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A comparison of the external morphology and functions of labial tip sensilla in semiaquatic bugs (Hemiptera: Heteroptera: Gerromorpha)

Jolanta BROŻEK[1] and Herbert ZETTEL[2]

[1]Department of Zoology, Faculty of Biology and Environmental Protection, University of Silesia, Bankowa 9, PL 40-007 Katowice, Poland; e-mail: jolanta.brozek@us.edu.pl

[2]Natural History Museum, Entomological Department, Burgring 7, 1010 Vienna, Austria; e-mail: herbert.zettel@nhm-wien.ac.at

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Abstract. The present study provides new data on the morphology and distribution of the labial tip sensilla of 41 species of 20 gerromorphan (sub)families (Heteroptera: Gerromorpha) obtained using a scanning electron microscope. There are eleven morphologically distinct types of sensilla on the tip of the labium: four types of basiconic uniporous sensilla, two types of plate sensilla, one type of peg uniporous sensilla, peg-in-pit sensilla, dome-shaped sensilla, placoid multiporous sensilla and elongated placoid multiporous subapical sensilla. Based on their external structure, it is likely that these sensilla are thermo-hygrosensitive, chemosensitive and mechano-chemosensitive. There are three different designs of sensilla in the Gerromorpha: the basic design occurs in Mesoveliidae and Hebridae; the intermediate one is typical of Hydrometridae and Hermatobatidae, and the most specialized design in Macroveliidae, Veliidae and Gerridae. No new synapomorphies for Gerromorpha were identified in terms of the labial tip sensilla, multi-peg structures and shape of the labial tip, but eleven new diagnostic characters are recorded for clades currently recognized in this infraorder. One synapomorphy is recorded for Hydrometridae + Hermatobatidae + Macroveliidae + Veliidae + Gerridae; five for Macroveliidae + Veliidae + Gerridae; one for Veliidae + Gerridae; and one for Gerridae alone. Within Gerridae, one possible autapomorphy is recorded for Trepobatinae, and two possible autapomorphies for Rhagadotarsinae. We also record a possible autapomorphy for Cylindrostethinae, which indicates that this taxon is monophyletic, as is indicated by other morphological characters. Finally, we record one putative diagnostic character for Macroveliidae + Veliidae, two families that are otherwise not considered sister groups. This new set of characters based on features of the mouthparts of gerromorphan bugs might provide new insights into the cladogenesis of the infraorder.

INTRODUCTION

Mouthparts of Gerromorpha, or semiaquatic bugs, are of the same piercing and sucking type found in other hemipterous insects. The rostrum or beak consists of a four-segmented, sheath-like labium enclosing two pairs of long stylets, the outer mandibular and inner maxillary pair (Cranston & Sprague, 1961; Cheng, 1966; Andersen, 1982; Schuh & Slater, 1995).

In Gerromorpha and other taxa of Heteroptera, the apical segment of the labium is tripartite and consists of two lateral lobes and a middle lobe (apical plate) situated on the ventral side. There are only sensory structures on the tips of the lateral lobes (Cobben, 1978; Hatfield & Frazier, 1980).

In hemipteran insects the labial tip sensilla monitor the outer surface of the plant or animal food source, whereas the inner sensory organs (e.g., cibarial sensilla) come into direct contact with the food as it is ingested (Miles, 1958; Backus, 1985; Chapman, 1998). Consequently, the labial tip sensilla can apparently perform both chemosensory and mechanosensory functions while bugs explore the surface of plants or animals with their labium.

On the tip of the labium of true bugs there are a number of differently shaped and differently sized chemo- (gustatory, contact chemoreceptors) and mechanosensilla. Different types of labial sensilla (chemo- and mechanosensilla) are recorded in several species of Nepomorpha (Benwitz, 1956; Lo & Acton, 1969; Cobben, 1978; Jarial, 2003; Brożek, 2008), Pentatomomorpha (Schoonhoven & Henstra, 1972; Khan, 1972; Peregrine, 1972; Gaffal, 1981; Rani & Madhavendra, 1995; Ventura et al., 2000; Ventura & Panizzi, 2005) and reduviids of the Cimicomorpha (Bernard, 1974; Catalá, 1996; Rosa et al., 1999; Brożek & Chłond, 2010). On the basis of a comparison of the morphological characteristics of labial sensilla and their distribution in Reduviidae (Triatominae and Peiratinae), it is suggested that interspecific diversity and intraspecific similarity in the shape and numbers of labial sensilla could be used as taxonomic/diagnostic characters (Catalá, 1996; Brożek & Chłond, 2010).

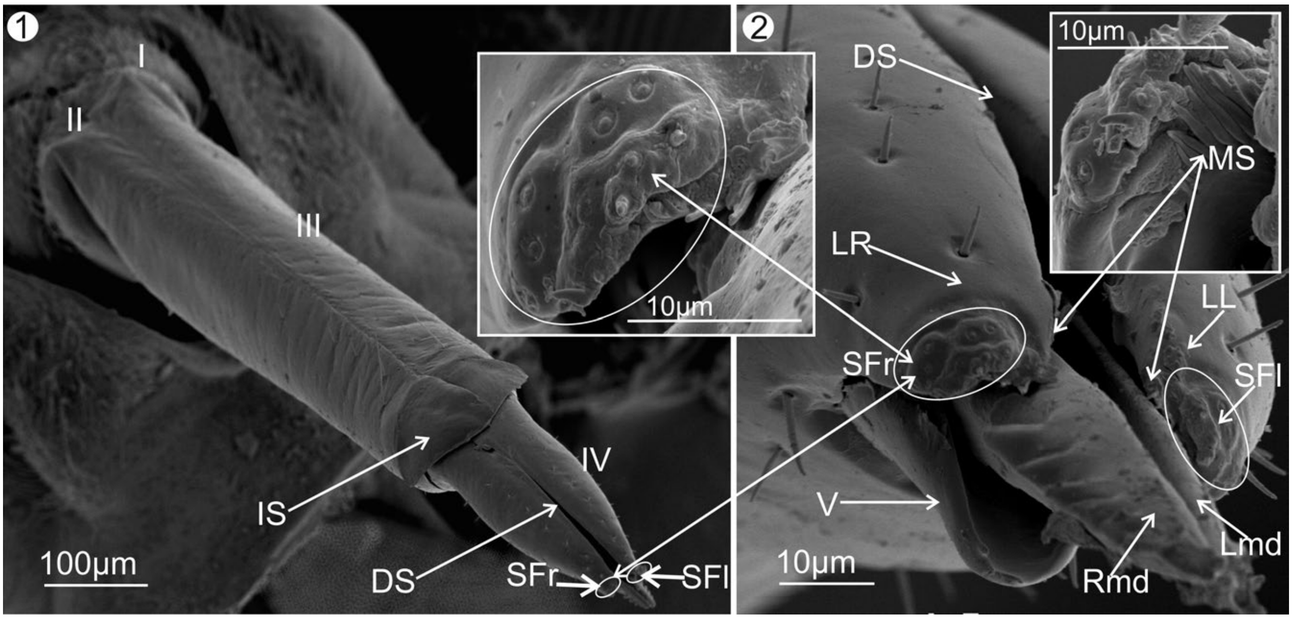
Little is known about the labial sensilla of Gerromorpha. In earlier studies it was revealed that the presence of sensory hairs on the labial tip is helpful in localizing suitable spots for penetration of the prey (Cheng, 1974; Andersen, 1976, 1977). Cobben (1978) indicates that in the gerrid *Aquarius najas* (De Geer) the terminal labial sensilla (which he called nipple-like sensilla) are more or less spherical and can be inserted into solid cuticle. There is little data on the typical gustatory sensilla in Gerromorpha, and only in the gerrid *Aquarius remigis* (Say) is the epipharyngeal sense organ described as gustatory (Cranston & Sprague, 1961). We decided to conduct a morphological study of the labial tip sensilla of gerromorphan groups in order to determine their diversity and phylogenetic significance.

Damgaard (2008) has proposed a new cladogenesis for the Gerromorpha and reclassified the superfamilies Ger-

TABLE 1. Description, terminology and definition of insects sensilla used in the present study with examples of sensilla on the labium of various hemipteran insects are also presented. Abbreviations used for gerromorphan taxa in the present study are explained in the last column.

Category and function of insect sensilla	Ultrastructure of insect sensilla	External morphology of insect sensilla	Types of (sub)apical sensilla on the labium in Hemiptera	Sensilla on labial tip in Gerromorpha
A. Bimodal no-pore (Np) sensilla: Hygrosensitive and thermosensitive (Altner & Prillinger, 1980; Chapman, 2003).	Three neurons. Dendrites of two are unbranched and extend into peg lumen; hygrosensitive, one responds to increasing humidity (moist receptor), the other to decreasing humidity (dry receptor). Third dendrite (thermosensitive) is folded into tightly packed lamellae or a whorl below peg base, responds to changes of temperature (cold receptor) (Altner, 1977; Altner et al., 1977; Altner & Loftus, 1985). All dendrites surrounded by a sheath (Altner & Prillinger, 1980; Chapman, 1998).	Short peg concealed in a pit or incompletely closed cavity in the cuticle (coeloconic sensilla) with an inflexible socket, lacking pores (except for terminal moulting pore) (Altner & Prillinger, 1980; Shields, 2010).	Peg in pit sensilla, apical: *Rhodnius neglectus*, *Triatoma infestans* (Catalá, 1996), *Peirates hybridus* (Brożek & Chłond, 2010). Peg in pit sensilla, distal on first labial segment in Peiratinae (*Lamotteus ornatus*, *Thymbreus crocinopterus*, *Brachysandalus bicolor*, *Melanolestes picipes*) (Brożek & Chłond, 2010).	Peg in pit sensilla (Np-pip).
B. Unimodal contact chemoreceptors (gustatory) with one terminal pore (Tp) (Altner & Prillinger, 1980; Zacharuk, 1980; Chapman, 1998).	Three to 10 neurons (Altner & Prillinger,1980; Chapman, 2003). Dendrites do not branch, extend along the length of the pegs and terminate just beneath the pore. Dendrites usually enclosed in a cuticular sheath (Altner & Prillinger, 1980; Zacharuk 1980).	Hair, basiconic, peg-, or plate-like structures, raised above the surface or flat, with inflexible socket. Single pore at the tip of the projection (Altner & Prillinger, 1980; Zacharuk, 1980, Mitchel et al., 1999). Pores may be simple or stellate, with grooves converging at the pore or with more complex fingerlike projections that surround the opening (Zacharuk, 1985; Mitchell et al., 1999).	Apical: Peg sensilla, *Parabemisia myricae* (Walker & Gordh, 1989). Basiconic sensilla, *Lygus lineolaris* (Avé et al., 1978). Peg sensilla: PP-S, Peiratinae (Brożek & Chłond, 2010); PS, Triatominae (Catalá, 1996). Papillate sensilla: PAS1 (short peg with a flattened tip) in Nepidae and Belostomatidae and PAS2 (short peg with a tappered tip) in remaining Nepomorpha (Brożek, 2013). Tall peg sensilla (PGUS1), short peg sensilla (PGUS2) and clavate sensilla (CLUS) in Fulgoromorpha (Brożek & Bourgoin, 2013). Subapical: Dome-shaped (PDS) and elongated dome-shaped (UDES) in Peiratinae (Brożek & Chłond, 2010).	Oval plate sensilla (Tp-opls), triangular plate sensilla (Tp-tpls), dome-shaped sensilla (Tp-ds).
C. Bimodal mechano- and contact chemoreceptors (tactile and gustatory) with one (sub)terminal pore (Tp) (Altner & Prillinger, 1980; Chapman, 1998).	Three to 10 neurons (Chapman, 2003). Chemosensitive dendrites do not branch, extend to tip of cone, entirely enclosed within dendritic sheath. One mechanosensitive dendrite ending in tubular body at the base of the cone (Chapman, 1998).	Hairs or various cones (peg and basiconic, short or tall) with single pore at or close to the tip. Sensilla are exposed and articulated in a flexible socket. Often tapering apically. Cuticular walls smooth, with a moulting pore near the base (Altner & Prillinger, 1980; Chapman, 1998).	Apical: Basiconic sensilla in *Dysdercus fulvoniger*, *D. koenigii*, *D. fasciatus*, *D. intermedius* (Gaffal, 1981), *Lygus lineolaris* (Avé et al., 1978), and *Parabemisia myricae* (Walker & Gordh, 1989). Peg sensilla (tall pegs and short peg) in *Odontopus nigricornis* and *Nezara viridula* (Rani & Madhavendra, 1995).	Sensilla basiconica: short (Tp-bss), tall or high (Tp-bhs), double (Tp-bds), with a flat socket (Tp-bfs), peg-like (Tp-ps).
D. Unimodal (olfactory) or bimodal (olfactory and thermosensitive) multiporous sensilla with wall pores (Wp) (Altner & Prillinger, 1980; Chapman, 1998).	Olfactory: One to 50 neurons. Dendrites have a sheath only within the receptor lymph cavity. Dendrites extending into the lumen of the cone lack a sheath, are branched or unbranched, may approach the cuticle of pore plates (Altner & Prillinger, 1980; Chapman, 1998). Olfactory and thermosensitive: One to 5 neurons, dendrites branched or not. One thermoreceptive dendrite (cold receptor), information on warm receptor is lacking, remaining neurons are olfactory (Altner & Prillinger, 1980).	Olfactory: Variable form and size: cones, bristles, placoid, elongate placoid, coeloconic, spherical or flattened porous cuticular areas (Altner & Prillinger, 1980; Zacharuk, 1980; Brożek & Chłond, 2010). Single-walled wall-pore sensilla of Altner & Prillinger (1980), multiporous sensilla of Zacharuk (1980), or thin-walled sensilla of Slifer (1970). Olfactory and thermoreceptive: Porous double walls, frequently pegs, basiconic or coeloconic (Altner and Prillinger, 1980). Both types of sensilla with inflexible sockets.	Apical, olfactory: Placoid (OPSM) in Nogodinidae, peg, complex peg, cupola- or dome-shaped in other Fulgoromorpha (Brożek & Bourgoin, 2013). Subapical, olfactory and thermosensitive: Sa-ECLT sensilla (elevated, cone-like to tubular) in Cixiidae, Meenoplidae and Lophopidae; Sa-TEBM sensilla (branched or multilobed tubular) in Delphacidae; however, the placoid sensilla (Sa-PFPL) in Ricaniidae, Dictyopharidae, Tropiduchidae, and Nogodinidae might respond only to odors (Brożek & Bourgoin, 2013), and sensilla placodea (PPLS) in Peiratinae (four species) presumably also have olfactory function (Brożek & Chłond, 2010).	Placoid sensilla (Wp-pls), subapical elongated placoid sensilla (Wp-ples).

