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Antennal and maxillary palp morphology, and sensillar equipment, of the spruce bark beetle predators, *Medetera signaticornis* and *Medetera infumata* (Diptera: Dolichopodidae)

Maria Sousa [a, *], Rickard Ignell [a], Marc Pollet [b], Kristina K. Green [a], Paul G. Becher [a, 1], Göran Birgersson [a, 1]

[a] Unit of Chemical Ecology, Department of Plant Protection Biology, Swedish University of Agricultural Sciences, P.O. Box 190, SE 234 22, Lomma, Sweden
[b] Research Institute for Nature and Forest (INBO), Herman Teirlinckgebouw, Havenlaan 88 Bus 73, B-1000, Brussels, Belgium

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ABSTRACT

Many long-legged *Medetera* flies are natural enemies of bark beetle pests, which they detect using olfactory cues, likely through olfactory sensilla on the antennae and maxillary palps. Morphological characterisation of olfactory sensilla among insects can provide a basis for future taxonomic, phylogenetic or electrophysiological studies. Scanning electron microscopy was used to describe the morphology of olfactory organs and sensillar equipment of *Medetera signaticornis* and *M. infumata*. Three different olfactory sensillum types were found in both fly species, sensilla trichodea, s. basiconica and grooved pegs. Based on size and wall structure, s. trichodea and s. basiconica were categorised into different subtypes. Sharp-tipped curved s. trichodea, and small, large and thin s. basiconica were found on the antennal postpedicel of *M. signaticornis* adults, while grooved s. basiconica were found in *M. infumata*. The density of sharp-tipped long s. trichodea was significantly higher in males compared to females, and in *M. signaticornis* compared to *M. infumata*. Long-grooved s. basiconica were found grouped in a small pit on the maxillary palps of both species. Comparison of our results with the limited available ecological data suggests that differences in numbers of specific sensillum types may reflect adaptations related to olfactory-driven behaviours such as host seeking.

1. Introduction

Medetera (Fischer von Waldheim, 1819) is by far the genus most rich in species within the subfamily Medeterinae (Diptera: Dolichopodidae). The genus includes over 300 species worldwide (Yang et al., 2006), with approximately 190 species reported from the Palaearctic realm, where it also reaches its highest species richness (Bickel, 1985; Pollet, 2011). Most flies of this genus are small (1.5–4.5 mm), and feature a metallic greenish to bluish body colour covered with small hair-like structures. Adults are commonly found on vertical substrates such as tree trunks, rocks or walls, while larvae are mainly confined to subcortical galleries of dead or weakened living trees (De Leon, 1935; Nuorteva, 1956; Pollet et al., 2011). Both adults and larvae are predators of a wide variety of small soft-bodied arthropods (Bickel, 1985). Several *Medetera* species are known to prey on early developmental stages of tree-killing bark beetles (Coleoptera: Curculionidae, Scolytinae) that are significant pests of coniferous forests (Beaver, 1966). As such, these species are considered as one of the most important natural enemies of bark beetle populations, and have the potential to be used for biological pest management (Dippel et al., 1997; Wermelinger, 2002; Hedgren and Schroeder, 2004). However, little is known about their life history, ecology and how they locate their prey. Previous studies have suggested that *Medetera* species use odorant chemical signals to locate spruce trees attacked by *Ips typographus* Linnaeus, 1758 (Hulcr et al., 2005, 2006), but the morphology of their peripheral olfactory organs and sensillar equipment is yet to be described.

The main olfactory organs in adult insects, i.e., the antennae, maxillary and labial palps, house various types of hair-like structures called sensilla, which are involved in the detection of chemical, mechanical and thermo-hygro stimuli in the environment (Schneider, 1964; Hansson and Stensmyr, 2011). These sensilla can be

* Corresponding author.
E-mail address: maria.sousa@slu.se (M. Sousa).
[1] equal author contribution.

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classified into different types based on their external wall-structure, pore density, shape, size and number of enclosed sensory neurons (Hallberg and Hansson, 1999; Lin and Potter, 2015). The types and abundance of these sensilla vary across insect species. Such variation in the morphology of the olfactory organs often reflects adaptations, both between species and sexes, to locate for example prey, habitat or mates (Hansson and Stensmyr, 2011). The arrangement of the olfactory organs and the diversity within the sensillar equipment can thus be used for taxonomic, phylogenetic or evolutionary ecological studies (Zhang et al., 2016). In addition, structural characterisation of the olfactory organs can provide the basis for future functional classification of olfactory sensory neurons, present within various sensillum types (De Bruyne et al., 1999, 2001).

In this study, we used scanning electron microscopy (SEM) in order to compare and describe the antennal morphology and sensillar equipment of two bark beetle predators, *Medetera signaticornis* Loew, 1857 and *M. infumata* Loew, 1857. We focused on these two species because they were the two most common species that were collected from bark beetle-infested trees during our field work. We hypothesized that flies of both species may display a similar morphology of their olfactory organs and sensillar equipment. The motivation for such hypothesis is because both species co-exist on coniferous trees, are known to oviposit on bark beetle-infested Norway spruce trees, and appear to be attracted by the spruce bark beetle pheromones (Hulcr et al., 2005; Wegensteiner et al., 2015).

2. Material and methods

2.1. Field collections of adult flies

The study material, males and females of *M. signaticornis* and *M. infumata*, was collected at two locations in Asa, Sweden (57.150°N, 14.765°E, and 57.127°N, 14.780°E, respectively) between May–August during 2018 and 2019. Adult flies were collected with a mouth aspirator from bark beetle-infested Norway spruce trees (*Picea abies*), and kept in individual vials with a humidified filter paper to prevent fly tissue dehydration, until further analysis.

2.2. Scanning electron microscopy

To prepare the antennae and the maxillary palps for SEM, the heads of the flies were detached from the bodies. Subsequently, the heads were immersed overnight in a fixative solution (2% paraformaldehyde, Tab Laboratory equipment, Aldermaston, UK) and 2.5% glutaraldehyde (Agar Scientific, Essex, UK), and washed in 0.1 M sodium cacodylate buffer (Agar Scientific, Essex, UK), with pH adjusted to 7.3. After fixation, each fly head was dehydrated in a graded series of ethanol (75%, 96% and 100% twice, for 15 min), followed by critical-point drying (030 Bal-Tec Inc, EM-Technology and Application, Büntle, Lichtenstein), using liquid carbon dioxide (CO_2). To obtain a full three-dimensional view of the antennae and the maxillary palps, heads were carefully affixed in frontal view on aluminium stubs with double-sided adhesive tape. Then, to increase conductivity, the dried heads were sputter-coated with gold ions (Sputter coater 108 auto, Cressington Scientific Instruments, Watford, UK) at 20 mA for 65 s. Imaging was performed with a high-resolution scanning electron microscope (SU3500, Hitachi high-tech, Tokyo, Japan) at 5 kV, at a working distance of 5–15 mm.

2.3. The antennal and maxillary palp morphology and sensillar equipment

For morphological measurements and sensillar counts in each species, six individuals from each sex were used. However, only the heads of the specimens that allowed a good lateral view of the inner part of the antennal postpedicel (i.e., the section directed towards the medial body plane) and the outer part of the maxillary palps were included in the analysis, i.e., *M. signaticornis:* females (n = 6) and males (n = 5); *M. infumata:* females (n = 5) and males (n = 4). For each individual, the length of the arista-like stylus, and the length and widths of the postpedicel and palp were recorded. Then, the lateral view of the inner part of the postpedicel and outer part of the palp was magnified, and the different morphological sensillum types were identified and counted. Furthermore, a subset of all sensillum types was selected for measurements of their length and basal width. All comparisons were done with similar magnifications.

