987). It is known that this species also is devoid of an olfactory center in the brain (Ehnbom 1948). Thus, the pseudoplacoid sensilla are a part of olfactory communicative system. Based on this inference, one can expect highly modified types of mate search and recognition in Lepidostomatidae and some Apataniidae.

Pseudoplacoid sensilla also are found on antennae outside the order Trichoptera in the representatives of primitive Lepidoptera. Mushroom-like pseudoplacoids have been reported by Faucheux (2004a, 2004b, 2004c) as "sensilla placodea" in Micropterigidae where they are observed in several different structural forms. Similar sensilla but in a derived form have been found in Agathiphagidae and Eriocraniidae (Faucheux 1990; Larsson *et al.* 2002) as "multiporous sensilla auricillica."

Our comparative analysis suggests that the antennal sensilla may be important characters in studies of taxonomy and evolution. This analysis is yet far from completion, and the lack of information for some key families necessary for taxonomy is obvious. Nonetheless, some characters, *e.g.*, formation of sensory fields, distribution of sensilla types, and development of peculiar types of sensilla are promising for taxonomy. The number and distribution of sensilla on the antennal segments are also very interesting and have potential as diagnostic and phylogenetic characters for less-inclusive taxonomic levels.

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