A non-typical intermediate (uniporous/multiporous) sensillum basiconicum D was described by Peregrine (1972) and Gaffal (1981) on the labial tip of *Dysdercus fasciatus* and *D. intermedius* (Heteroptera: Pentatomomorpha: Pyrrhocoridae). This sensillum is short (5–7 µm height) and differs in ultrastructure from the tall (20 µm) sensilla basiconica A (10 pairs). The basal two-thirds of the shaft is thick-walled due to the presence of a lamellated endocuticular layer and traversed by perforations to about the same extent as the surrounding labial cuticle. The apical third lacks an endocuticular layer and is more extensively perforated with a system of pore tubules extending into the shaft lumen. The sensillum is innervated by two dendrites, one of which has a six-fold greater diameter (1.2 µm) than the other (0.2 µm). Both dendrites extend to the tip of the sensillum and are surrounded by a dendritic sheath whose apical part is irregularly wrinkled. This folded part has thinner walls and opens into the lumen of the sensillum. Many tubules terminate immediately at the tip of the dendritic sheath. Based on this description, the sensillum may represent an intermediate form between a single-walled type of wall-pore olfactory sensillum and a terminal-pore gustatory sensillum. Similar intermediate type of sensillum basiconicum has been described in other species of Pyrrhocoridae, *Dysdercus fulvoniger* and *D. koenigii*, by Schoonhoven & Henstra (1972).



Figs 1–2. General organization of the labium and the sensory field at the tip of the labium in Gerromorpha [the actual structures are those of *Velia caprai* (Veliinae)]. I–IV, number of labial segments; DS – dorsal side; IS – internal sclerites; Lmd – left mandible; LL – left lobe; LR – right lobe; MS – multi-peg structures (arrows indicate their location) on inner side of lobes (LL and LR); Rmd – right mandible; SFl – left sensory field; SFr – right sensory field; V – ventral lobe.

roidea and Hydrometroidea, which previously were distinguished by Andersen (1982), Muraji & Tachikawa (2000), Andersen & Weir (2004) and Damgaard et al. (2005). He suggests a close relationship between Hydrometridae and Hermatobatidae, and indicates a sister-group relationship between Hermatobatidae + Hydrometridae and Hebridae (although this was poorly supported and there were no convincing diagnostic morphological synapomorphies). Moreover, he also points out that Veliidae are a non-monophyletic group and proposes that the subfamilies Ocelloveliinae, Veliinae, Rhagoveliinae, Perittopinae, and Microveliinae + Haloveliinae be raised to family rank.

Recently, Perez-Goodwyn et al. (2009) have shown, that the gait (double tripod) in Hermatobatidae is intermediate between that of Mesoveliidae, Hebridae, Macroveliidae, and Hydrometridae, in which the gait (double tripod) is a plesiomorphic character, and the clade Gerridae + Veliidae with a gait that is autapomorphic (synchronous rowing). These authors have also identified a new synapomorphic character (horizontally directed meso- and metacoxa) in the superfamily Gerroidea (Hermatobatidae, Gerridae and Veliidae). These results are consistent with previous classifications of the Gerroidea: Hermatobatidae, Veliidae + Gerridae (Andersen, 1982; Andersen & Weir, 2004; Damgaard et al., 2005).

Many unresolved questions and absence of a strong confirmation of relationships between some of the gerromorphan groups are good reasons for looking for a new set of characters for establishing the monophyly of groups and their close relationships.

The aim of this paper is to find a new set of characters in Gerromorpha. The objectives include: 1. Determine whether there are differences in structure, distribution and number of the labial tip sensilla in the various (sub)families. 2. Attempt to identify the probable functions of the sensilla. 3. Identify the characters of the labial tip sensilla in the different systematic groups of Gerromorpha, which might be useful in future phylogenetic studies.

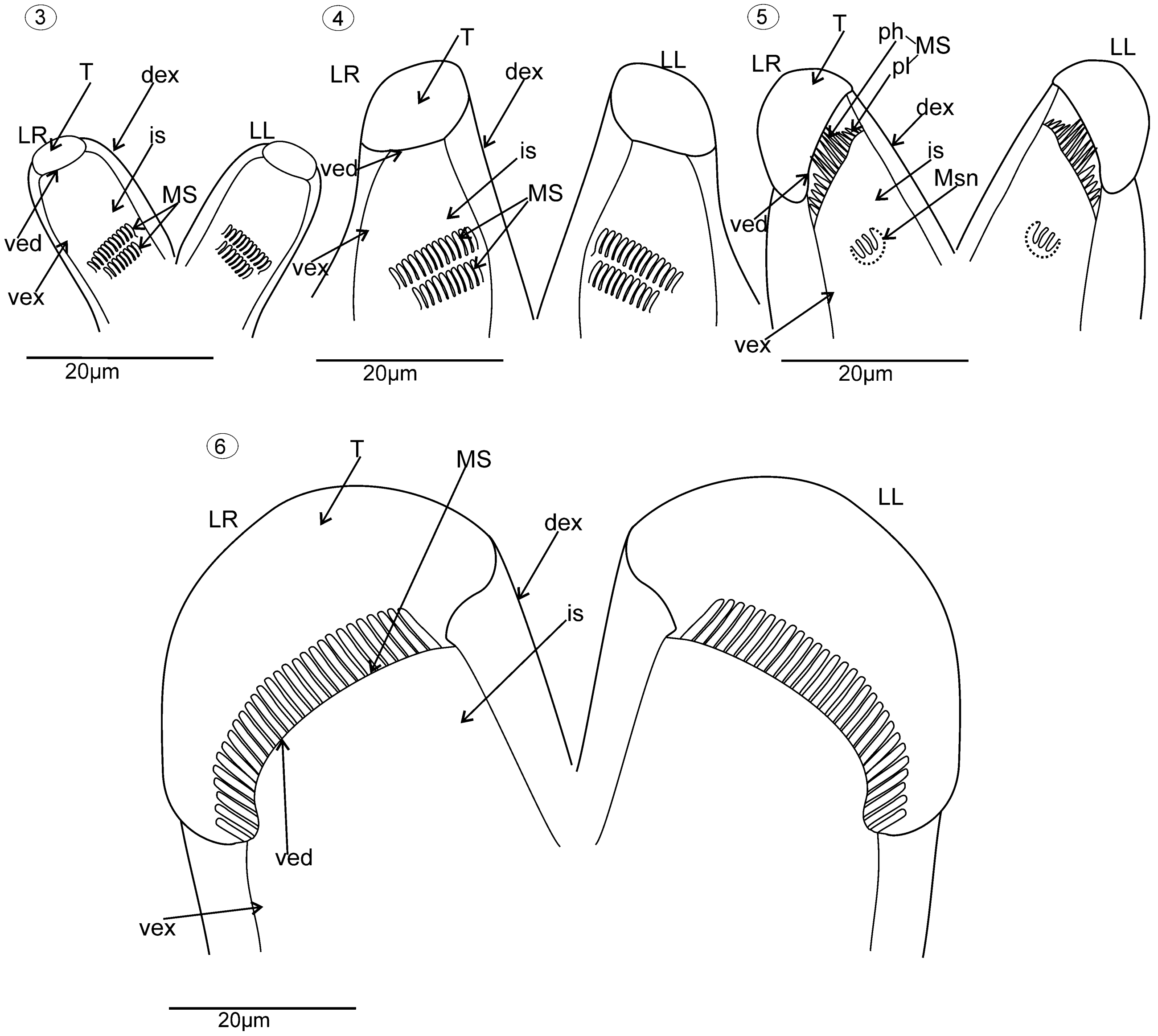
MATERIAL AND METHODS

Terminology used to describe apical sensilla

In this study, the terminology and classification of the apical labial sensilla is mainly based on the morphological criteria of sensilla established by Altner & Prillinger (1980) and Zacharuk (1980). The proposed functions of the sensilla of gerromorphan species are based on the morphological and ultrastructural characteristics of the receptors of insects described by several authors (Slifer, 1970; Altner & Prillinger, 1980; Zacharuk, 1980; Chapman, 1998, 2003). The ultrastructural and general morphological characteristics of sensilla of insects, as well as some examples of sensilla in different hemipteran insects similar to the currently described shapes and functions of labial tip sensilla of the Gerromorpha, are presented in Table 1 (except for the unimodal no-pore mechanosensitive sensilla such as tactile hairs and campaniform sensilla which have not been identified on the labial tip). Some of the information on the structure of sensilla used to describe previously unrecorded labial tip sensilla such as sensillum basiconicum, double – (Tp-bds), sensillum basiconicum with a flat socket – (Tp-bfs), oval plate sensilla – (Tp-opls), triangular plate sensilla – (Tp-tpls), and elongated placoid sensilla (Wp-ples), came from the interpretation of insect sensilla by the aforementioned authors. The remaining types of sensilla mentioned in the present paper (Table 1) were previously described by the following authors: Altner & Prillinger (1980), Zacharuk (1980), Chapman (1998), Brożek & Chłond (2010).

Taxa sampled

This study is based on dry material of 41 species belonging to 20 (sub)families (listed in Table 2). All material was dissected (i.e., all heads) and the basal part of the head with the labium was glued vertically onto the stage of a scanning microscope, coated



Figs 3–6. Locations of multi-peg structures (MS). 3 – Mesoveliidae and Hebridae; 4 – Hermatobatidae; 5 – Macroveliidae and Veliidae; 6 – Gerridae. dex – dorsal side; is – internal side; LL – left lobe; LR – right lobe; MS– wide row of multi-peg structures; Msn – narrow row of multi-peg structures, ph – tall pegs; pl – short pegs; T – labial tip; ved – ventral edge; vex – ventral side. Figs 3–4 – multi-peg structures do not occur on the ventral edge of the labium; Fig. 5 – a few of the multi-peg structures occur on the ventral edge; Fig. 6 – multi-peg structures occur on the ventral edge. Scale bar = 20 μm.

with a 65–70 μm film of gold and photographed using a Jeol scanning electron microscope. The specimens examined belong to the Natural History Museum, Vienna (NHMW).

Specimens of the subfamilies Madeoveliinae (Mesoveliidae), Heterocleptinae and Limnobatodinae (Hydrometridae), and of the family Paraphrynoveliidae were not included.

Photographs of the SEM images and several drawings of the labial tip sensilla and multi-peg structures of Gerromorpha subunits are presented in Figs 1–74.

Figs 3–6 and Figs 17–38 were prepared on the basis of several images at the same scale in order to present uniformly the sizes of multi-peg structures (Figs 3–6) and labial tip sensilla as well as the pattern of their distribution (Figs 17–38) on the labial tips of individual species.

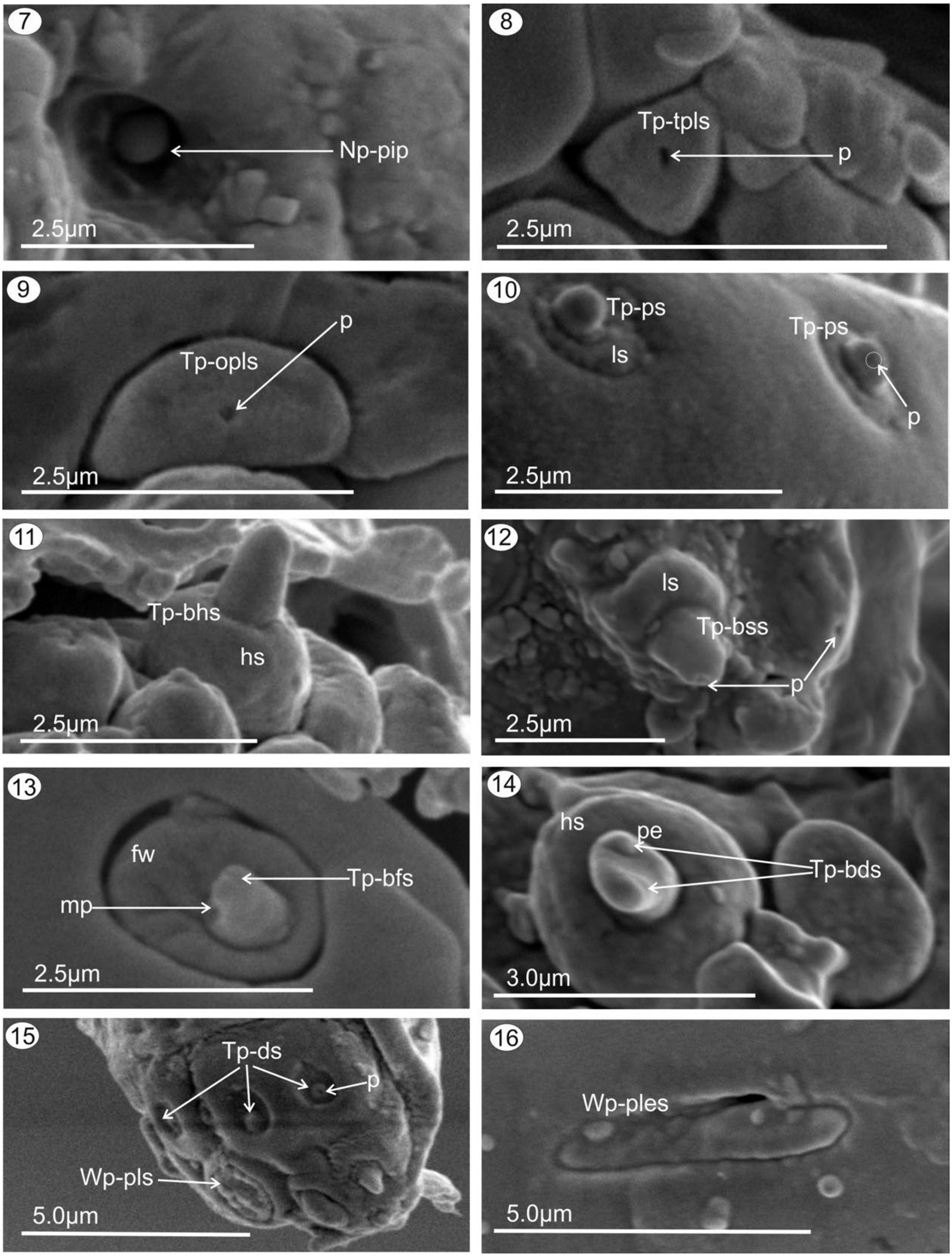
The original phylogenetical tree of Damgaard (2008) is inserted in Fig. 75, in order to present the relationships of gerromorphan families proposed by this author.

Schemas of the shapes and number of labial tip sensilla in individual species are summarized in Table 2.