To compare the sensillum density between adults of *M. signaticornis,* which are larger in body size compared to *M. infumata*, the surface area of the postpedicel and palps was estimated, similar to Pitts and Zwiebel (2006). For each specimen, the basic formula of an ellipse (r1*r2 *π) was used, in order to estimate the surface area of the inner part of the postpedicel and outer part of maxillary palps. The largest and the smallest diameters of the postpedicel or maxillary palps, respectively, were measured and half their lengths defined as r1 and r2. Then, the sensillum density on the postpedicel and maxillary palps was calculated by dividing the total number of sensilla by the surface area, in which the particular type of sensillum was found. Two-way analysis of variance (ANOVA) was used to compare the relative measurements of the *(i)* length of the arista-like stylus, (*ii*) the surface area of the postpedicel and palp; and *(iii)* the densities of the different sensillum types. Pairwise multiple-comparison post-hoc tests were carried out for the multiple comparisons between sexes, species and statistical interaction between these two variables (sex*species). Statistical analyses were performed using *aov ()* and *Emmeans ()* functions from R studio (version 3.6.1; RStudio-Team, 2018).

3. Results

The criteria for identification and classification of the antennal morphology and sensilla types in this study followed those of Shanbhag et al. (1999), Hallberg and Hansson (1999) and Keil (1999).

3.1. General morphology of the olfactory organs

3.1.1. Antennae

The antennae of adult *M. signaticornis* and *M. infumata* species are located frontally between the large compound eyes (Fig. 1A and B). Each antenna consists of three distinct segments: the scape, the pedicel and the postpedicel with an arista-like stylus (Fig. 1A and B). The postpedicel is oval in shape, and the surface area is significantly larger ($F = 56.5$; $df = 1, 16$; $P < 0.001$) in *M. signaticornis* compared to *M. infumata* (Fig. 1C and D). However, no significant differences in size are observed between sexes ($F = 1.6$; $df = 1, 16$; $P > 0.05$), and neither do the variables of sex and species statistically interact ($F = 1.4$; $df = 1, 16$; $P > 0.05$; Table 1). The terminal arista-like stylus is rigid and long (400 μm–480 μm), and it is located at the end (top) of the postpedicel (Fig. 2A–C). No significant differences are observed in the relative length of the terminal arista-like stylus between sexes ($F = 0.4$; $df = 1, 17$; $P > 0.05$) or species ($F = 1.0$; $df = 1, 17$; $P > 0.05$), nor do the variables of sex and species influence each other by statistical interaction ($F = 0.4$; $df = 1, 17$; $P > 0.05$). This indicates that the lengths of the arista-like stylus are similar between individuals of the different sexes and species.

In both species, a large number of non-innervated microtrichia (Shanbhag et al., 1999) are found on the scape, pedicel, postpedicel

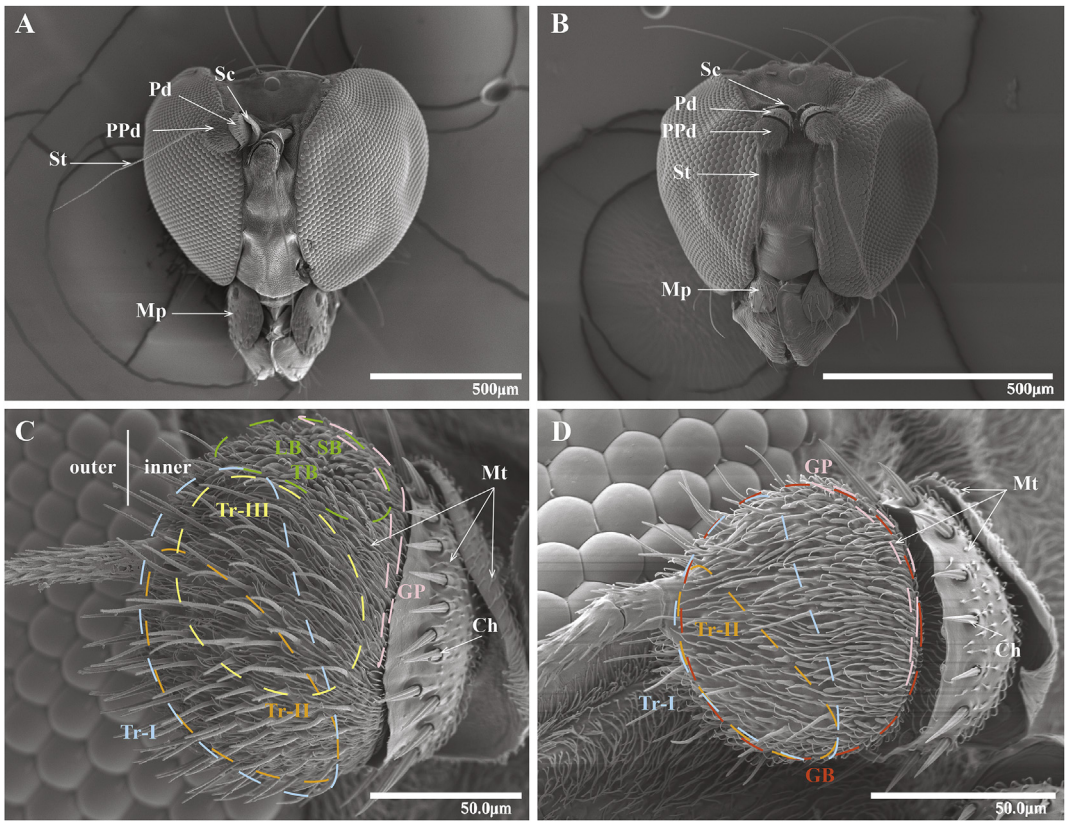

Fig. 1. Morphology of the antenna, maxillary palps and the sensillar arrangement in *Medetera signaticornis* and *Medetera infumata*. **A.** Frontal view of the heads of female *M. signaticornis* and **B.** *M. infumata,* respectively. **C.** Lateral view of the inner part of the postpedicel of female *M. signaticornis* and **D.** *M. infumata*, respectively. Abbreviations: Sc, scape; Pd, pedicel; PPd, postpedicel; St, arista-like stylus; Mp, maxillary palps; LB, large s. basiconica; SB, small s. basiconica; TB, thin s. basiconica and GB, grooved s. basiconica; Tr-I, long s. trichodea; Tr-II, short s. trichodea and Tr-III, curved s. trichodea; GP, grooved pegs; Ch, s. chaetica and Mt, microtrichia. Colored dashed lines indicate the areas where the specific types and subtypes of olfactory sensilla are found.

Table 1
Lengths (µm) of the arista-like stylus and surface areas (µm^2) of the inner part of the postpedicel and the outer part of the maxillary palps are shown as means ± standard errors. Data were analysed for significant differences dependent on sex or species, as well as for statistical interaction between these two variables. Different small letters (a,b,c) following the measures of length and surface area indicate significant differences between sexes or species according to post-hoc tests following two-way ANOVA. F-values provide a measure for variation between samples, df abbreviates the degrees of freedom and $P < 0.05$ provides a measure for significant difference between means.

	M. signaticornis		*M. infumata*		Variables		
	Females	Males	Females	Males	Sex	Species	Sex*Species
Length of the arista-like stylus	472.7 ± 28.4	438.3 ± 11.8	472.0 ± 13.7	465.0 ± 12.9	$F = 1.0$; $df = 1, 17$; $P > 0.05$	$F = 0.4$; $df = 1, 17$; $P > 0.05$	$F = 0.4$; $df = 1, 17$; $P > 0.05$
Surface area of the postpedicel	10218.1 ± 932.6**a**	8642.8 ± 457.5**a**	4372.4 ± 12.9**b**	4403.3 ± 92.0**b**	$F = 1.6$; $df = 1, 16$; $P > 0.05$	$F = 56.5$; $df = 1, 16$; $P < 0.001$	$F = 1.4$; $df = 1, 16$; $P > 0.05$
Surface area of the maxillary palps	18761.5 ± 2160.2**a**	14789.4 ± 1373.3 **ab**	8154.2 ± 412.2**bc**	6329.1 ± 142.4**c**	$F = 3.4$; $df = 1, 14$; $P > 0.05$	$F = 33.9$; $df = 1, 14$; $P < 0.001$	$F = 0.4$; $df = 1, 14$; $P > 0.05$

and arista-like stylus (Fig. 1C and D; Fig. 2A–F). Besides microtrichia no other structures are found on the scape (Fig. 2D). The pedicel is the only antennal segment that houses mechanosensory bristles known as s. chaetica (Ch) (Fig. 1C and D; Fig. 2 D, G, H). While, the postpedicel features three different putative olfactory sensilla types: s. trichodea, s. basiconica and grooved pegs (GP) (Fig. 1C and D).

3.2. Maxillary palps

The maxillary palps in adults of *M. signaticornis* and *M. infumata* are attached to the side of the basodorsal part of the proboscides (Fig. 1A and B), with both species displaying a similar maxillary palp morphology, in regards to the shape and location of the different sensillum types (Fig. 3A and B). The palp surface area of *M. signaticornis* is significantly larger ($F = 33.9$; $df = 1, 14$; $P < 0.001$) compared to *M. infumata*, and although females have a slightly larger palp area compared to males, the difference is not significant ($F = 3.4$; $df = 1, 14$; $P > 0.05$), and no statistical interaction between sex and species is found, i.e., the larger surface in *M. signaticornis* is independent from any variation between sexes ($F = 0.4$; $df = 1, 14$; $P > 0.05$) (Table 1). Each palp consists of a single oval segment, with two different subtypes of Ch (as described below) distributed from the centre to the distal end (Fig. 3A–D). Few microtrichia are distributed along the proximate rim of the palp and over the edges (Fig. 3A, B, E) and a group of long grooved s. basiconica (MpGB) are found in a pit (Fig. 3A, B, F).

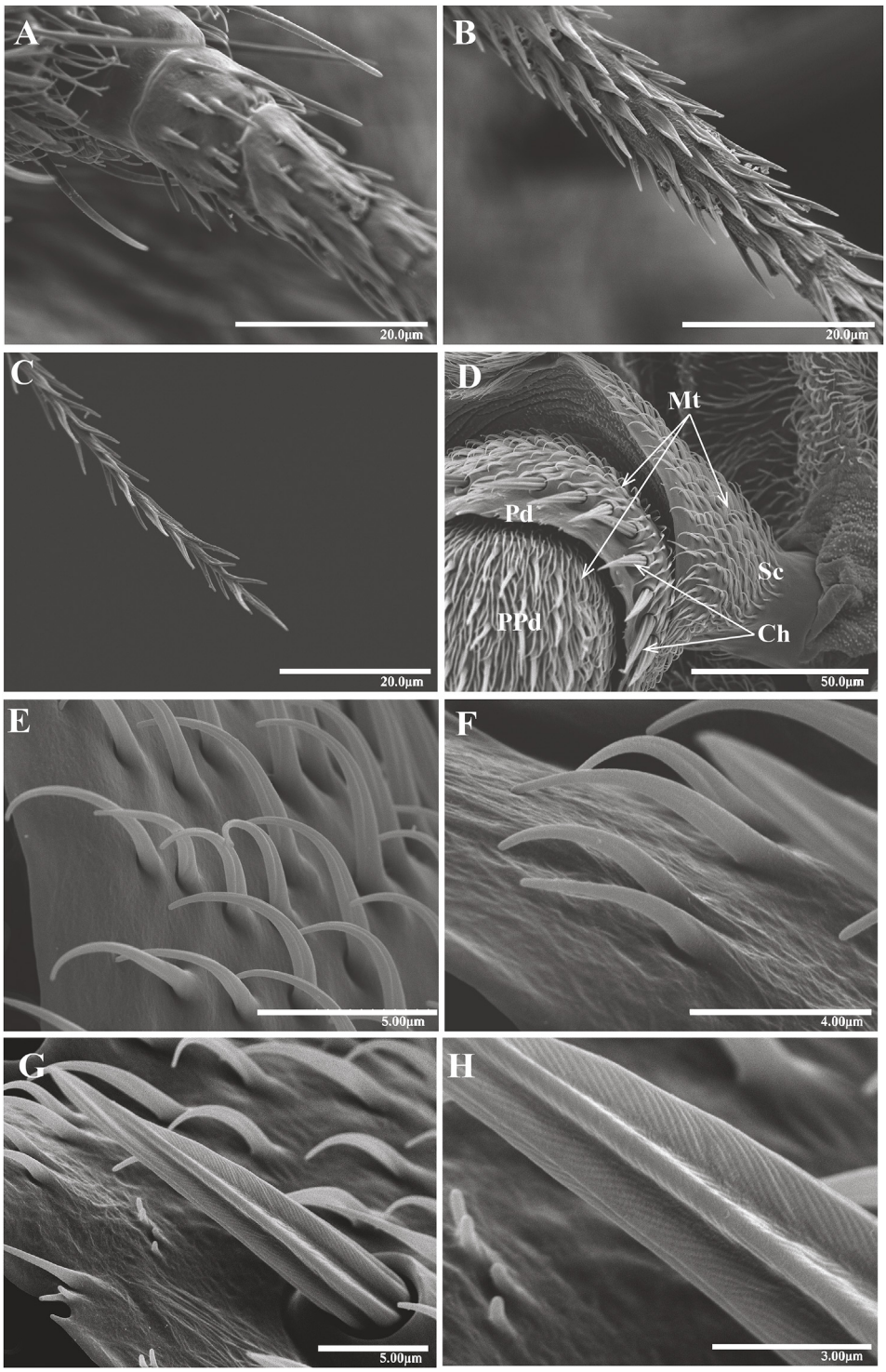

Fig. 2. Arista-like stylus, scape and pedicel of *Medetera signaticornis* and *Medetera infumata*. **A-C**. Different parts (base, middle and tip, respectively) of the arista-like stylus of male *M. infumata*. **D-H.** Pictures from female *M. signaticornis*. **D.** Lateral view of the scape and pedicel. **E-F.** High-resolution of microtrichia from the scape and pedicel, respectively. **G-H.** High-resolution images of s. chaetica from the circumference of the pedicel. Abbreviations: Sc, scape; Pd, pedicel; PPd, postpedicel; Ch, s. chaetica; Mt, microtrichia.