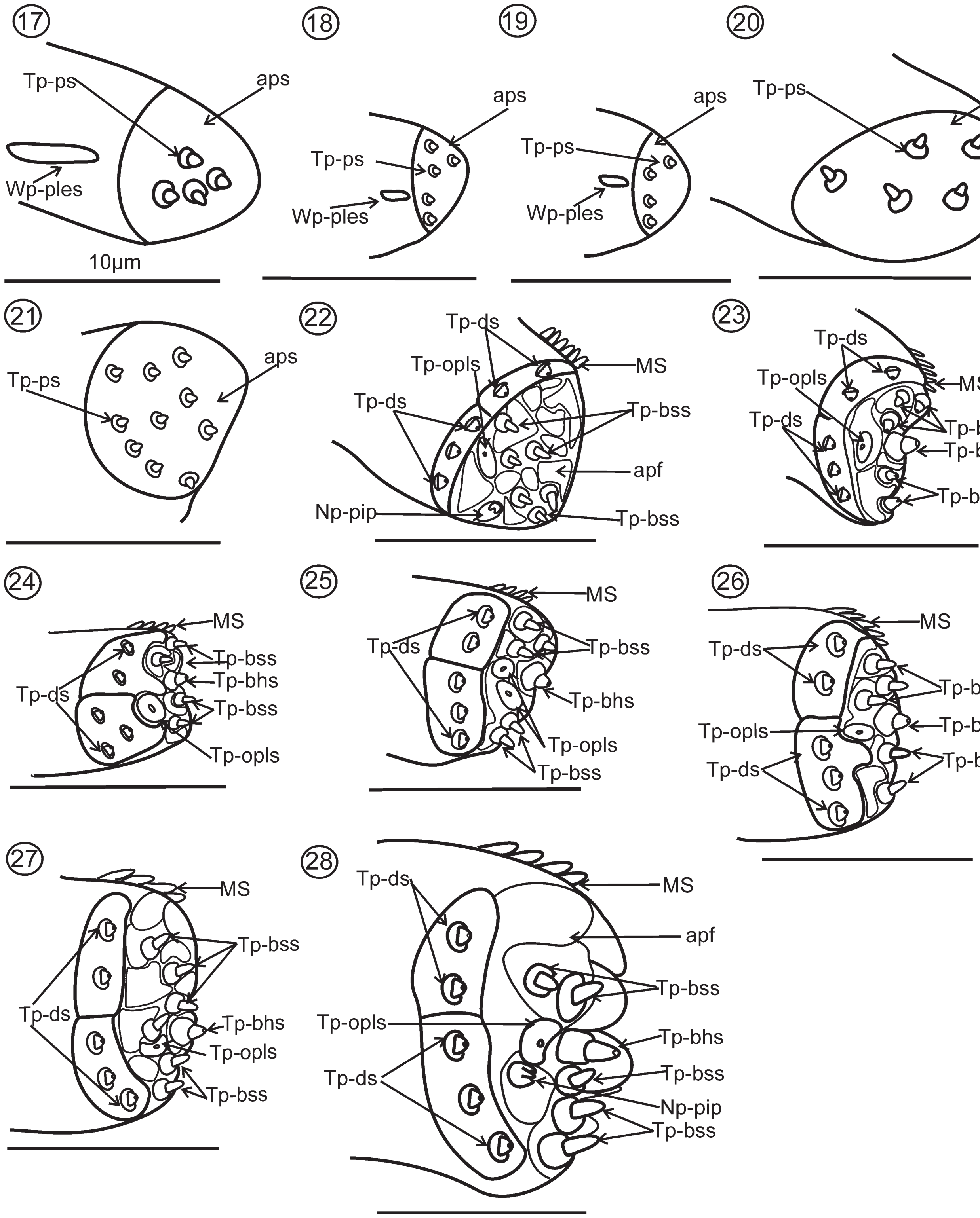
RESULTS

Structure of the labial apex and labial tip sensilla

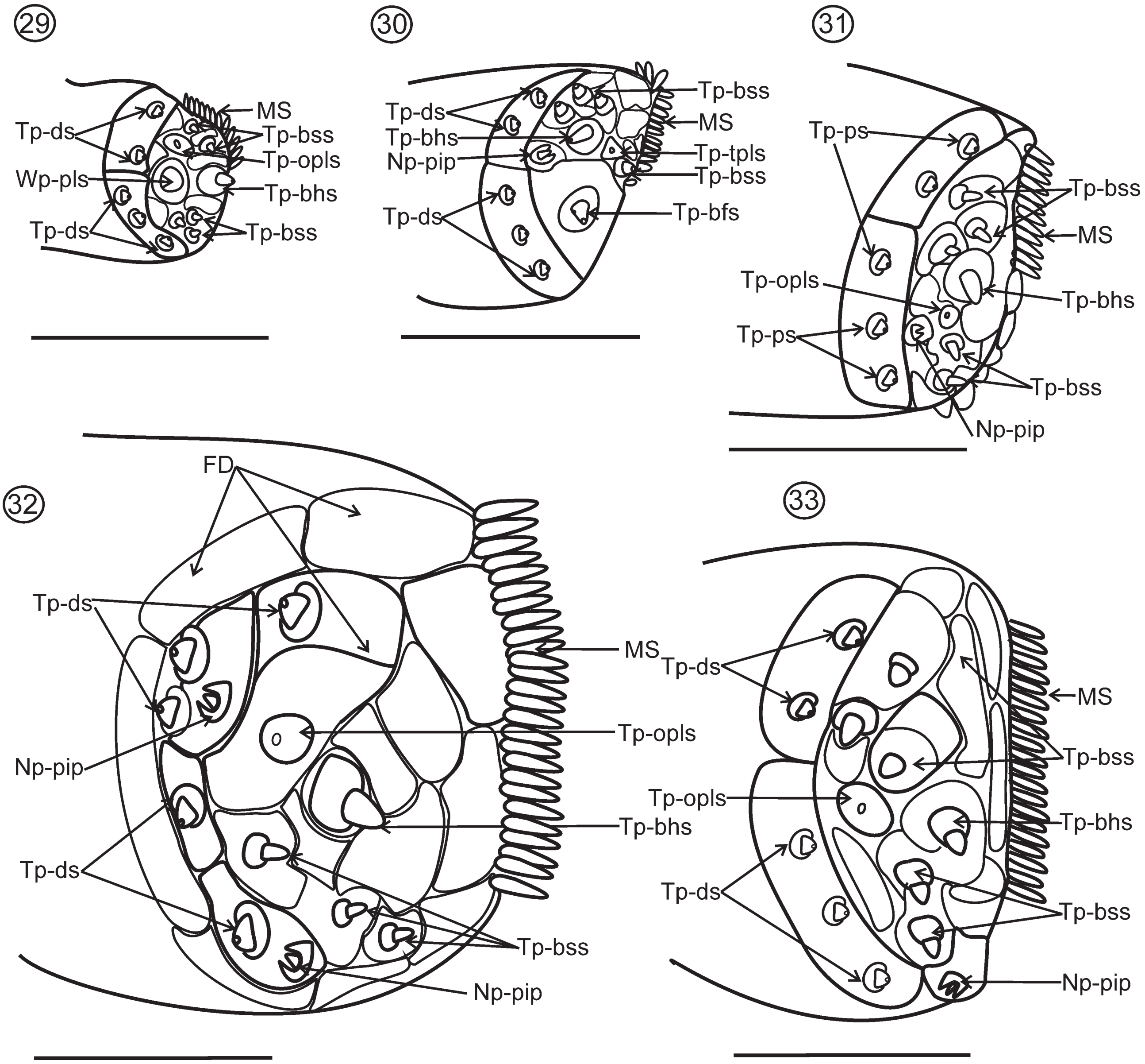
In semiaquatic bugs, the tip of the elongated labium (Fig. 1) is slightly rounded with two lateral lobes (left – LL and right – LR) and a ventral (V) lobe (Figs 1–2). The apical surface of the lateral lobes is smooth (Figs 17–21; Figs 39–44) or is divided by deep furrows into several folds (Figs 22–38; Figs 45–66), which resemble rounded knobs. At the tip of both lateral lobes there are sensory fields (SF: SFl – left and SFr – right) (Fig. 2), in which there are various morphological types of sensilla: plate (Figs 8–9), peg (Fig. 10), basiconica (Figs 11–14), placoid and dome-shaped sensilla (Fig. 15). Most of the labial tip sensilla are embed-



Figs 7–16. The different types of labial tip sensilla in Gerromorpha. 7 – Np-pip – peg-in-pit sensillum = coeloconic sensillum (*Paravelia basalis*); 8 – Tp-tpls – triangular plate sensillum with a terminal pore (*Rhagadotarsus kraepelini*); 9 – Tp-opls – oval plate sensillum with a terminal pore (*Velia caprai*); 10 – Tp-ps – peg sensillum with a terminal pore (*Hermatobates marchei*); 11 – Tp-bhs – tall basiconic sensillum with a terminal pore (*Amemboa brevifasciata*); 12 – Tp-bss – short basiconic sensillum with a terminal pore (*Velia caprai*); 13 – Tp-bfs – basiconic sensillum with a terminal pore and a flat socket (*Rhagadotarsus kraepelini*); 14 – Tp-bds – double basiconic sensillum with a terminal pore (*Potamobates tridentatus*); 15 – Tp-ds – dome-shaped sensillum with a terminal pore, Wp-pls – placoid sensillum with a multiporous wall (*Naboandelus signatus*); 16 – Wp-ples – elongated placoid sensillum with a multiporous wall (*Mesovelia furcata*). fw – flat and wide socket; hs – tall socket; ls – short socket; mp – a moulting pore; p – a terminal pore; pe – short peg.



Figs 17–28. The right sensory field; types and distribution of labial tip sensilla. 17 – *Mesovelia furcata*, (Mesoveliinae); 18 – *Timasius miyamotoi* (Hebrinae); 19 – *Nieserius subaquaticus* (Hyrcaninae); 20 – *Hydrometra aculeata* (Hydrometridae); 21 – *Hermatobates marchei* (Hematobatidae); 22 – *Macrovelia hornii* (Macroveliidae); 23 – *Ocellovelia fusca* (Ocelloveliinae); 24 – *Halovelia esakii* (Haloveliinae); 25 – *Microvelia douglasi* (Microveliinae); 26 – *Rhagovelia sumatrensis* (Rhagoveliinae); 27 – *Perittopus asiaticus* (Perittopinae); 28 – *Paravelia basalis* (Veliinae). apf – folded apex; aps – smooth apex; MS – multi-peg structures; Np-pip – peg-in-pit sensillum no-pore; p – pore; Tp-bhs – tall basiconic sensillum with a terminal pore; Tp-bss – short basiconic sensillum with a terminal pore; Tp-ds – dome-shape sensillum with a terminal pore; Tp-opls – oval plate sensillum with a terminal pore; Tp-ps – peg sensillum with a terminal pore; Wp-ples – elongated placoid sensillum, multiporous, subapical. Scale bar = 10 µm.



Figs 29–33. The right sensory field; different types of the sensilla and their distribution in Gerridae: 29. *Naboandelus signatus* (Trepobatinae); 30. *Rhagadotarsus kraepelini* (Rhagadotarsinae); 31. *Brachymetra albinervis* (Charmatometrinae); 32. *Limnometra nigripennis* (Gerrinae); 33. *Eurygerris fuscinervis* (Gerrinae). MS – multi-peg structures; Np-pip – peg-in-pit sensillum, no-pore; Tp-bfs – basiconic sensillum with a terminal pore inserted in flat socket; Tp-bhs – tall basiconic sensillum, with a terminal pore; Tp-bss – short basiconic sensillum, with a terminal pore; Tp-ds – dome-shaped sensillum with a terminal pore; Tp-opls – oval plate-like sensillum with a terminal pore; Tp-tpls – triangular plate-like sensillum with a terminal pore; Wp-pls – placoid sensillum, multiporous. Scale bar = 10 µm.

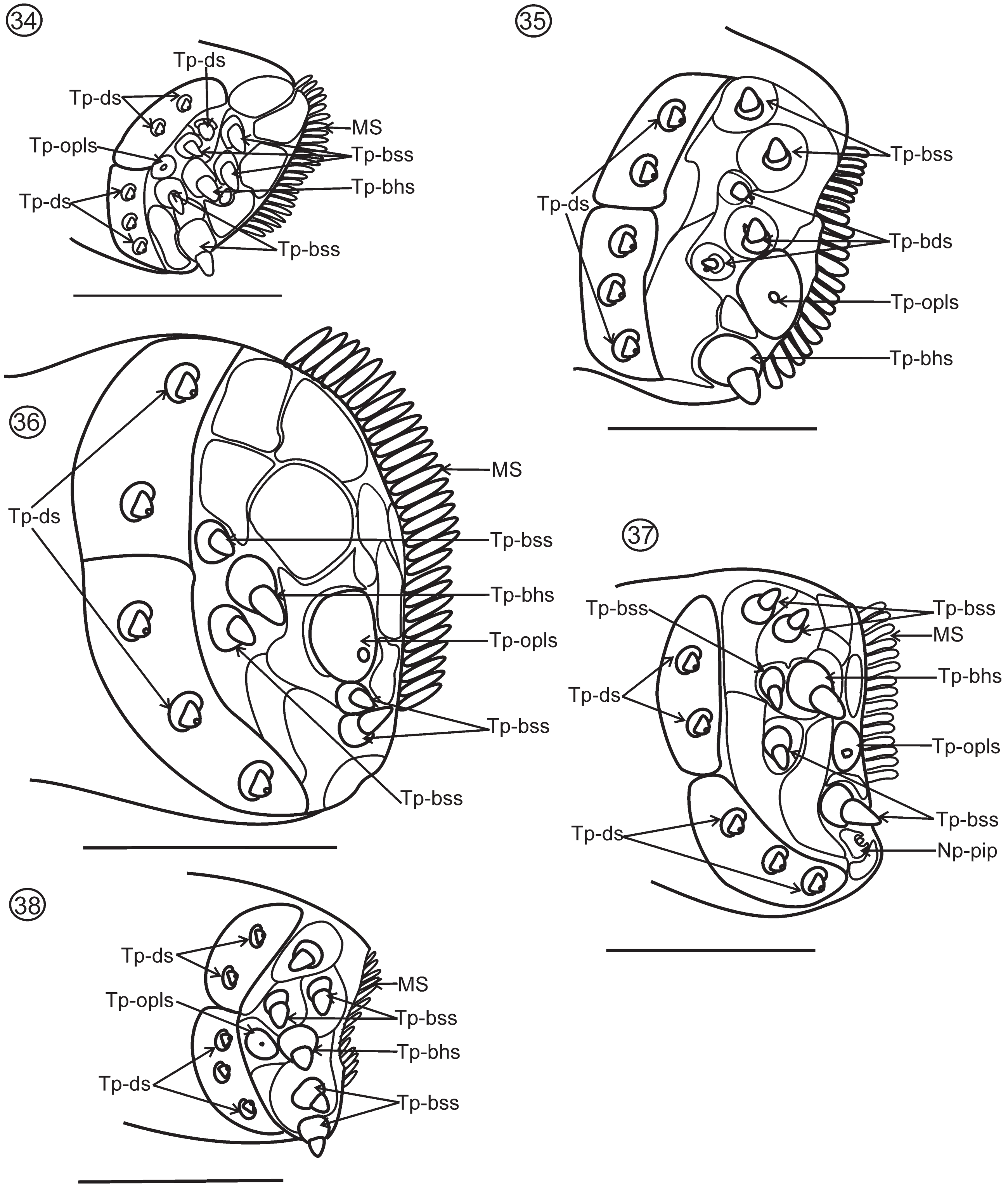
ded in sockets between the folds. Some sockets are short (ls) (Figs 10, 12), others are tall (hs) (Figs 11, 14) and flat and wide (fw) (Fig. 13), either allowing the sensillum to move (flexible sockets, Figs 10–14) or not (inflexible sockets, Figs 7–9; Figs 15–16).