3.3. Sensillum types

3.3.1. Sensilla chaetica (CH)

The Ch arise from a flexible socket, and are cylindrical at the base, and then gradually taper into a long straight hair with a sharp tip. The surface has prominent longitudinal grooves with no discernible wall pores (Fig. 2G and H; Fig. 3C and D). This type of sensillum is present in both species, and is distributed evenly around the circumference of the pedicel (Fig. 1C and D) and from the centre to the distal end of the outer part of the maxillary palp (Fig. 3A and B). According to their length and position, the Ch sensilla on the maxillary palps are classified as Ch-I and Ch-II (Table 2). The density of Ch on the pedicel and Ch-I on the maxillary palps found in *M. infumata* is significantly higher than in

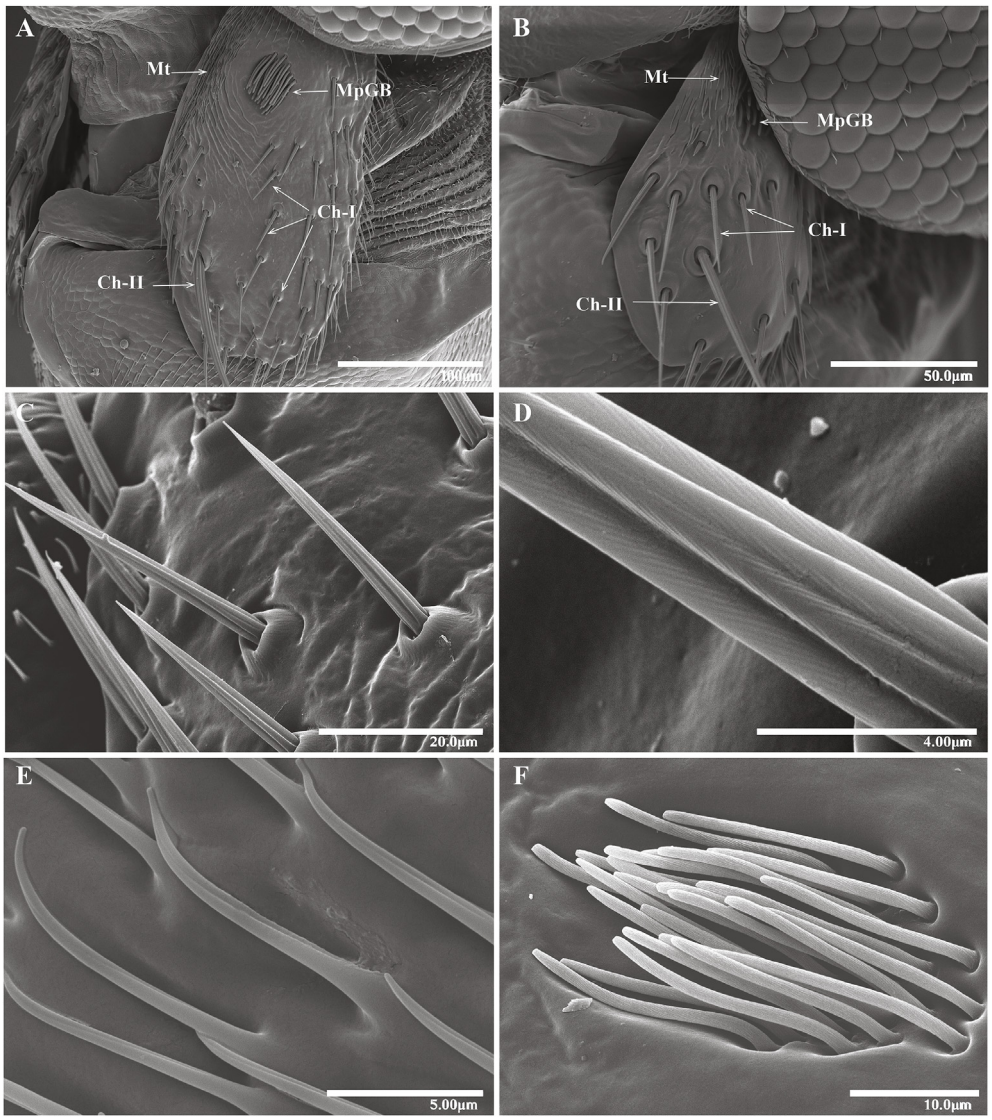

Fig. 3. Morphology of the maxillary palps of *Medetera signaticornis* and *Medetera infumata*. **A-B**. Lateral view of the outer part of maxillary palp of female *M. signaticornis* and *M. infumata,* respectively. **C**–**F.** Pictures from the outer part of the maxillary palp of female *M. signaticornis*. **C-D.** High-resolution of the palpal sensilla chaetica. **E.** High-resolution of microtrichia from the proximate rim of the palp. **F.** Pit with the long grooved s. basionica. Abbreviations: Mt, microtrichia; MpGB, long grooved s. basiconica; Ch-I, s. chaetica subtype I; Ch-II, s. chaetica subtype II.

M. signaticornis (Ch: $F = 71.4$; $df = 1, 13$; $P < 0.001$, Ch-I: $F = 24.7$; $df = 1, 11$; $P < 0.001$), however, no significant differences are observed between sexes (Ch: $F = 0.39$; $df = 1, 13$; $P > 0.05$, Ch-I: $F = 0.9$; $df = 1, 11$; $P > 0.05$) and no statistical interaction is found between the variables of species and sex (Ch: $F = 1.19$; $df = 1, 13$; $P > 0.05$, Ch-I: $F = 4.5$; $df = 1, 11$; $P > 0.05$) (Table 3). Only one long Ch-II sensillum is found on each palp in both species (Fig. 3A and B).

3.4. Sensilla trichodea

Sensilla trichodea are the most abundant sensillum type found on the postpedicel of *M. signaticornis*, and the second most common type found on the postpedicel of *M. infumata* (Fig. 1C and D; Table 2). According to differences in morphology and length, the sharp-tipped s. trichodea may be sub-divided into long (Tr-I), short (Tr-II) and curved s. trichodea (Tr-III) (Fig. 4A–F; Table 2). The Tr-I and Tr-II sensilla are found closely packed along the lateral margin of the postpedicel in both species (Fig. 1 C, D). The Tr-III subtype is only found on the postpedicel of *M. signaticornis*, and is distributed diagonally over the disto-lateral part of both the inner and outer side of the postpedicel. The size of Tr-III is intermediate when compared to Tr-I and Tr-II (Table 2). The cuticle of the Tr-I and Tr-II sensilla is relatively smooth compared to Tr-III, which is characterised by elevated ridges (Fig. 4A–F). All three subtypes have evenly distributed pores and a non-accentuated basal drum. The density of Tr-I found on the postpedicel of *M. signaticornis* is higher compared to *M. infumata* ($F = 21.8$; $df = 1, 16$; $P < 0.001$), and in both cases, males have more Tr-I compared to the females ($F = 13.2$; $df = 1, 16$; $P < 0.01$) (Table 3).

3.5. Sensilla basiconica

The sensilla basiconica are the most common sensillum type found on the postpedicel of *M. infumata* and second most common found on the postpedicel of *M. signaticornis*. According to the morphology and size, these sensilla can be divided into four subtypes; large (LB), small (SB), thin (TB) and grooved (GB) (Fig. 4-G-J)

Table 2
Types, location, numbers and dimensions of sensilla found on the antenna and maxillary palps. Lengths (L) and basal widths (BW) expressed in μm were measured from samples containing males and females and are shown as means ± standard errors. N° represents the numbers of sensilla found on the inner part of the antenna or on the outer part of the maxillary palps. As some types of sensilla are more common than others, different numbers (n) of sensilla were used for the evaluation of L and BW.

Sensilla	Location of the sensilla		*M. signaticornis*					*M. infumata*				
	Antennae	Maxillary palps	N° of sensilla females	N° of sensilla males	L	BW	n	N° of sensilla females	N° of sensilla males	L	BW	n
S. chaetica (Ch)	x		16.5 ± 0.9	15.0 ± 0.6	22.4 ± 1.1	3.3 ± 0.1	15	12.0 ± 0.8	11.5 ± 0.4	22.1 ± 1.5	3.1 ± 0.1	15
S. chaetica subtype I (Ch-I)		x	31.5 ± 1.9	27.5 ± 2.8	31.2 ± 1.6	3.1 ± 0.1	15	17.2 ± 0.4	17.4 ± 1.2	34.0 ± 1.1	2.7 ± 0.1	15
S. chaetica subtype II (Ch-II)		x	1.0 ± 0.0	1.0 ± 0.0	85.0 ± 3.1	7.5 ± 0.4	5	1.0 ± 0.0	1.0 ± 0.0	77.5 ± 2.6	5.0 ± 0.2	5
Long s. trichodea (Tr-I)	x		69.2 ± 3.2	76.6 ± 3.7	23.3 ± 0.4	1.9 ± 0.0	25	24.4 ± 1.8	28.3 ± 0.9	21.2 ± 0.4	1.9 ± 0.0	10
Short s. trichodea (Tr-II)	x		20.2 ± 2.5	14.2 ± 2.0	9.9 ± 0.5	1.9 ± 0.0	12	5.8 ± 1.0	7.5 ± 1.1	10.0 ± 0.3	2.0 ± 0.0	5
Curved s. trichodea (Tr-III)	x		24.5 ± 2.8	28.0 ± 1.2	14.3 ± 0.6	1.8 ± 0.0	12					
Small s. basiconica (SB)	x		27.2 ± 1.6	21.0 ± 3.6	6.7 ± 0.2	1.8 ± 0.0	20					
Large s. basiconica (LB)	x		38.8 ± 3.0	34.0 ± 3.9	4.5 ± 0.2	2.0 ± 0.1	20					
Thin s. basiconica (TB)	x		8.7 ± 0.8	9.2 ± 0.6	8.2 ± 0.3	1.7 ± 0.2	10					
Grooved s. basiconica (GB)	x							47.6 ± 0.6	41.5 ± 2.5	7.6 ± 0.2	1.6 ± 0.0	20
Long grooved s. basiconica (MpGB)		x	31.2 ± 2.2	25.5 ± 1.5	18.6 ± 0.3	1.4 ± 0.1	30	19.5 ± 1.1	12.0 ± 0.5	12.5 ± 0.2	1.9 ± 0.1	30
Grooved pegs (GP)	x		8.5 ± 0.5	8.4 ± 1.0	3.6 ± 0.2	1.6 ± 0.1	10	5.0 ± 0.9	2.3 ± 0.7	3.5 ± 0.3	2.0 ± 0.1	5

Table 3
Sensilla densities (number of sensilla per μm^2 of surface area) found on the inner part of the postpedicel and outer part of the maxillary palps. Data were analysed for significant differences dependent on sex or species, as well as for statistical interaction between these two variables. Different small letters (a,b,c) indicate significant differences between sexes or species according to post-hoc tests following two-way ANOVA. F-values provide a measure for variation between samples, df abbreviates the degrees of freedom and $P < 0.05$ provides a measure for significant difference between means.

Sensilla	*M. signaticornis*		*M. infumata*		Variables		
	Females	Males	Females	Males	Sex	Species	Sex*Species
S. chaetica (Ch)	$1.5 \times 10^{-3} \pm 7.7 \times 10^{-5}$**b**	$1.7 \times 10^{-3} \pm 1.8 \times 10^{-4}$**b**	$2.8 \times 10^{-3} \pm 2.0 \times 10^{-4}$**a**	$2.6 \times 10^{-3} \pm 5.8 \times 10^{-5}$**a**	F = 0.39; df = 1, 13; P > 0.05	F = 71.4; df = 1, 13; P < 0.001	F = 1.19; df = 1, 13; P > 0.05
S. chaetica subtype I (Ch-I)	$1.7 \times 10^{-3} \pm 9.9 \times 10^{-5}$**b**	$1.6 \times 10^{-3} \pm 1.8 \times 10^{-4}$**b**	$2.1 \times 10^{-3} \pm 7.5 \times 10^{-5}$**a**	$2.5 \times 10^{-3} \pm 1.1 \times 10^{-4}$**ab**	F = 0.9; df = 1, 11; P > 0.05	F = 24.7; df = 1, 11; P < 0.001	F = 4.5; df = 1, 11; P > 0.05
Long s. trichodea (Tr-I)	$6.9 \times 10^{-3} \pm 3.4 \times 10^{-4}$**b**	$8.9 \times 10^{-3} \pm 4.1 \times 10^{-4}$**a**	$5.6 \times 10^{-3} \pm 4.5 \times 10^{-4}$**c**	$6.4 \times 10^{-3} \pm 2.2 \times 10^{-4}$**b**	F = 13.5; df = 1, 16; P < 0.01	F = 21.4; df = 1, 16; P < 0.001	F = 1.95; df = 1, 16; P > 0.05
Short s. trichodea (Tr-II)	$2.1 \times 10^{-3} \pm 2.7 \times 10^{-4}$	$1.7 \times 10^{-3} \pm 2.5 \times 10^{-4}$	$1.3 \times 10^{-3} \pm 2.5 \times 10^{-4}$	$1.7 \times 10^{-3} \pm 2.5 \times 10^{-4}$	F = 0.02; df = 1, 16; P > 0.05	F = 1.9; df = 1, 16; P > 0.05	F = 1.7; df = 1, 16; P > 0.05
Curved s. trichodea (Tr-III)	$2.4 \times 10^{-3} \pm 2.4 \times 10^{-4}$	$3.3 \times 10^{-3} \pm 3.1 \times 10^{-4}$			F = 4.01; df = 1, 9; P > 0.05		
Small s. basiconica (SB)	$2.8 \times 10^{-3} \pm 3.5 \times 10^{-4}$	$2.6 \times 10^{-3} \pm 5.8 \times 10^{-4}$			F = 0.14; df = 1, 9; P > 0.05		
Large s. basiconica (LB)	$4.0 \times 10^{-3} \pm 4.5 \times 10^{-4}$	$4.1 \times 10^{-3} \pm 6.7 \times 10^{-4}$			F = 0.01; df = 1, 9; P > 0.05		
Thin s. basiconica (TB)	$8.6 \times 10^{-4} \pm 5.2 \times 10^{-5}$	$1.1 \times 10^{-3} \pm 8.6 \times 10^{-4}$			F = 4.16; df = 1, 9; P > 0.05		
Grooved s. basiconica (GB)			$1.9 \times 10^{-2} \pm 1.5 \times 10^{-4}$	$9.5 \times 10^{-3} \pm 6.7 \times 10^{-4}$	F = 4.2; df = 1, 7; P > 0.05		
Long grooved s. basiconica (MpGB)	$1.7 \times 10^{-3} \pm 2.6 \times 10^{-4}$	$1.8 \times 10^{-3} \pm 4.1 \times 10^{-5}$	$2.4 \times 10^{-3} \pm 1.7 \times 10^{-4}$	$1.9 \times 10^{-3} \pm 8.9 \times 10^{-5}$	F = 0.5; df = 1, 14; P > 0.05	F = 3.2; df = 1, 14; P > 0.05	F = 2.1; df = 1, 14; P > 0.05
Grooved pegs (GP)	$8.7 \times 10^{-4} \pm 8.3 \times 10^{-5}$	$9.9 \times 10^{-4} \pm 1.4 \times 10^{-4}$	$1.1 \times 10^{-3} \pm 2.5 \times 10^{-4}$	$5.3 \times 10^{-4} \pm 1.6 \times 10^{-4}$	F = 0.95; df = 1, 14; P > 0.05	F = 0.06; df = 1, 14; P > 0.05	F = 4.7; df = 1, 14; P = 0.05

(Table 2). The LB, SB and TB subtypes are only found on the postpedicel of *M. signaticornis*, while the GB subtype is only found on the postpedicel of *M. infumata*.