At the rear, dorsal edge of the sensory field there is a series of transversely arranged dome-shaped sensilla (Fig. 15). This series is divided into two parts: one contains two sensilla (usually no 9–10) and the other three sensilla (usually no 11–13) (Figs 48–49; Fig. 51; Figs 53–54; Figs 56–57; Fig. 59). On the front edge of the top of the labium basiconica, peg and plate sensilla are arranged symmetrically on both lobes.

One pair of elongated placoid sensilla (Wp-ples) is located sub-apically on each side of the labium (Figs 17–19; Figs 39–42).

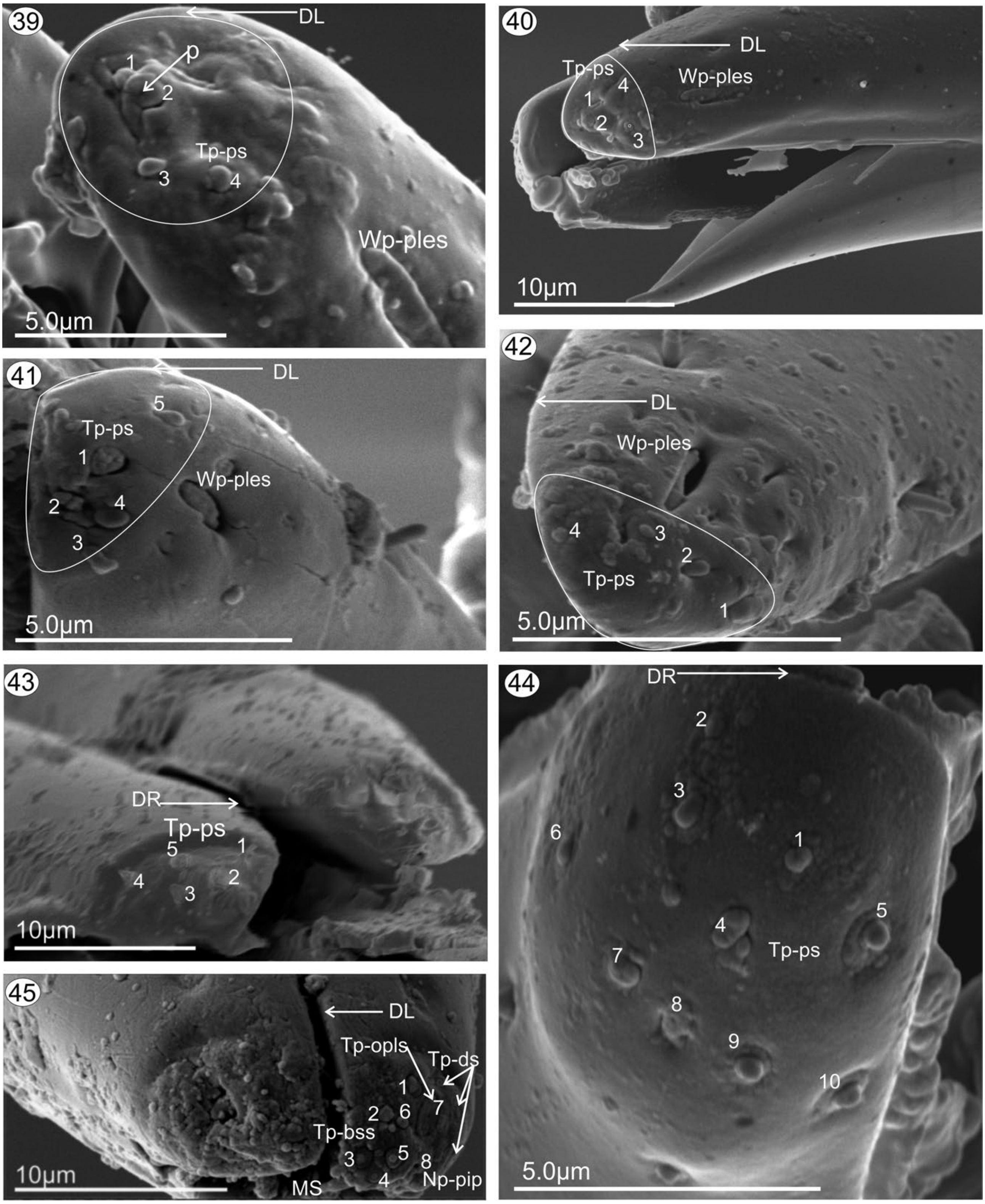
Distribution of the multi-peg structures

There are multi-peg structures (MS) on the ventral (vex) and internal sides (is) of the labial tip (e.g., Figs 3–6). These structures include numerous tall (ph) and short (pl) pegs, grouped on the inner side of the labium in two transverse rows near the apex (e.g., Fig. 5). Both rows are either formed by identical wide structures (MS) (Fig. 3 – Mesoveliidae and Hebridae; Fig. 4; Figs 68–69 – Hermatobatidae) or consist of rows of both narrow (Msn) and wide (MS) structures (Fig. 5; Figs 70–71 – Veliidae).

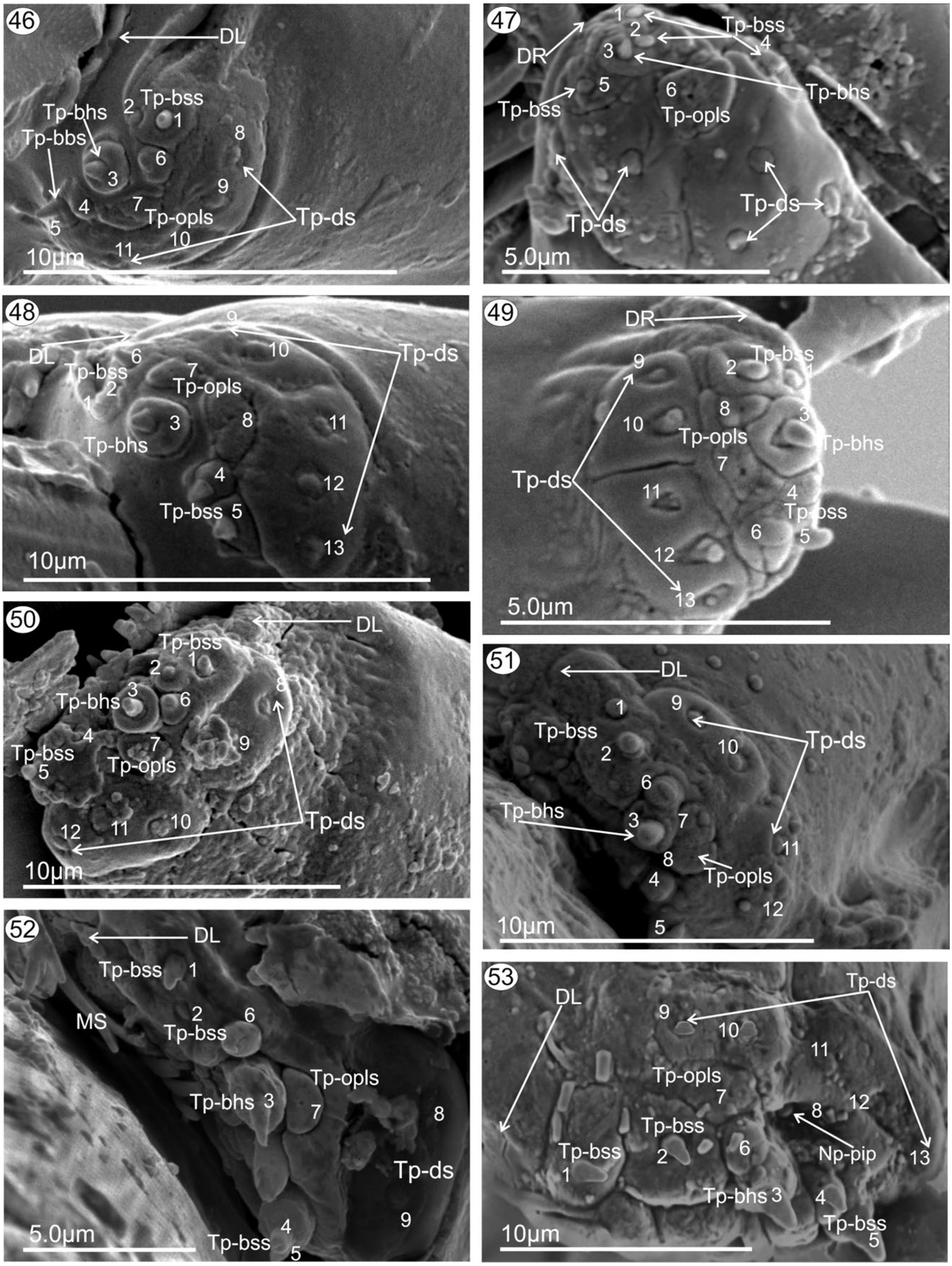


Figs 34–38. The right sensory field; different types of the sensilla and their distribution in Gerridae: 34 – *Amemboa brevifasciata* (Eotrechinae); 35 – *Potamobates tridentatus* (Cylindrostethinae); 36 – *Ptilomera tigrina* (Ptilomerinae); 37 – *Potamometroides madagascariensis* (Ptilomerinae); 38 – *Metrocoris nigrofascioides* (Halobatinae). MS – multi-peg structures; Np-pip – peg-in-pit, no-pore sensillum; Tp- bds – double basiconic sensillum; Tp-bhs – tall basiconic sensillum with a terminal pore; Tp-bss – short basiconic sensillum with a terminal pore; Tp-ds – dome-shaped sensillum with a terminal pore; Tp-opls – oval plate-like sensillum with a terminal pore. Scale bar = 10 µm.

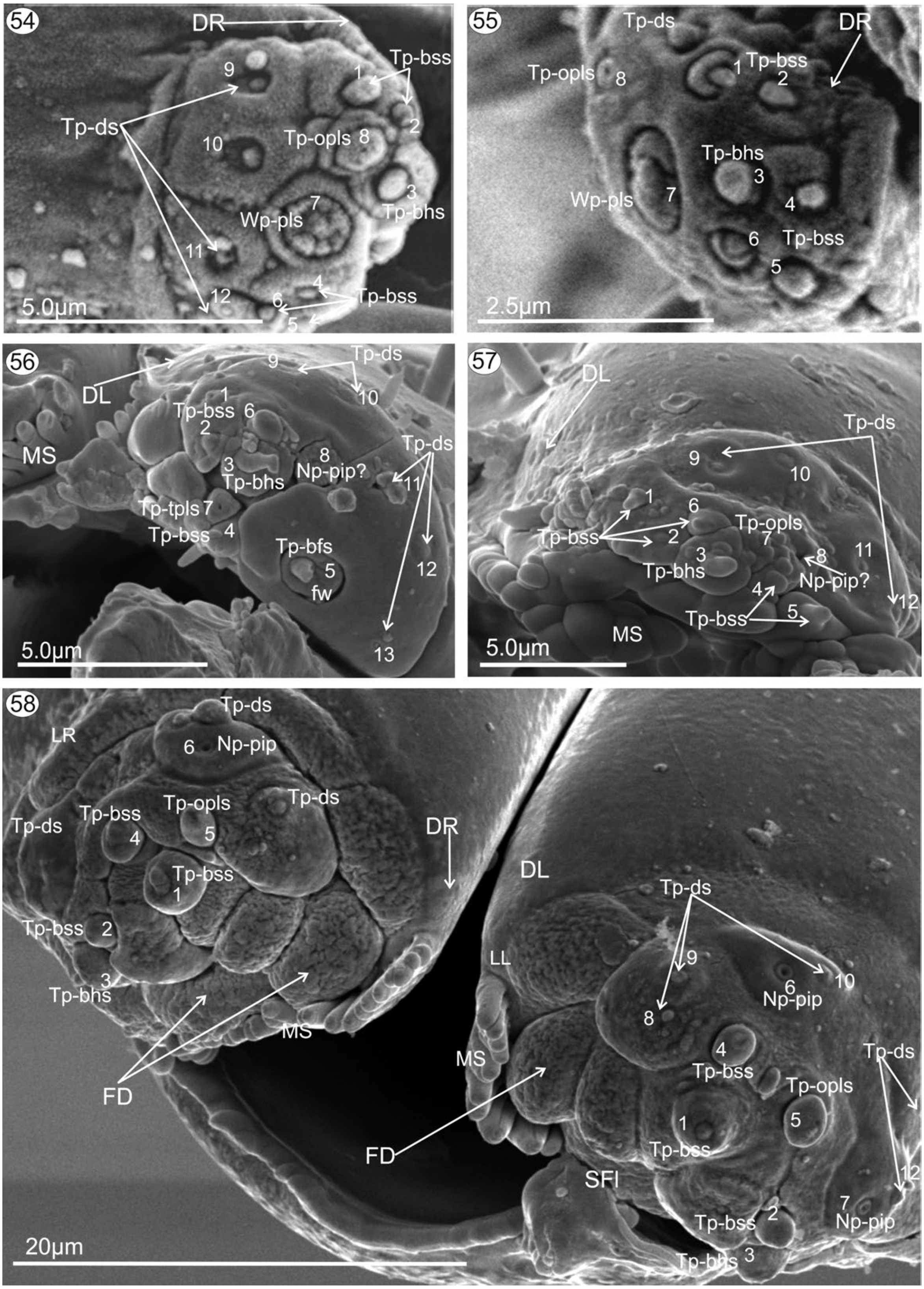
The two wide rows (Fig. 3; Fig. 67 – Mesoveliidae and Hebridae; Fig. 4; Figs 68–69 – Hermatobatidae and Fig. 43 – Hydrometridae) are located below the ventral edge (ved) of the labial tip (not reaching ventral edge of labium), or a wide row is located near its apex (partly reaching it) (Fig. 5; Figs 70–71 – Veliidae, Fig. 45 – Macroveliidae), or actually located on the ventral edge of the of the labial tip (Fig. 6; Figs 72–74 – Gerridae). The narrow row (Msn) is



Figs 39–45. Types and distribution of labial tip sensilla: 39–40 – *Mesovelia furcata* (Mesoveliinae); 41 – *Nieserius subaquaticus* (Hyrcaninae); 42 – *Timasius miyamotoi* (Hebrinae); 43 – *Hydrometra aculeata* (Hydrometridae); 44 – *Hermatobates marchei* (Hermatobatidae); 45 – *Macrovelia hornii* (Macroveliidae). DL – left dorsal side of the sensory field; DR – right dorsal side of the sensory field; p – pore; Tp-bss – short basiconic sensillum with a terminal pore; Tp-ds – dome-shape sensillum with terminal pore; Tp-opls – oval plate sensillum with a terminal pore; Tp-ps – peg sensillum with a terminal pore; Wp-ples – elongated placoid sensillum, multiporous, subapical.