In *M. signaticornis*, s. basiconica are situated within a shallow depression at the top part of the postpedicel (Fig. 1C). The LB is the most common sensillum subtype (Fig. 4G; Table 2) and is present in various forms, which not always end up in a rounded tip. The SB are mostly distributed around the LB sensilla, and are considerably longer than the LB but smaller than the TB (Fig. 4H; Table 2). Both SB and LB sensilla have a smooth cuticular surface with a high density of pores and a seemingly uniform distribution. The TB sensilla are less common on the postpedicel of *M. signaticornis*

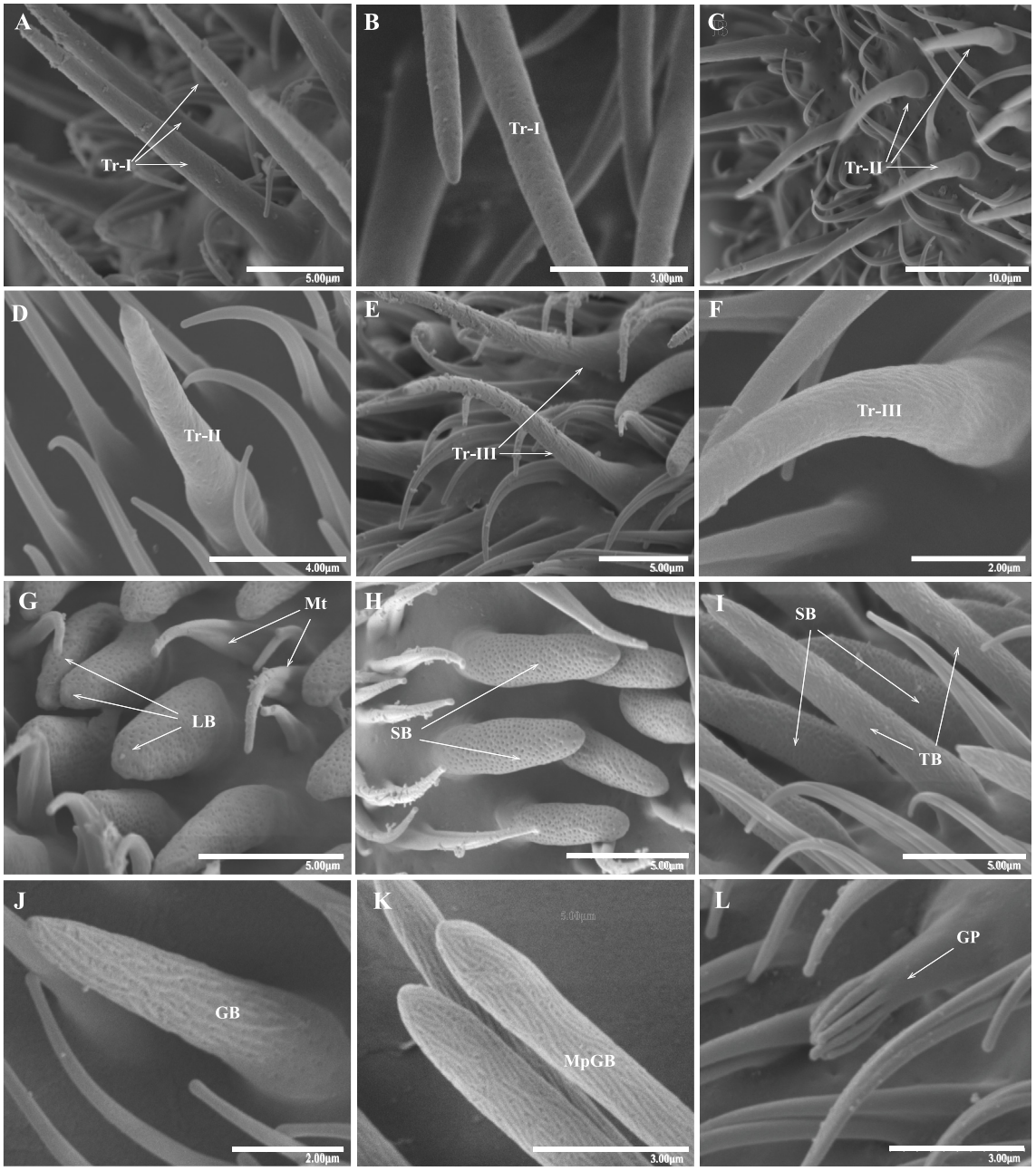

Fig. 4. High-resolution scanning micrographs showing the morphologically different olfactory sensillum types. **A-I** All pictures from the inner part of the postpedicel of female *M. signaticornis*. **A-B.** Long sensilla trichodea (Tr-I). **C-D.** Short s. trichodea (Tr-II). **E-F.** Curved s. trichodea (Tr-III). **G.** Large s. basiconica (LB) and microtrichia (Mt). **H.** Small s. basiconica (SB). **I.** Thin s. basiconica (TB) and SB. **J.** Grooved s. basiconica (GB) from the inner part of the postpedicel of a male *M. infumata*. **K.** Long grooved s. basiconica (MpGB) from the outer part of maxillary palp of a female *M. signaticornis*. **L.** Grooved peg sensillum (GP) from the postpedicel of a male *M. signaticornis*.

compared to the other two subtypes found in this species. This sensillum subtype is mainly located at the narrow edges of the shallow depression at the top medial part of the postpedicel. The TB sensilla were the longest s. basiconica subtype detected (Table 2). The TB sensilla have a sharp tip and a ridged cuticular surface with sparse pores (Fig. 4I).

The GB sensilla (Fig. 4J) are uniformly distributed on both the inner and outer sides of the postpedicel of *M. infumata* (Fig. 1D). Although the *M. infumata* GB and *M. signaticornis* TB sensilla found on the postpedicel are similar in length (Table 2), the cuticular surface of the GB sensilla contains more prominent ridges and a lower number of visible pores compared to the TB sensilla. Similar GB sensilla are also found grouped in a pit on the maxillary palps of both species (Fig. 3A, B, F). However, these sensilla are longer, blunt-tipped and are defined as MpGB (Fig. 4K; Table 2). No significant differences between densities MpGB on the maxillary palps are observed between species ($F = 3.2$; $df = 1, 14$; $P > 0.05$) or sexes ($F = 0.5$; $df = 1, 14$; $P > 0.05$), and the variables sex and species do not affect each other ($F = 2.1$; $df = 1, 14$ $P > 0.05$) (Table 3).

3.6. Grooved pegs

The GP are the smallest and least abundant sensillum type found in both species (Table 2). This sensillum type is located

mainly around the basal part of the postpedicel, close to pedicel. These sensilla are characterised by finger-like processes that extend from an otherwise smooth cuticular shaft (Fig. 4L). No significant differences in the density of GP are observed between species ($F = 0.06$; $df = 1, 14$; $P > 0.05$) or sexes ($F = 0.95$; $df = 1, 14$; $P > 0.05$), and no statistical interaction is seen between these two variables ($F = 4.7$; $df = 1, 14$ $P > 0.05$) (Table 3).

4. Discussion

Many *Medetera* species are predators on bark beetles, which they locate using olfaction. Through a comparative analysis of the main olfactory organs of *M. signaticornis* and *M. infumata*, this study demonstrates significant differences between species in relation to surface areas of the postpedicel and the maxillary palps, the subtypes of antennal sensilla (trichodea and basiconica) and the sensillum densities on the antennae and the maxillary palps. The olfactory system is known to reflect insect phylogeny, ecology and ethology (Hansson and Stensmyr, 2011) and the observed differences in morphology likely reflect evolutionary adaptations related to ecologically relevant behaviours, such as host finding and reproduction. In contrast, the shape and location of the different sensilla found on the maxillary palps are well conserved.