Figs 46–53. Types and distribution of labial tip sensilla in Veliidae: 46 – *Ocellovelia fusca* (Ocelloveliinae); 47 – *Halovelia esakii* (Haloveliinae); 48 – *Microvelia douglasi* (Microveliinae); 49 – *Pseudovelia pusilla* (Microveliinae); 50 – *Rhagovelia sumatrensis* (Rhagoveliinae); 51 – *Perittopus asiaticus* (Perittopinae); 52 – *Velia caprai* (Veliinae); 53 – *Paravelia basalis* (Veliinae). DL – left dorsal side of the sensory field; DR – right dorsal side of the sensory field; MS – multi-peg structures; Np-pip – peg-in-pit sensillum no-pore; Tp-bhs – tall basiconic sensillum with a terminal pore; Tp-bss – short basiconic sensillum with a terminal pore; Tp-ds – dome-shaped sensillum with a terminal pore; Tp-opls – oval plate-like sensillum with a terminal pore.



Figs 54–58. Different types of sensilla and their distribution on the tip of the labium in Gerridae: 54. *Naboandelus signatus* (Trepobatinae); 55. *Pseudohalobates inobonto* (Trepobatinae); 56. *Rhagadotarsus kraepelini* (Rhagadotarsinae); 57. *Brachymetra albinervis* (Charmatometrinae); 58. *Limnometra nigripennis* (Gerrinae). DL – left dorsal side of sensory field; DR – right dorsal side of sensory field; FD – folds on the tip of the labium; fw – flat and wide socket; LL – left lobe of labium, LR – right lobe of labium, MS – multi-peg structures; Np-pip – peg-in-pit sensillum, no-pore; Tp-bfs – basiconic sensillum with a terminal pore inserted in a flat socket; Tp-bhs – tall basiconic sensillum with a terminal pore; Tp-bss – short basiconic sensillum with a terminal pore; Tp-ds – dome-shaped sensillum with a terminal pore; Tp-opls – oval plate-like sensillum with a terminal pore; Tp-tpls – triangular plate-like sensillum with a terminal pore; Wp-pls – placoid sensillum, multiporous.

usually located distant from the labial tip (Figs 5, 71). The pegs of these structures are directed towards the end of the terminal segment and are connected with its inner side.

Morphological types, classification and functions of the labial tip sensilla

The labial tip sensilla are classified into four (I–IV) main morphological and functional categories, within which there are currently eleven types of sensilla (Np-pip, Tp-tpls, Tp-opls, Tp-ds, Tp-ps, Tp-bhs, Tp-bss, Tp-bfs, Tp-bds, Wp-pls, Wp-ples) differentiated on the basis of their external appearance and location. The criteria for recognition of these sensilla are based on external morphological characters, identifying the types of sensilla by the system of pores (visible or not), the relative position of the sensilla with respect to the surface of the labium, whether short or tall (flexible or inflexible sockets), and the general shape of the sensilla. Their presumed functions correspond with external morphology (Table 1).

I. Np – no-pore sensilla with inflexible sockets (bimodal hygrosensitive and thermosensitive sensilla) (Table 1A).

Np-pip – peg-in-pit sensillum (poreless coeloconic sensillum) (Fig. 7). The short and smooth peg is concealed in a depression in the surface with the apex of the peg not projecting from the pit.

This type of sensillum occurs in *Macrovelia hornii* (sensillum no. 8, Fig. 45; Macroveliidae), *Paravelia basalis* (sensillum no. 8, Veliinae; Fig. 53), *Limnometra nigripennis* (sensilla no. 6–7, Fig. 58), *Eurygerris fuscinervis* (sensillum no. 7, Fig. 59), *Gerris argentatus*, *G. odontogaster* (all in Gerrinae); *Amemboa brevifasciata* (sensillum no. 8, Fig. 60), *A. javanica* (sensillum no. 8, Fig. 61), and *Onychotrechus esakii* (all in Eotrechinae).

II. Tp – sensilla with the terminal pore (uniporous) inserted in an inflexible socket (unimodal chemosensitive sensilla: gustatory) (Table 1B).

On the tip of the labium of Gerromorpha there are three morphological forms of sensilla:

Tp-tpls – triangular plate sensillum (Fig. 8). This is a flat triangular plate on the same level as the general surface. There is one pore visible in the centre of the plate. This type of sensillum is specific for Rhagadotarsinae, *Rhagadotarsus kraepelini* (sensillum no. 7, Fig. 56) and *Rheumatobates crassifemur*.

Tp-opls – oval plate sensillum (Fig. 9). This flat oval sensillum has one pore in the centre of the plate. This sensillum slightly protrudes above the surface.

Oval plate sensilla usually occur individually at the end of the labium (no. 6–7 or 8 in Figures), as in *Macrovelia hornii* (Fig. 45; Macroveliidae), *Ocellovelia fusca* (Fig. 46; Ocelloveliinae), *Halovelia esakii* (Fig. 47) and *Strongylovelia philippinensis* (both in Haloveliinae); *Microvelia douglasi* (Fig. 48), *Pseudovelia pusilla* (Fig. 49), and *Neoalardus typicus* (all in Microveliinae); *Rhagovelia sumatrensis* (Fig. 50) and *Rhagovelia kawakamii* (both in Rhagoveliinae), *Perittopus asiaticus* (Fig. 51; Perittopinae), *Velia caprai* (Fig. 52) and *Paravelia basalis* (Fig. 53) (both in Veliinae); *Naboandelus signatus* (Fig. 54) and *Pseudohalobates inobonto* (Fig. 40) (both in Trepobatinae); *Limnometra nigripennis* (sensillum no. 5, Fig. 58), *Eurygerris fuscinervis* (Fig. 44), *Gerris argentatus*, and *G. odontogaster* (all in Gerrinae); *Amemboa brevifasciata* (Fig. 60), *A. javanica* (Fig. 61), and *Onychotrechus esakii* (all in Eotrechinae); *Potamobates tridentatus* (Fig. 62) and *Cylindrostethus costalis* (both in Cylindrostethinae); *Ptilomera tigrina* (sensillum no. 5, Fig. 63), *Potamometroides madagascariensis* (Fig. 64), and *Rheumatogonus luzonicus* (all in Ptilomerinae); *Ventidius werneri* (Fig. 65), *Metrocoris nigrofasciodes* (Fig. 66), and *Halobates hayanus* (all in Halobatinae). Only in the three species of Microveliinae analyzed (*Microvelia douglasi* (Fig. 48), *Pseudovelia pusilla* (Fig. 49), and *Neoalardus typicus*) are there two oval plate sensilla.

Tp-ds – dome-shaped sensillum (Fig. 15). These peg sensilla have a slightly rounded tip and one pore situated apically. They are embedded in shallow open cavities and occur in one row at the back of the sensory field. The row is divided into two areas, with two sensilla in one area and three in the other. This type of sensillum occurs in all species of Macroveliidae, Veliidae and Gerridae examined (Figs 45–66).

III. Tp – sensillum with (sub)terminal pore (uniporous) and a flexible socket (bimodal mechano-chemoreceptive sensilla: tactile and gustatory) (Table 1C).

In the present study these sensilla can be subdivided into five distinct forms:

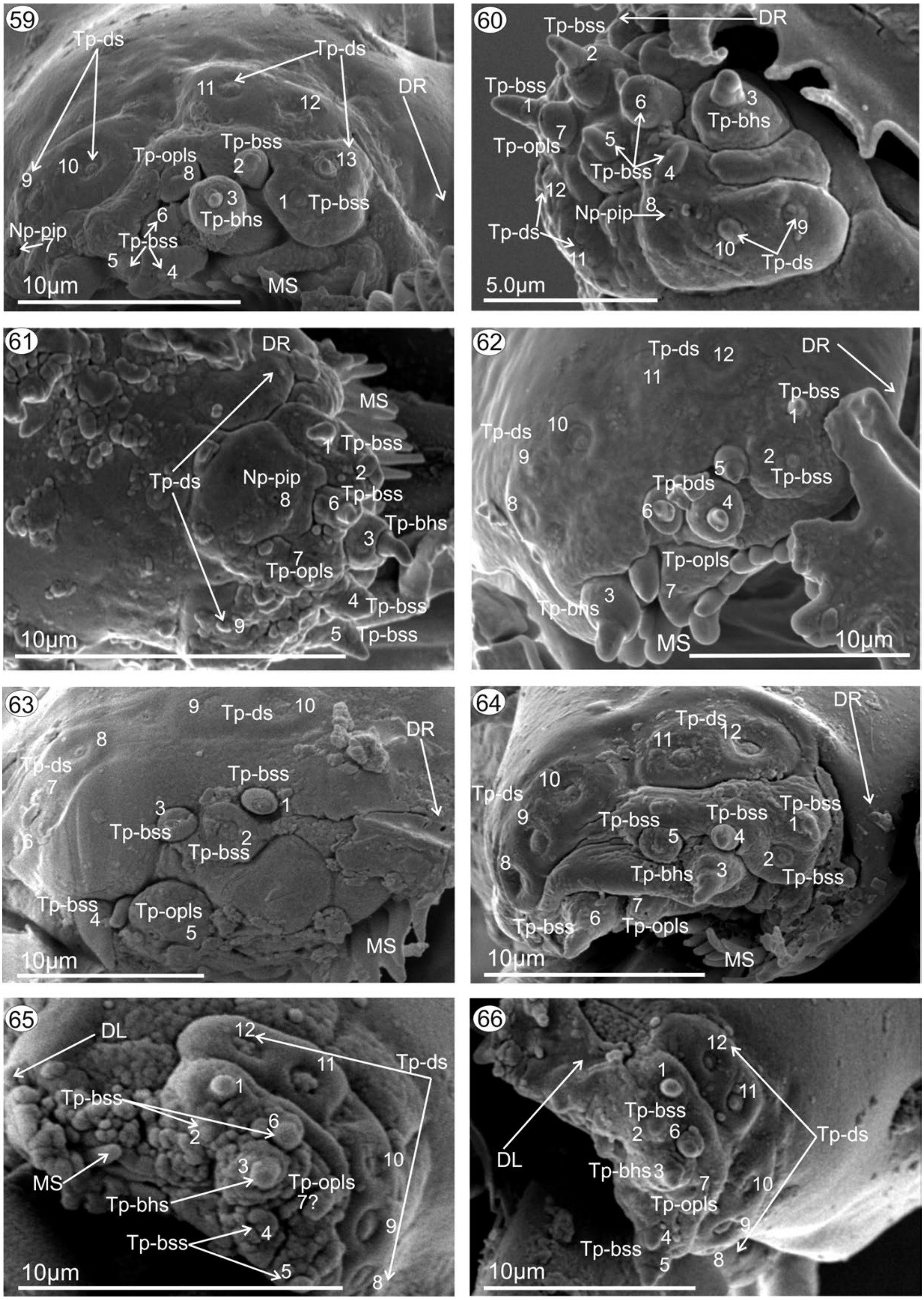
Tp-ps – peg sensillum (Fig. 10). This sensillum is short, with a rounded apex and a socket (ls). The pore (p) is frequently visible. This kind of sensillum designated as no. 1–5 occurs in species of Mesoveliinae, Hebrinae, Hyrcaninae, and Hydrometridae (Figs 39–43), and as no. 1–10 in Hermatobatidae (Fig. 44).

Tp-bhs – tall basiconic sensillum (Fig. 11). This cone-shaped sensillum has a tapered tip with one apical pore. Cone and socket (hs) are tall and this type of sensillum is larger than the other labial tip sensilla. In most species of veliids and gerrids it is designated no. 3 (Figs 46–66).

Tp-bss – short basiconic sensillum (Fig. 12). This sensillum is inserted in a socket (ls), which raises the sensory cone above the general surface of the cuticle. The sensory cone is blunt with one terminal pore. This type of sensillum is usually designated no. 1–2, 4–6, and is pointed in species of macroveliids, veliids and gerrids (Figs 45–66).

Tp-bfs – basiconic sensillum with flat and wide socket (Fig. 13). Cone-shaped sensillum with tapered apex and two pores (mp – moulting pore nearer to base and p – terminal pore, chemical) inserted in a flat and wide socket (fw). It is only found in Rhagadotarsinae, *Rhagadotarsus kraepelini* (sensillum no. 5, Fig. 56) and *Rheumatobates crassifemur*.

Tp-bds – double basiconic sensillum (Fig. 14). This sensillum consists of a tall cone with a single terminal pore and a short peg (pe). The peg is on the wall of the cone. This type of sensillum is embedded in a tall socket (hs). It is a very specific type of sensillum occurring only in Cylindrostethinae, *Potamobates tridentatus* (sensilla no. 4–6, Fig. 62) and *Cylindrostethus costalis*.



Figs 59–66. Different types of the sensilla and their distribution on the tip of the labium in Gerridae: 59. *Eurygerris fuscinervis* (Gerrinae); 60. *Amemboa brevifasciata* (Eotrechinae); 61. *Amemboa javanica* (Eotrechinae); 62. *Potamobates tridentatus* (Cylindrostethinae); 63. *Ptilomera tigrina* (Ptilomerinae); 64. *Potamometroides madagascariensis* (Ptilomerinae); 65. *Ventidius werneri* (Halobatinae); 66. *Metrocoris nigrofascioides* (Halobatinae). DL – left dorsal side of sensory field; DR – right dorsal side of sensory field; MS – multi-peg structures; Np-pip – peg-in-pit, no-pore sensillum; Tp-bds – double basiconic sensillum with terminal pore; Tp-bhs – tall basiconic sensillum with a terminal pore; Tp-bss – short basiconic sensillum with a terminal pore; Tp-ds – dome-shaped sensillum with a terminal pore; Tp-opls – oval plate-like sensillum with a terminal pore.

IV. Wp – sensillum with wall pores (multiporous) with an inflexible socket (unimodal chemosensitive sensillum: olfactory) (Table 1D).

Two types of sensilla are identified that have the morphological characteristics connected with olfaction:

Wp-pls – placoid sensillum (Fig. 15). Flat, oval plate raised above the surface the walls of which are covered with multipores. This type of sensillum (no. 7) occurs in Trepobatinae, *Naboandelus signatus* (Fig. 54) and *Pseudohalobates inobonto* (Fig. 55).

Wp-ples – elongated placoid sensillum (Fig. 16). Flat and elongated plate, inserted in a shallow depression. There are multipores in the wall of this sensillum. It is specific to Mesoveliidae, *Mesovelia furcata* (Figs 39–40) and *Mesovelia vittigera*, and Hebridae, *Timasius miyamotoi* (Fig. 41), *Hebrus philippinus, Nieserius subaquaticus* (Fig. 42) and *Hyrcanus varicolor*.

DISCUSSION

The present study provides a comparison of the morphological characters of the labial tip sensilla of 20 gerromorphan taxa belonging to different subfamilies and families. The tip of the labium bears a set of different types of sensilla, which presumably function as gustatory, tactile and gustatory, and olfactory (Table 1). In addition, the multi-peg structures situated on the ventral and internal sides of the labial tip are included in this study.

Morphological characteristics and presumed function of the labial tip sensilla

The labial tip sensilla in Gerromorpha as described in this paper morphologically correspond with similar types of sensilla described in other insects (McIver, 1975; Altner & Prillinger, 1980; Zacharuk, 1980, 1985). Based on the external structure we assign tentative functions to the labial sensilla according to existing examples in many papers (McIver, 1975; Altner & Prillinger, 1980; Zacharuk, 1980, 1985; Keil & Steinbrecht, 1984, 1997; Chapman, 1998; Keil, 1998; Hartenstein, 2005).

The **peg-in-pit** sensilla (poreless coeloconic sensilla, Table 1A) present in some of gerromorphans are very similar to the poreless coeloconic sensilla responsible for thermo- and hygroreception (Altner, 1977). Generally, these sensilla are not numerous and often occur as single pegs with inflexible sockets inside pits or cavities. They are often concentrated on lateral surfaces of antennomeres and only rarely on other parts in many insect orders (McIver, 1973; Boo & McIver, 1975; McIver & Siemicki, 1976; Altner et al., 1977, 1978; Altner et al., 1981; Altner et al., 1983; Altner & Loftus, 1985; Steinbrecht, 1994). The present study indicates that a characteristic example of this type of sensillum occurs in one veliid species (*Paravelia basalis*) and is located in the centre of the tip of the labium. This sensillum on the labial tip also occurs in Macroveliidae, *Macrovelia hornii* (Fig. 45), two species of Gerrinae, *Limnometra nigripennis* (Fig. 58) and *Eurygerris fuscinervis* (Fig. 59), and in Eotrechinae (Figs 60-61). Our results cannot rule out presence of such sensillum in other species of Gerromorpha because their location makes them difficult to observe and identification using SEM is also difficult. A morphologically similar sensillum appears to be present in most species of Nepomorpha (Heteroptera) (Brożek, 2008, 2013) and several species of Peiratinae (Heteroptera: Cimicomorpha: Reduviidae) (Brożek & Chłond, 2010). One or two pairs of poreless coeloconic sensilla occur on the labial tip in most auchenorrhynchans (fulgoromorphans) (Foster et al., 1983; Backus, 1985). This type of sensillum may occur also elsewhere on the labium in gerromorphan species; in some Reduviidae (Cimicomorpha) the poreless coeloconic sensilla are scattered over the labial tip [Triatominae: *Rhodnius neglectus* Lent, *Triatoma infestans* (Klug): (Catalá, 1996); Peiratinae: *Peirates hybridus* (Scopoli), *Lamotteus ornatus* Villiers, *Thymbreus crocinopterus* Stål, *Brachysandalus bicolor* Villiers, *Melanolestes picipes* (Herrich-Schaeffer): Brożek & Chłond, 2010].

Plate- (triangular or oval) and **dome-shaped** sensilla are presumed to be gustatory sensilla in the species of Gerromorpha (Table 1B) because of the central/terminal pore; similar sensilla occur in many insects (Cook, 1972; Zacharuk, 1980, 1985; Altner & Prillinger, 1980; Mitchell et al., 1999). For instance, a gustatory plate-like (A1) sensillum occurs on the clypeolabrum of *Locusta migratoria migratorioides* (Reiche & Fairmaire) (Cook, 1972). Flattened plate-like papillae on the epipharyngeal organ of aphids are gustatory (Wensler & Filshie, 1969). Oval plate-like sensilla occur singly in the some species of gerromorpha studied (Table 2), whereas the triangular plate-like sensilla occur only in Rhagadotarsinae. There is no information on the shape of these plate-like labial sensilla in the literature on heteropterans. In the Macroveliidae, Veliidae and Gerridae the dome-shaped sensilla are always five in number and do not differ morphologically.

In a previous study, similar but more sub-apical gustatory sensilla [peg sensilla (PP-S), dome-shaped (PDS), elongated plate sensilla (UDES)] were recorded in the Reduviidae: Peiratinae (Brożek & Chłond, 2010). In Nepomorpha there are two types of uniporous gustatory papillae on the labial tip. The first type (PAS1) characteristically has a flattened tip and resembles plate sensilla (Nepidae and Belostomatidae), while the second type (PAS2) in the remaining 11 families of Nepomorpha is similar to peg sensilla (Brożek, 2013). In several species of fulgoromorphan families there are four morphological types of uniporous gustatory peg sensilla on the labial tip [pit peg sensilla (PPSU), peg sensilla tall (PGSU1), peg sensilla short (PGSU2), clavate sensilla (CLSU)] (Brożek & Bourgoin, 2013). Peg and basiconic gustatory sensilla are present also in some other hemipterans. In the tarnished plant bug *Lygus lineolaris* (Palisot de Beauvois) (Heteroptera: Cimicomorpha: Miridae) there are eleven sensilla basiconica (Avé et al., 1978). Walker and Gordh (1989) reported that three of seven pairs of sensilla symmetrically positioned on either side of the tip of the labial groove of *Parabemisia myricae* (Kuwana) of Aleyrodidae (Hemiptera: Sternorrhyncha) are gustatory. These sensilla are small uniporous pegs (generally ranging between 1–4 µm in height and 0.1–0.6 µm in width). There is disagreement about the function of these sensilla in Reduviidae; Catalá (1996) records gustatory peg sensilla on the labial tip in Triatominae even though previously Bernard (1974) suggested that they were tonic mechanoreceptors. Generally, gustatory short pegs and/or dome-shaped sensilla are present in most insects (Zacharuk, 1980).

In hemipteran insects a labial tapping of host surfaces prior to feeding probably exposes the mechano- and contact chemoreceptive sensilla to tactile and chemical stimuli (Backus, 1988). According to the latter author, Heteroptera and Auchenorrhyncha, although rather diverse, are rather similar in their labial sensory system.

These **peg** (Tp-ps) and **basiconic** (Tp-bhs, Tp-bss, Tp-bfs and Tp-bds) mechano-chemoreceptive sensilla (Table 1C) are rather numerous on the labial tip of Gerromorpha (Table 2). Peg sensilla are present mainly in basal groups of gerromorphan insects (Figs 39–44) and morphologically all peg sensilla are very similar with no clear differences in their structure. Basiconic sensilla occur at the tip of the labium in Macroveliidae (Fig. 45), Veliidae (Figs 46–53) and Gerridae (Figs 54–66). The dominant (i.e. the largest) sensillum, which usually distinctly protrudes from the labial tip, is the tall basiconic sensillum (Tp-bhs), which is characteristic of Veliidae and Gerridae. This position, together with its perpendicular orientation, probably results in the Tp-bhs sensillum being the first to come into direct contact with the surface. The basiconic sensilla (Tp-bss) identified in the present study are similar to those in *Aquarius najas*, which were called nipple-like sensilla and have the same function (Cobben, 1978).

Mechano-chemoreceptive peg sensilla have also been recorded on the labial tip of other Heteroptera. Rani & Madhavendra (1995) describe 10 such peg sensilla on the labial tip of *Odontopus nigricornis* (Pentatomomorpha: Pyrrhocoridae) and 11 on that of *Nezara viridula* (Pentatomidae). The nine basiconic sensilla and two chaetic sensilla on the labial tip in species of Pyrrhocoridae (*Dysdercus fulvoniger*, *D. koenigii*: Schoonhoven & Henstra, 1972; *D. fasciatus*: Peregrine, 1972; *D. intermedius*: Gaffal, 1981), Miridae (*Lygus lineolaris*: Avé et al., 1978), and one basiconic sensillum in *Parabemisia myricae* (Aleyrodidae: Walker & Gordh, 1989) are thought to be dual mechano- chemoreceptors. In both these types of sensilla only one dendrite is terminated in the tubular body while the remaining dendrites (2-6) are terminated in the tip of sensillum.

Generally, all types of uniporous sensilla that respond to gustatory stimuli can also respond to strong odours (Zacharuk, 1980). An intermediate type of basiconic sensillum (D) described in *Dysdercus fasciatus* and *D. intermedius* has typical terminal pore and a multiporous wall, suggestive of gustatory and olfactory functions (Peregrine, 1972; Gaffal, 1981). Perhaps for these reasons, specialized olfactory sensilla seldom occur on the labium of heteropterans.

Placoid (Wp-pls) and **elongated placoid** (Wp-ples) sensilla are thought to be olfactory (Table 1D) because the multiporous placoid sensillum is single-walled and provides only olfactory function (Altner & Prillinger, 1980).

Two species of gerrids (Figs 54–55) have the placoid sensilla on the labial tip whereas in species of the subfamilies Mesoveliinae, Hebrinae and Hyrcaninae an elongated placoid sensillum occurs in shallow cavities subapically on the labium. In remaining studied species of Gerromorpha, such sensilla have not been identified. A similar situation is recorded for the multiporous placoid sensilla (PPLS) of Reduviidae: Peiratinae: Of the nineteen species examined, four species of different genera have such sensilla situated subapically on labium, whereas the others do not (Brożek & Chłond, 2010). Based on morphological characters, the elongated placoid sensillum of the reduviids *Platychiria murrayi* Signoret, *Cethera musiva* (Germar), and *Ectrichodia distincta* (Signoret) (Brożek & Chłond, unpublished data), and of *Prostemma* sp. (Nabidae) (Schuh & Slater, 1995: Fig. 10.7 B, p. 52), is identical to the elongated placoid sensillum of Mesoveliidae and Hebridae, and is thus presumed to have an olfactory function. In contrast, placoid or other olfactory sensilla have not been found in Nepomorpha (Cobben, 1978; Brożek, 2008, 2013) and in species of Pentatomidae and Miridae (Avé et al., 1978; Hatfield & Frazier, 1980; Rani & Madhavenda, 1995).

The five different multiporous sensilla on the labial tip of fulgoromorphans [placoid (OPSM), peg, peg-complex, cupola, dome-shaped] probably function as olfactory receptors (Brożek & Bourgoin, 2013). In many fulgoromorphan families there are several different sub-apical sensilla (multiporous, multilobed and branched or placoid, placed subapically on the labium in a cavity: Foster et al., 1983; Backus, 1985; Liang, 2005; Brożek & Bourgoin, 2013); possible olfactory and thermosensitive functions have been suggested (Table 1D). They have different structure and distribution of dendrites in comparison with the multiporous sensillum on the tip of labium, but their exact function has not been identified (Foster et al., 1983; Backus, 1985). Preliminarily they can be regarded as dual-function sensilla.

Generally, the labial sensilla of Gerromorpha need to be studied ultracturcturally to further improve and reinforce the conclusions on their function.

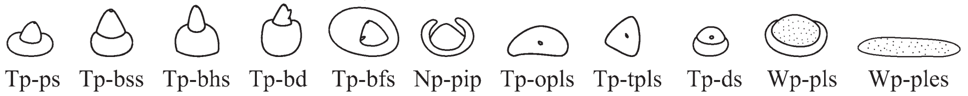
The types and distributions of labial tip sensilla in Gerromorpha

Based on the currently accepted phylogenies of Gerromorpha (reviewed by Damgaard, 2008) the families included in this study are: the Mesoveliidae, Hebridae, Hydrometridae + Hermatobatidae, Macroveliidae + Paraphrynoveliidae, Veliidae (includes Oceloveliidae) and Gerridae. The sensory endings on the labial tip and other labial structures of these families are analyzed below.

I. Mesoveliid and hebrid pattern. Four pairs of pegs scattered over the smooth apex and one pair of elongated placoid sensilla positioned sub-apically constitute the basal pattern of Mesoveliinae (Fig. 17). A very similar pattern to that occurring in mesoveliids, with four or five pegs and one pair of subapical sensilla occurs in both subfamilies of Hebridae, Hebrinae (Fig. 18) and Hyrcaninae (Fig. 19) (Table 2).

TABLE 2. Detailed descriptions of the sizes, numbers and shapes of the labial tip sensilla of the species of gerromorphan subfamilies studied.

Schema of various shapes of sensilla (description in text, particular elements of sensilla are shown in Figs 7–16)