4.1. Antennal morphology

The antennae of *M. signaticornis* and *M. infumata* are composed of three distinct segments: the scape, the pedicel and the postpedicel with a terminal arista-like stylus, similar to the antennal morphology in most fly species (Diptera: Brachycera) (Cumming and Wood, 2017). The scape and the pedicel have been suggested to have a baroreceptor role in the majority of families of Diptera (McAlpine, 2011). Within the genus *Medetera*, the scape is usually relatively short and sometimes rudimentary, but some *Medetera* species can have a more elongated scape compared to the pedicel (Bickel, 1985). Within the Dolichopodidae, the pedicel can also be round and laterally compressed or featuring a finger-like inner projection (e.g., in species from the genus *Syntormon* Loew, 1857), which penetrates the inner side of the postpedicel (Grichanov, 2007). The external structure of the pedicel is taxonomically variable across different dipteran families (Cumming and Wood, 2017). In more distantly-related dipteran species, the pedicel can be enlarged (e.g., members of family Tabanidae), elongated (e.g., members of families Conopidae and Sciomyzidae) or it can be marked dorsally by a longitudinal "antennal seam" (e.g., members of families Muscidae and Calyptratae) (McAlpine et al., 1981; McAlpine, 2011). The functional relevance for the observed morphological variation in scape and pedicel is yet unknown. In all cases, the pedicel connects to the third antennal segment, the postpedicel.

As compared to other dolichopodids, both *M. signaticornis* and *M. infumata* have a relatively small postpedicel of oval shape. Previous studies have shown that shape and size of postpedicel varies across *Medetera* species from elongated triangular (e.g., *M. ambigua* Zetterstedt, 1843) to large triangular (e.g., *M. pinicola* Kowarz, 1878 and *M. melancholica* Lundbeck, 1912) or quadrate of various sizes (e.g., other species of the *M. signaticornis-pinicola* group) (Bickel, 1985). Postpedicel size and shape also differ substantially between genera within the same dolichopodid subfamilies (Negrobov et al., 2015). While not observed in our study, in other fly species representing several dolichopodid genera like e.g., *Argyra* Macquart, 1834; *Dolichopus* Latreille, 1796; *Rhaphium* Meigen, 1803; *Syntormon* and some *Sybistroma* Meigen, 1824, a sexual dimorphism can be found in the shape or size of the postpedicel (Pollet, 2000; Negrobov et al., 2015). Whether this dimorphism reflects a function in sexual communication remains to be determined.

The arista-like stylus has previously been described within the *Medetera* genus as long, bi-segmented and borne apically in a slight notch almost at the tip of the postpedicel (Bickel, 1985). The arista-like stylus is bi-segmented in all dolichopodids, varies strongly in length and can be positioned in various places along the dorsal side of the postpedicel (from basodorsal to apical). However, in some cases within the Dolichopodidae the second segment of the arista-like stylus can be extended (e.g., species of the genera *Chrysosoma* Guerin-Meneville, 1831 and *Plagiozopelma* Enderlein, 1912) (Negrobov et al., 2015). It can also be bare (e.g., species of the genus *Tachytrechus* Haliday, 1851), have short hairs (e.g., species of the genus *Medetera*) or be very pilose (e.g., species of the genus *Poecilobothrus* Mik, 1857) (Negrobov et al., 2015). Still, within the Dolichopodidae family, some species (e.g., genus *Sybistroma*) show apical and even median flags on the second segment of the arista-like stylus (Grichanov, 2007).

Similar arista-like stylus morphology, as observed in both of the studied *Medetera* species, has been described in members of other Diptera families, such as species of genera *Callomyia* Meigen, 1804 (Diptera: Platypezidae) (Cumming and Wheeler, 2016), *Macalpinomyia* Li and Yeates, 2018 (Diptera: Ironomyiidae) (Li and Yeates, 2019), *Megaselia* Rondani, 1856 (Diptera: Phoridae) and *Pseudacteon* Coquillett, 1907 (Diptera: Phoridae) (Pfeil et al., 1994; Sukontason et al., 2005; Chen and Fadamiro, 2008; Lu, 2012). However, other dipteran species can have a subterminal or terminal stylus, which usually is short (e.g., *Mallophora ruficauda* Wiedemann, 1828 (Diptera: Asilidae) (Groba et al., 2014) and *Rhamphomyia bhagati* sp. nov. (Diptera: Tabanidae) (Barták et al., 2021)). Alternatively, dipteran species can have a bristle-like arista, which originates from the inner or outer surface, near the lateral edge, of the postpedicel (e.g., *Gymnosoma rotundatum* Linnaeus, 1758 (Diptera: Tachinidae) (Roh et al., 2020)) or from the dorso-proximal end of the postpedicel (e.g., species of genus *Drosophila* Fallén, 1823 (Diptera: Drosophilidae) (Shanbhag et al., 1999; Gao et al., 2020)). In *Drosophila melanogaster* Meigen, 1830 (Diptera: Drosophilidae), the arista has been demonstrated to play a role in both humidity (Sayeed and Benzer, 1996; Ji and Zhu, 2015) and auditory sensing (Yorozu et al., 2009). However, the function of the arista-like stylus of *Medetera* and other flies remains to be understood.

4.2. Antennal sensillar equipment

In both *Medetera* species, the sensilla of type Ch are found to be organized in a ring around the pedicel. This is similar to that described for most members of the Dolichopodidae family (Grichanov, 2007), with the exception of the *M. aberrans* Wheeler, 1899 group, which has a reduced number of this sensillum type (Bickel, 1985), likely rendering them less capable of detecting mechanosensation, i.e., the sensory modality conveyed by these sensilla (Shanbhag et al., 1999).

In comparison with other families of flies, the distribution of this sensillum type varies considerably. The distribution can be confined to only the scape or the pedicel (e.g., *G. rotundatum* (Roh et al., 2020)) or both the scape and the pedicel can have this sensillum type. Examples of the latter can be found in species such as *M. ruficauda* and *Eupeodes corollae* Fabricius, 1794 (Diptera: Syrphidae) and in species of the genera *Tabanus* Linnaeus, 1758 (Diptera: Tabanidae) and *Simulium* Latreille, 1802 (Diptera: Simuliidae) (Mercer and McIver, 1973; Parashar et al., 1994; Groba et al., 2014; Jia et al., 2019). In Simuliidae, the arrangement of sensilla type Ch around the distal boundary of the scape and pedicel suggests that they may detect the direction and degree of bending of the scape and pedicel, emphasizing a role in assessing air movement over the antenna (Mercer and McIver, 1973).

Sensilla trichodea are one of the most abundant sensillum type found in both *M. signaticornis* and *M. infumata*. This is similar to other fly species (e.g., species from genus *Pseudacteon* (Chen and Fadamiro, 2008; Lu, 2012), *E. corollae* (Jia et al., 2019) and *M. ruficauda* (Groba et al., 2014)). Similar to *Medetera*, the abundance of this sensillum type has been observed to increase from the base to the distal end of the postpedicel in species of genera *Pseudacteon*, *Megaselia* and *Apystomyia* Melander, 1950 (Diptera: Apystomyiidae) (Chen and Fadamiro, 2008; McAlpine, 2011; Lu, 2012). Based on their ultrastructure, s. trichodea have been attributed an olfactory function, and shown to respond to chemical signals used for e.g., foraging, oviposition and mate seeking by dipterans (De Bruyne et al., 2001; Qiu et al., 2006; Hill et al., 2009; Siju et al., 2010). Given the higher abundance of s. trichodea on the postpedicel in males of both studied *Medetera* species, it is a possibility that this sensillum type may be tuned to detect pheromones, as in *D. melanogaster* (Clyne et al., 1997), although pheromone compounds are yet to be identified in Dolichopodidae.

Sensilla basiconica are another sensillum type found with uniform distribution on the postpedicel of *M. infumata*, and are concentrated in a shallow depression at the top part on the postpedicel of *M. signaticornis*. Morphologically, similar subtypes of s. basiconica have been described in *Pseudacteon tricuspis* Borgmeier, 1925 (Diptera: Phoridae) (Chen and Fadamiro, 2008), *M. ruficauda* (Groba et al., 2014), and *G. rotundatum* (Roh et al., 2020). However, the density and distribution of this sensillum type in members of these and other families of flies differs from the two studied *Medetera* species (Shanbhag et al., 1999; Chen and Fadamiro, 2008; Groba et al., 2014; Roh et al., 2020). Functional analysis of s. basiconica in other species has demonstrated that this sensillum type responds to a variety of odorants, including those involved in the detection of food and oviposition sites (De Bruyne et al., 1999, 2001; Elmore et al., 2003). The differences we found in relation to the number and subtypes of s. basiconica between the two *Medetera* species, might reflect species-specific habitat preference. *M. signaticornis* is mainly known to be associated with coniferous forests where bark beetle damage occurs. In contrast, *M. infumata* belongs to a species group that is not confined to tree trunks but also occurs on dry sandy soils (Bickel, 1985; Pollet et al., 2011). Recently, *M. infumata* has been recorded from wooded habitats with coniferous trees, where it is found on both tree trunks and rocky substrates (Pollet, pers. comm.). Accordingly, in slight difference to our hypothesis, the olfactory organs and sensillar equipment show dissimilarities, which might reflect adaptations in relation to species-specific ecology and behaviours, despite common coexistence in coniferous forest, egg-laying on bark beetle-infested trees and attraction to bark beetle pheromones. Future functional analysis is required to assess a possible correlation between this sensillum type, specific chemosensory stimulants and behavioural preference.

The GP described in both *M. signaticornis* and *M. infumata* have previously been found in both members of closely and distantly-related families of dipteran flies, such as *Megaselia scalaris* Loew, 1866 (Diptera: Phoridae) (Sukontason et al., 2005), *P. tricuspis* (Chen and Fadamiro, 2008), *Trichopoda pennipes* Fabricius, 1781 (Diptera: Tachinidae) (Giangiuliani et al., 1994), *Haematopota pandazisi* Krober, 1936 (Diptera: Tabanidae) (Pezzi et al., 2018), *D. melanogaster* (Shanbhag et al., 1999), *Culicoides obsoletus* Meigen, 1818 (Diptera: Ceratopogonidae) (Isberg et al., 2013; Urbanek et al., 2014) and *Anopheles stephensi* Liston, 1901 (Diptera: Culicidae) (Boo and McIver, 1976; Hempolchom et al., 2017). This type of sensillum is ancestral and seems to be conserved through hundreds of millions of years of insect evolution as it can be found in many, if not in all, insect orders (Steinbrecht, 1997; Yao et al., 2005). However, the distribution of this sensillum type on the antenna varies greatly across insect families. Most of the work on the GP has been done in *D. melanogaster* showing that it is tuned to carboxylic acids and amines, expresses olfactory receptors of the ionotropic receptor family but also plays a role in other sensory modalities (Meijerink et al., 2001; Yao et al., 2005; Ghaninia et al., 2008).

4.3. Maxillary palp

The maxillary palp of both *M. signaticornis* and *M. infumata* consists of one small, flat and oval segment. This seems to be similar for the majority of the species of *Medetera* genus (Bickel and Arnaud Jr, 2011). In other genera, within the Dolichopodidae family, the shape of maxillary palps varies substantially e.g., it can also be subquadrate with rounded corners (e.g., *Chrysotus* Meigen, 1824), or rather narrow and pointed apically (e.g., *Amblypsilopus* Bigot, 1888) (Grichanov, 2007). The size also varies from small (e.g., *Sympycnus* Loew, 1857) to large (e.g., *Tachytrechus*) (Brooks and Cumming, 2008) or extended (e.g., *Chrysotus*) (Capellari, 2015; Runyon and Capellari, 2018). Compared to other fly families, the morphology of the maxillary palp varies in relation to the number of palpal segments, orientation (e.g., arched, straight, curved or C-shaped), length and attachment (e.g., connected directly to stipes, separated from stipes, connected to an external sclerite or palpifer) (Sinclair and Cumming, 2006). Additionally, although not observed in our study, sexual dimorphism can be found in relation to the length and shape of the maxillary palps (Runyon, 2020; Pezzi et al., 2021).

4.4. Palpal sensillar equipment

On the maxillary palps of both *Medetera* species, two subtypes of sensilla Ch were found, differentiated based on their size and position. The small Ch-I were distributed from the centre to the distal end of the maxillary palp, while only one long Ch-II was found in the medial part of the palp. In the descriptions of *Medetera* species, the maxillary palp has been mentioned as bearing apical small hairs on the outer side and one long bristle at the apex (Bickel, 1985; Grichanov, 2007). Apical hairs, and one or several long bristles, are also common in distantly-related species such as *D. melanogaster* (Shanbhag et al., 1999) and *Bactrocera dorsalis* Hendel, 1912 (Diptera: Tephritidae) (Liu et al., 2021).

In addition to Ch-I and II, the maxillary palps of both *Medetera* species carry the sensilla MpGB grouped in a pit. Similar sensory pits can be found in closely-related families of predatory and parasitoid flies (e.g., *Hilara maura* Fabricius, 1776 (Diptera: Empididae), *Stenopogon inquinatus* Loew, 1866 (Diptera: Asilidae) and *Lomatia belzebul* Fabricius, 1794 (Diptera: Bombyliidae) (Yeates, 1994; Sinclair and Cumming, 2006), and in distantly-related flies (e.g., species within the genus *Culicoides* Latreille, 1809 (Diptera: Ceratopogonidae) (Isberg et al., 2013). Single sensillum recordings of the papal s. basiconica in different mosquito species (e.g., species within the genera *Anopheles* Meigen, 1818; *Culex* Linnaeus, 1758 and *Culicoides*) have shown that this sensillum type detects carbon dioxide (CO_2), which is a generic cue shared by all vertebrate hosts (Grant and Kline, 2003; Grant et al., 1995). Similarly, CO_2 might be a cue used for example by predatory flies to detect small soft-bodied arthropods that they feed on.

We hypothesized similarity in the morphology of the olfactory organs and sensillar equipment between *M. signaticornis* and *M. infumata,* as based on their close phylogenetic relation and overlap in their ecology and behaviour. In conclusion of our study, we found that the general morphology of the antennae and maxillary palps, in relation to the shape, size and position is similar between *M. signaticornis* and *M. infumata*, but the antennal sensillar equipment varies across species. Different sensillum subtypes and

distributions might indicate that *M. signaticornis* and *M. infumata* process different environmental cues or process the same cues in a different way. However, future studies need to be done to gain a better understanding of the diversity, physiological function and evolution of sensilla types within this taxonomic group. Investigations of the sensorial structures in the *Medetera* genus may establish a base for studies that aim at understanding how these predators find their hosts, mates and oviposition sites. Better understanding of the host finding behaviour might advance the development of biological control of bark beetles with *Medetera* flies.

Author contributions

MS, **PGB**, **KKG** and **GB** planned and conceived the study. **MS** Collected, analysed the data and wrote the original draft of the manuscript. **RI** assisted with the identification of the different olfactory sensillum types, structure and revision of the manuscript. **MP** identified the specimens and gave guidance during the early stage of the study. **GB** initiated the project. All co-authors contributed to the revision of the manuscript and have approved the last version of the manuscript.

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