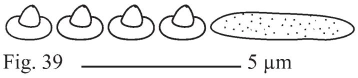
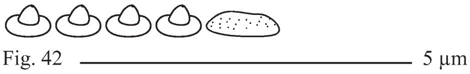
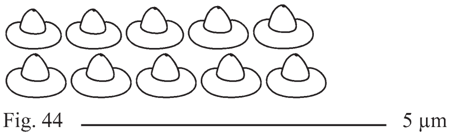
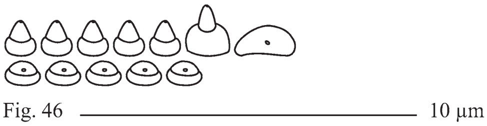
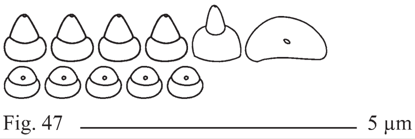
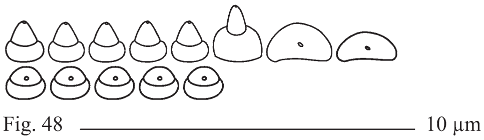
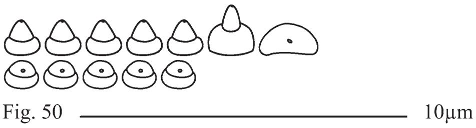
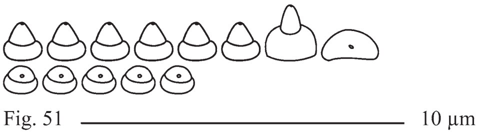
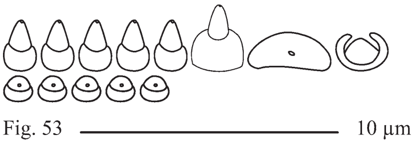
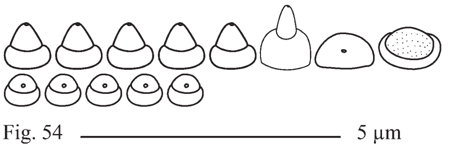
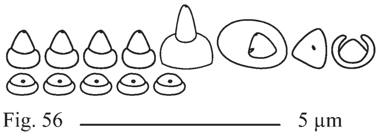
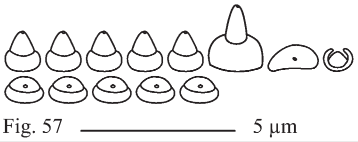
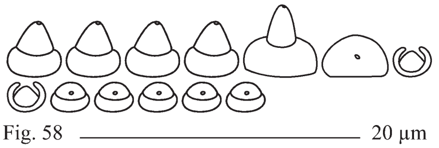
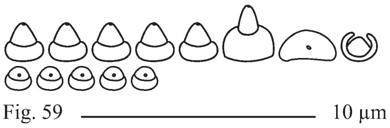
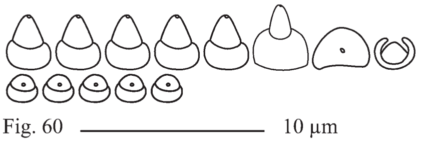
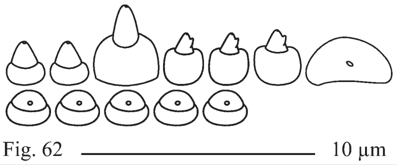
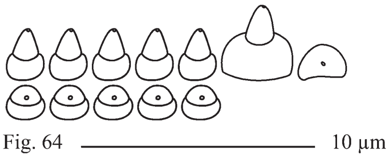
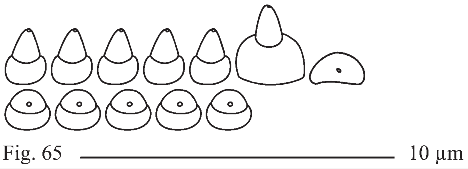
Taxa	Numbers of labial tip sensilla (refer to both lobes of the labium, right and left)	Shape of labial tip sensilla (numbers are for one lobe of the labium), same scale as in Figs 39–66
Mesoveliinae: *Mesovelia furcata* Mulsant & Rey (Figs 17, 39–40) *Mesovelia vittigera* (Horváth)	4 pairs peg sensilla (uniporous) (Tp-ps) 1 pair elongated placoid sensilla (Wp-ples)	 Fig. 39
Hebrinae: *Hebrus philippinus* Zettel *Timasius miyamotoi* Andersen (Figs 18, 41)	5 pairs peg sensilla (uniporous) (Tp-ps) 1 pair elongated placoid sensilla (Wp-ples)	 Fig. 41
Hyrcaninae: *Hyrcanus varicolor* Andersen *Nieserius subaquaticus* Zettel (Figs 19, 42)	4 pairs peg sensilla (uniporous) (Tp-ps) 1 pair elongated placoid sensilla (Wp-ples)	 Fig. 42
Hydrometridae: *Hydrometra aculeata* Montrouzier (Figs 20, 43) *Hydrometra stagnorum* (Linnaeus)	5 pairs peg sensilla (uniporous) (Tp-ps)	 Fig. 43
Hermatobatidae: *Hermatobates marchei* (Coutiere & Martin) (Figs 21, 44)	10 pairs peg sensilla (uniporous) (Tp-ps)	 Fig. 44
Macroveliidae: *Macrovelia hornii* Uhler (Figs 22, 45)	6 pairs short basiconic sensilla (uniporous) (Tp-bss) 1 pair oval plate sensilla (uniporous) (Tp-opls) 1 pair peg-in-pit sensilla (nonporous) (Np-pip) 5 pairs dome-shaped sensilla (uniporous) (Tp-ds)	 Fig. 45
Ocelloveliinae: *Ocellovelia fusca* (Germar) (Figs 23, 46)	5 pairs short basiconic sensilla (uniporous) (Tp-bss) 1 pair tall basiconic sensilla (uniporous) (Tp-bhs) 1 pair oval plate sensilla (uniporous) (Tp-opls) 5 pairs dome-shaped sensilla (uniporous) (Tp-ds)	 Fig. 46
Haloveliinae: *Halovelia esakii* Andersen (Figs 24, 47) *Strongylovelia philippinensis* Zettel	4 pairs short basiconic sensilla (uniporous) (Tp-bss) 1 pair tall basiconic sensilla (uniporous) (Tp-bhs) 1 pair oval plate sensilla (uniporous) (Tp-opls) 5 pairs dome-shape sensilla (uniporous) (Tp-ds)	 Fig. 47
Microveliinae: *Microvelia douglasi* Scott (Figs 25, 48) *Pseudovelia pusilla* Hecher (Fig. 49) *Neoalardus typicus* (Distant)	5 pairs short basiconic sensilla (uniporous) (Tp-bss) 1 pair tall basiconic sensilla (uniporous) (Tp-bhs) 2 pairs oval plate sensilla (uniporous) (Tp-opls) 5 pairs dome-shape sensilla (uniporous) (Tp-ds)	 Fig. 48
Rhagoveliinae: *Rhagovelia sumatrensis* Lundblad (Figs 26, 50) *Rhagovelia kawakamii* (Matsumura)	5 pairs short basiconic sensilla (uniporous) (Tp-bss) 1 pair tall basiconic sensilla (uniporous) (Tp-bhs) 1 pair oval plate sensilla (uniporous) (Tp-opls) 5 pairs dome-shape sensilla (uniporous) (Tp-ds)	 Fig. 50
Perittopinae: *Perittopus asiaticus* Zettel (Figs 27, 51)	6 pairs short basiconic sensilla (uniporous) (Tp-bss) 1 pair tall basiconic sensilla (uniporous) (Tp-bhs) 1 pair oval plate sensilla (uniporous) (Tp-opls) 5 pairs dome-shaped sensilla (uniporous) (Tp-ds)	 Fig. 51
Veliinae: *Velia caprai* Tamanini (Fig. 52) *Paravelia basalis* (Spinola) (Figs 28, 53)	5 pairs short basiconic sensilla (uniporous) (Tp-bss) 1 pair tall basiconic sensilla (uniporous) (Tp-bhs) 1 pair oval plate-like sensilla (uniporous) (Tp-opls) 1 pair peg-in-pit sensilla (nonporous) (Np-pip) (only visible in *Paravelia basalis*) 5 pairs dome-shaped sensilla (uniporous) (Tp-ds)	 Fig. 53

TABLE 2 (continued).

Schema of various shapes of sensilla (description in text, particular elements of sensilla are shown in Figs 7–16)

Tp-ps Tp-bss Tp-bhs Tp-bd Tp-bfs Np-pip Tp-opls Tp-tpls Tp-ds Wp-pls Wp-ples

Taxa	Numbers of labial tip sensilla (refer to both lobes of the labium, right and left)	Shape of labial tip sensilla (numbers are for one lobe of the labium), same scale as in Figs 39–66
Trepobatinae: *Naboandelus signatus* (Distant) (Figs 29, 54) *Pseudohalobates inobonto* Polhemus & Polhemus (Fig. 55)	5 pairs short basiconic sensilla (uniporous) (Tp-bss) 1 pair tall basiconic sensilla (uniporous) (Tp-bhs) 1 pair oval plate sensilla (uniporous) (Tp-opls) 1 pair placoid sensilla (multiporous) (Wp-pls) 5 pairs dome-shape sensilla (uniporous) (Tp-ds)	 Fig. 54
Rhagadotarsinae: *Rhagadotarsus kraepelini* Breddin (Figs 30, 56) *Rheumatobates crassifemur* Esaki	4 pairs short basiconic sensilla (uniporous) (Tp-bss) 1 pair tall basiconic sensilla (uniporous) (Tp-bhs) 1 pair basiconic sensilla, flat socket (uniporous) (Tp-bfs) 1 pair triangular plate sensilla (uniporous) (Tp-tpls) 1 pair peg-in-pit sensilla (nonporous) (Np-pip) 5 pairs dome-shaped sensilla (uniporous) (Tp-ds)	 Fig. 56
Charmatometrinae: *Brachymetra albinervis* Serville (Figs 31, 57)	5 pairs short basiconic sensilla (uniporous) (Tp-bss) 1 pair tall basiconic sensilla (uniporous) (Tp-bhs) 1 pair oval plate sensilla (uniporous) (Tp-opls) 1 pair peg-in-pit sensilla (nonporous)?(Np-pip) 5 pairs dome-shaped sensilla (uniporous) (Tp-ds)	 Fig. 57
Gerrinae: *Limnometra nigripennis* Mayr (Figs 32, 58)	4 pairs short basiconic sensilla (uniporous) (Tp-bss) 1 pair tall basiconic sensilla (uniporous) (Tp-bhs) 1 pair oval plate sensilla (uniporous) (Tp-opls) 2 pair peg-in-pit sensilla (nonporous)? (Np-pip) 5 pairs dome-shape sensilla (uniporous) (Tp-ds)	 Fig. 58
Gerrinae: *Eurygerris fuscinervis* (Berg) (Figs 33, 59) *Gerris argentatus* Schummel *Gerris odontogaster* (Zetterstedt)	5 pairs short basiconic sensilla (uniporous) (Tp-bss) 1 pair tall basiconic sensilla (uniporous) (Tp-bhs) 1 pair oval plate sensilla (uniporous) (Tp-opls) 1 pair peg-in-pit sensilla (nonporous) (Np-pip) 5 pairs dome-shape sensilla (uniporous) (Tp-ds)	 Fig. 59
Eotrechinae: *Amemboa brevifasciata* Miyamoto (Figs 34, 60) *Amemboa javanica* Lundblad (Fig. 61) *Onychotrechus esakii* Andersen	5 pairs short basiconic sensilla (uniporous) (Tp-bss) 1 pair tall basiconic sensilla (uniporous) (Tp-bhs) 1 pair oval plate sensilla (uniporous) (Tp-opls) 1 pair, peg-in-pit sensilla (nonporous)? (Np-pip) 5 pairs dome-shaped sensilla (uniporous) (Tp-ds)	 Fig. 60
Cylindrostethinae: *Potamobates tridentatus* Esaki (Figs 35, 62) *Cylindrostethus costalis* Schmidt	2 pairs short basiconic sensilla (uniporous) (Tp-bss) 1 pair tall basiconic sensilla (uniporous) (Tp-bhs) 3 pairs double basiconic sensilla (uniporous) (Tp-bds) 1 pair oval plate sensilla (uniporous) (Tp-opls) 5 pairs dome-shaped sensilla (uniporous) (Tp-ds)	 Fig. 62
Ptilomerinae: *Ptilomera tigrina* Uhler (Figs 36, 63) *Potamometroides madagascariensis* Hungerford (Figs 37, 64) *Rheumatogonus luzonicus* (Kirkaldy)	5 pairs short basiconic sensilla (uniporous) (Tp-bss) 1 pair tall basiconic sensilla (uniporous) (Tp-bhs) 1 pair oval plate sensilla (uniporous) (Tp-opls) 5 pairs dome-shaped sensilla (uniporous) (Tp-ds)	 Fig. 64
Halobatinae: *Ventidius werneri* Hungerford & Matsuda (Fig. 65) *Metrocoris nigrofascioides* Chen & Nieser (Figs 38, 66) *Halobates hayanus* White	5 pairs short basiconic sensilla (uniporous) (Tp-bss) 1 pair tall basiconic sensilla (uniporous) (Tp-bhs) 1 pair oval plate sensilla (uniporous) (Tp-opls) 5 pairs dome-shaped sensilla (uniporous) (Tp-ds)	 Fig. 65

II. Hydrometrid and hermatobatid pattern. This pattern consists of five (in Hydrometridae, Fig. 20) to ten pairs (in Hermatobatidae, Fig. 21) of identical peg sensilla. Surprisingly, in both families this one type of sensillum functions as a contact chemoreceptive sensillum and occurs in large numbers on the smooth apex of the labium.

III. Macroveliid, veliid and gerrid pattern. A comparison of the mesoveliid pattern with that of the evolutionary advanced taxa Macroveliidae, Veliidae and Gerridae reveals significant differences. Most of all, these families display a much greater diversity of types and numbers of sensilla (Table 2). The labial tip is folded. Sensilla basiconica are inserted in distinct sockets. Usually, one plate-like sensillum is visible in the centre of the tip of the labium among several short basiconic sensilla. Another diagnostic feature is the presence of a row of five dome-shaped sensilla at the back of the tip. In general, the sensilla are numerous (10–15 pairs) and morphologically varied (peg-in-pit, plate-like, basiconic, dome-shaped, placoid sensilla).

The distribution of sensilla on the labial tip of Veliidae is fairly homogeneous (Table 2). Only in *Paravelia basalis* (the Veliinae) is a clearly distinguishable coeloconic sensillum present. A coeloconic sensillum is also present in Macroveliidae and several subfamilies of Gerridae [Charmatometrinae, Rhagadotarsinae, Gerrinae and Eotrechinae (Table 2)]. This sensillum is usually not clearly visible in most veliids and gerrids because it is probably in a deep hole in the folded surface of the labial apex. Due to the fact that a coeloconic sensillum occurs in Macroveliidae and several species of Veliidae and Gerridae this sensillum may also be present in the remaining subfamilies of these groups. In Gerridae the presence of significantly different types of basiconic sensilla is a new characteristic. Another significant feature is the presence of olfactory-placoid sensilla. There are morphological peculiarities in various subfamilies of Gerridae. A placoid sensillum is characteristic of Trepobatinae, a basiconic sensillum with wide sockets and a triangular plate sensillum are characteristic only of Rhagadotarsinae and a double basiconic characteristic of Cylindrostethinae.

The type, distribution and number of labial tip sensilla determines the pattern. The species of the same gerromorphan subfamilies have identical patterns (Table 2). The patterns vary slightly among the different (sub)families: pattern I, II and III. In subfamilies of Gerridae there are several different forms of sensilla and thus more variation than in other families of Gerromorpha. In some other heteropteran families there are also differences in distributions and shapes of labial tip sensilla; e.g., such differences occur in Reduviidae between Triatominae (Catalá, 1996) and Peiratinae (Brożek & Chłond, 2010), i.e., the sensilla are similar in species belonging to the same subfamily.

Other structures on the apical labial segment

In addition to the labial sensilla, the SEM micrographs show multi-peg structures distributed in rows on the inner side of the apical segment of some Gerromorpha (Figs 3–6; 67–74). These multi-peg structures may have a sensory function. Cranston & Sprague (1961) have interpreted them as sense organs in *Aquarius remigis*. In contrast, Cobben (1978) describes them as comb-like and suggests they might have a mechanical function, recording friction between mandibles during sucking.

It is interesting that the special location of these structures is similar in the taxa studied. We identified a distinct difference between (1) the more basal taxa (Mesoveliinae, Hebrinae, Hyrcaninae, Hydrometrinae, and Hermatobatidae) in which the multi-peg structures do not occur on the ventral edge of the tip of the labium; (2) the Macroveliidae and Veliidae in which some multi-peg structures occur on the ventral edge; and (3) the Gerridae in which all structures occur on the ventral edge.

In terms of the surface of the tip the labium it is smooth in species of Mesoveliinae, Hebrinae, Hyrcaninae, Hydrometrinae and Hermatobatidae and folded in Macroveliidae, Veliidae and Gerridae.

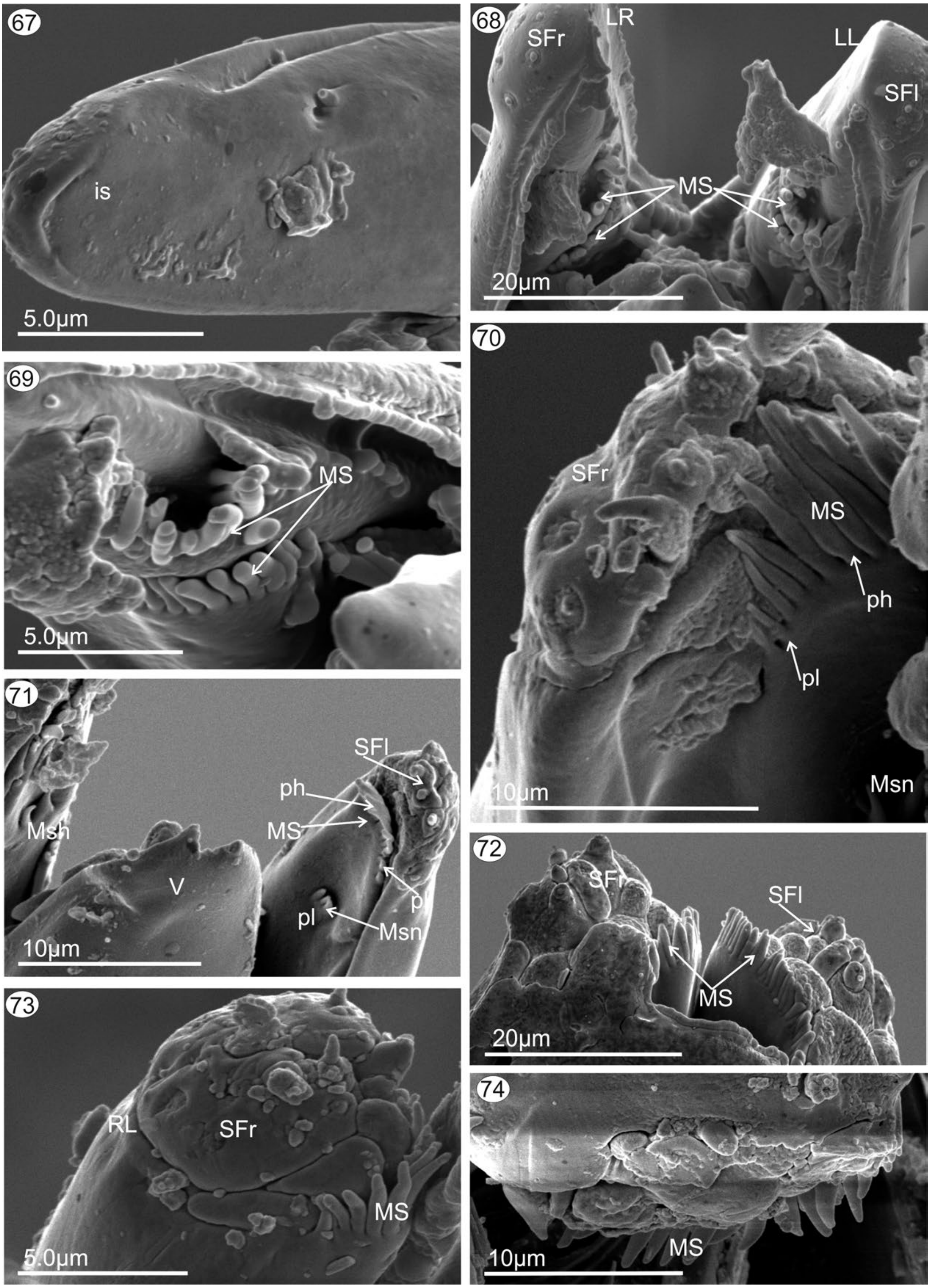
Structure of the sensilla and the phylogenetic history of semiaquatic bugs

The labial tip sensilla are of a similar type (peg sensilla) in Mesoveliidae, Hebridae, Hydrometridae, and Hermatobatidae and a similar but different type (basiconic short sensilla and dome-shape sensilla) in Macroveliidae, Veliidae and Gerridae. There is only a slight difference in the elongated placoid sensillum of Mesoveliidae and Hebridae. The elongated placoid sensillum in the first two families seems to be a plesiomorphic condition, which contrasts with the absence of this sensillum in the other taxa (synapomorphy for Hydrometridae, Hermatobatidae, Macroveliidae, Veliidae, and Gerridae).

In the Hydrometridae and Hermatobatidae the sensilla are of an intermediate type. The presence of peg sensilla (plesiomorphic character) places these taxa closer to Mesoveliidae and Hebridae. In turn, the lack of elongated placoid sensilla in hydrometrids and hermatobatids places them closer to Macroveliidae, Veliidae and Gerridae (synapomorphy of these five families). Similarly, based on the mode of locomotion Perez-Goodwyn et al. (2009) indicate that the gait of hermatobatids is intermediate between that of Mesoveliidae, Hebridae, Macroveliidae, and Hydrometridae (plesiomorphic character of the gait) and the clade Gerridae + Veliidae, in which it is autapomorphic.

Moreover, there is strong evidence that the types and distribution patterns of the apical sensilla are essentially the same (Figs 22–38) in Macroveliidae, Veliidae, and Gerridae. The presence of basiconic short sensilla, oval plate-like and dome-shaped sensilla are synapomorphies for Macroveliidae, Veliidae, and Gerridae, but not Rhagadotarsinae (Gerridae), which have a triangular plate-like sensillum that is homologous with an oval plate-like sensillum. This is interpreted as a new autapomorphic state of the sensillum in this subfamily. The process of differentiation of the apical sensilla into tall basiconic sensilla is evident in Veliidae and Gerridae, so for them this type is a synapomorphy.

A trend towards a modified type of basiconic sensilla seems to have taken place in subfamilies of Gerridae. This variation in the shape of the sensilla is a new autapomorphic character; a basiconic sensillum with wide sockets is an autapomorphy in Rhagadotarsinae; and a double basiconic sensillum an autapomorphy in Cylindrostethinae. Another example of further differentiation of the apical sensilla can be found in Trepobatinae. A new type of sensillum (placoid sensillum with an olfactory function) is an autapomorphy for this subfamily. Probably, this sensillum is a modified form of the elongated placoid sensillum in Mesoveliidae



Figs 67–74. Multi-peg structures on the terminal segment of the labium in Gerromorpha. 67 – *Hyrcanus varicolor* (Hyrcaninae); 68–69 – *Hermatobates marchei* (Hermatobatidae); 70 – *Velia caprai* (Veliinae); 71 – *Microvelia douglasi* (Microveliinae); 72 – *Limnometra nigripennis* (Gerrinae); 73 – *Rhagadotarsus kraepelini* (Rhagadotarsinae); 74 – *Ptilomera tigrina* (Ptilomerinae). is – internal side of the terminal segment of the labium; LL – left lobe of the labium; LR – right lobe of the labium; MS – multi-peg structures (wide row); Msn – multi-peg structures (narrow row); ph – tall pegs; pl – short pegs; SFl – left sensory field; SFr – right sensory field; V – ventral lobe.

and Hebridae, which occurs only in Trepobatinae; it seems likely that basiconic sensilla evolved from peg sensilla.

In addition, a pair of coeloconic sensilla occur only in several gerromorphan taxa (such as the genera *Macrovelia* and *Paravelia* or subfamilies Charmatometrinae, Rhagadotarsinae, Gerrinae, and Eotrechinae). Moreover, there are two pairs of coeloconic sensilla in *Limnometra nigripennis* (Gerrinae). Consequently, the presence of such sensilla in advanced taxa can be regarded a putative synapomorphy; conversely, the absence of a coeloconic sensillum in other gerromophan groups should be interpreted as plesiomorphic. This type of sensillum probably evolved independently of other sensilla.

There are variations in the number of sensilla. The number of sensilla increases from four or five pairs in Mesoveliidae, Hebridae and Hydrometridae to ten pairs in Hermatobatidae and even more pairs, i.e., from 11 to 14, in other families of Gerromorpha. Moreover, in several groups of Heteroptera similar numbers occur, i.e., twelve sensilla occur in species of Pentatomomorpha (Shoonhoven & Henstra, 1972) and from 10 to 16 on the labial tip of species in nepomorphan families (Brożek, 2008, 2013). Probably the lower number of sensilla is a characteristic of basal taxa such as in Gerromorpha. A similar situation occurs in the basal taxa of Nepomorpha: 9 pairs of sensilla in Nepidae and 16 pairs in the advanced taxon Naucoridae.

The distribution of several labial structures other than the labial tip sensilla vary in Gerromorpha. Multi-peg structures do not occur on the ventral edge of the labial tip and this character is specific to and a symplesiomorphy of Mesoveliinae, Hebrinae, Hyrcaninae, Hydrometrinae, and Hermatobatidae. Multi-peg structures that occur on the ventral edge are a synapomorphy of Macroveliidae and Veliidae and these structures occur on the ventral edge and are an autapomorphy of Gerridae.

Differences in the distributions of these multi-peg structures might indicate they are derived from a basal position in which they do not occur on the ventral edge, via an intermediate position as in macroveliids and veliids to the final state as in gerrids. Multi-peg structures are homologous in all gerromorphan taxa, however, these structures are polymorphic and can evolve into quite different shapes.

In addition, the smooth surface of the tip of the labium is probably a symplesiomorphy for Mesoveliidae, Hebridae, Hydrometidae and Hermatobatidae, however, the folded apex in Macroveliidae, Veliidae, and Gerridae is for them a synapomorphy.

CONCLUSIONS

The aforementioned new apomorphic characters should be included in a future cladistic analysis of Gerromorpha. There are several significant indications of the relationship of the families of Gerromorpha that can be pointed out based on their current characters (apomorphies).

1. Apparently, characteristics of those labial tip sensilla (tall basiconic sensilla) viewed as a synapomorphy in the present study provide support for the monophyly of Veliidae and Gerridae. This provides support for solutions proposed by Andersen (1982), Andersen & Weir (2004) and Perez-Goodwyn et al. (2009).

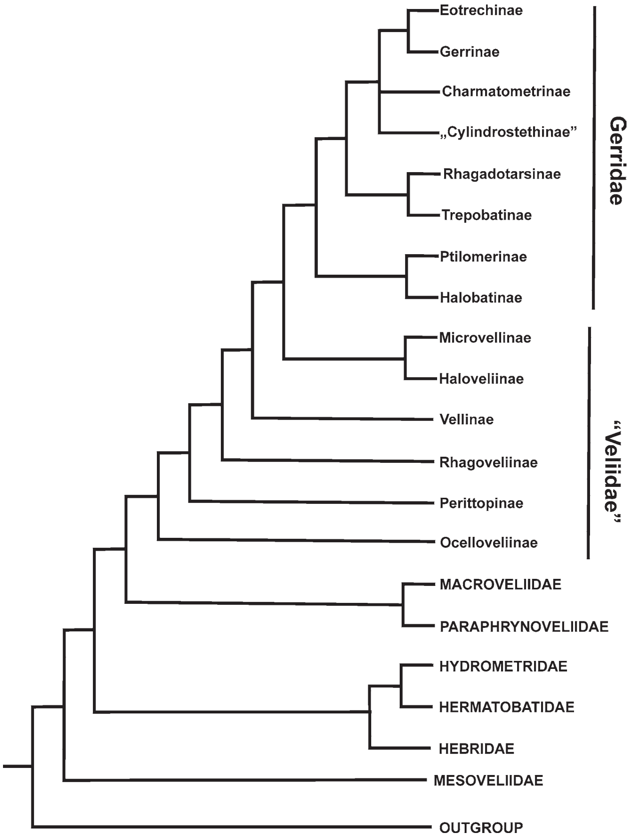


Fig. 75. A phylogenetic tree of the relationships among gerromorphan bugs, which is based on an analysis of both morphological and molecular data (Damgaard, 2008).

2. This study of labial tip sensilla has provided evidence of the monophyly of Cylindrostethinae, Trepobatinae, and Rhagadotarsinae. The autapomorphic character (double basiconic sensillum) is an especially important indicator of the monophyly of Cylindrostethinae as Damgaard (2008) evaluated Cylindrostethinae as paraphyletic, due to the lack of convincing apomorphic characters but stated that "within the Gerridae, the lack of monophyly in the 'Cylindrostethinae' is surprising, since this subfamily has been diagnosed previously and currently it is also supported by the 16S rRNA". The monophyly of the two subfamilies: Trepobatinae and Rhagadotarsinae, suggested in previous studies, is confirmed.

3. In the present study one synapomorphy (lack of an elongated placoid sensillum) is regarded as evidence that Hydrometridae, Hermatobatidae, Macroveliidae, Veliidae and Gerridae separated from the basal lineage of Mesoveliidae and Hebridae (unfortunately there is no synapomorphy in Gerromorpha).

4. Short sensilla basiconica, oval plate-like sensillum, dome-shaped sensilla and folded labial tip are four synapomorphies and coeloconic sensillum is a putative synapomorphy of Macroveliidae, Veliidae, and Gerridae

5. In this study, the autapomorphic character, multi-peg structures, is thought to indicate that the Gerridae is a monophyletic group. The monophyly of Gerridae sug-

gested in many previous studies is confirmed (Andersen, 1982; Muraji & Tachikawa, 2000; Andersen & Weir, 2004; Damgaard et al., 2005; Damgaard, 2008). In addition, the position of the multi-peg structures may be a synapomorphy of the Macroveliidae + Veliidae. However, it is not supported by additional characters and might be shown to be a homoplasy in future studies.

Even though the characteristics of labial tip sensilla and multi-peg structures and the surface of the labial tip were recognizable at the (sub-)family level in the present study, these characters do not provide support for the superfamilies identified by Andersen (1982), Muraji & Tachikawa (2000), Andersen & Weir (2004), Damgaard et al. (2005), and Perez-Goodwyn et al. (2009) or for the alternative cladogenetic solutions proposed by Damgaard (2008) (Fig. 75), who left unanswered several major questions regarding the future systematics of Gerromorpha.

This study revealed similarities in the labial tip sensilla in particular taxa of Gerromorpha. Currently, in terms of a higher classification, three groups can be clearly distinguished based on the pattern of types and distribution of apical sensilla: (1) Mesoveliidae and Hebridae; (2) Hydrometridae and Hermatobatidae; (3) Macroveliidae, Veliidae (including Ocelloveliidae sensu Damgaard, 2008) and Gerridae. In addition, the multi-peg structures provide evidence of a division between the lineage including Mesoveliinae, Hebrinae, Hyrcaninae, Hydrometrinae, and Hermatobatidae and that of Macroveliidae and Veliidae from the Gerridae. Slightly different arrangements of the families are obtained based on the type of surface of the labial tip; they are: (1) Mesoveliinae, Hebrinae, Hyrcaninae, Hydrometrinae and Hermatobatidae and (2) Macroveliidae, Veliidae and Gerridae.

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