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Mouthpart dimorphism in male and female wasps of *Vespula vulgaris* and *Vespula germanica* (Vespidae, Hymenoptera)

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Abstract

Social wasps perform a variety of tasks with their mouthparts. Female workers use them to feed on carbohydrate-rich fluids, to build nests by collecting wood fibers and forming paper, to hunt and manipulate insect prey for feeding larvae as well as for brood care. Since male wasps neither feed on insects nor participate in nest building, sex-specific differences in mouthpart morphology are expected. Despite these different applications, general mouthpart morphology of male and female wasps from the genus *Vespula* was similar. However, males possessed significantly shorter mandibles with fewer teeth than females. Furthermore, the adductor muscles of the mandibles were distinctly smaller in males than in females. Male wasps showed a higher number of sensilla on the mandibles and the labial palpi. Mouthpart dimorphism and functional morphology of fluid uptake are discussed.

Key Words

mandible
sensilla
morphology
feeding
social insects
sexual dimorphism

Introduction

Insect mouthparts are composed of a set of homologous organs that are derived from appendages of head segments adapted to various tasks in context of feeding, defence and nesting. The mouthparts are composed of an unpaired labrum plate in front of the mouth, paired mandibles and paired maxillae as well as an unpaired labium extending from the last head segment (Snodgrass 1935, Seifert 1995). In general, the mandibulate mouthparts of Hymenoptera are characterized by the labio-maxillary complex which is formed by components of the labium and the maxillae (Duncan 1939, Krenn et al. 2005). This unique functional unit of the mouthparts as well as the four-segmented labial palpus are regarded as autapomorphies of the Hymenoptera (Krenn 2007). Adaptations of the labio-maxillary complex for nectar feeding evolved several times independently in many Hymenoptera (Jervis 1998, Jervis and Vilhelmsen 2000). Especially in social wasps, the mouthparts are functionally versatile allowing their use in various kinds of tasks that are reflected by the well-developed biting mandibles and the labio-maxillary complex which is used to take up nectar and other kinds of fluids (Schremmer 1962).

Social wasps collect two main kinds of food. Adult wasps nourish themselves with liquid carbohydrates obtained from honeydew, ripe fruits, flower nectar and sometimes tree sap (Matsuura and Yamane 1990). Female wasps are involved in brood care, nest building and hunting prey, while male wasps do not forage (Schremmer 1962, Spradbery 1973). Females prey mainly on other insects, bite off the wings, legs, and head of the captured prey and convert the remaining parts into a meatball, which is fed to the larvae in the nest (Berland 1928, Schremmer 1962). In addition to supplying themselves and their brood with food, female wasps use their mouthparts for cutting and scraping off plant fibers during nest building, for picking up soil and stones when colonizing underground cavities, as well as for the uptake of water. Hence the mandibles and labio-maxillary complex can be compared to a set of microtools for different kinds of tasks. By contrast, male wasps are not involved in brood care and feed on nectar obtained from flowers with freely accessible nectaries (Schremmer 1962, Matsuura and Yamane 1990).

The mouthparts of some *Vespula* species were previously examined in detail (Kirmayer 1909, Duncan 1939, Spradbery 1973). They consist of the large biting mandibles and the labio-maxillary complex (Fig. 1). Each maxilla consists of the slender cardo and the flat stipes with the small lacinia, the lateral galea and the 6-segmented maxillary palpus. The labium can be divided into the submentum, forming the lateral connection to the cardines, the roof-shaped mentum and the prementum bearing the 4-segmented labial palpi as well as the median ligula, composed of the united glossae and paired paraglossae (Duncan 1939, Seifert 1995). The labrum (termed as epipharynx in Seifert 1995) is situated under the frontal rim of the clypeus (termed as labrum in Seifert 1995).

Wasps from the genus *Vespula* are widely distributed in the Northern hemisphere (Greene 1991, Kimsey and Carpenter 2012). During the last decades, researchers focused mainly on behavioural studies of these social wasps (e.g., Matsuura and Yamane 1990, Mauss 2007). The principle composition of the mouthparts is well studied and was found to be very similar in female workers and queens (Kirmayer 1909, Duncan 1939, Spradbery 1973). However, the mouthparts of male wasps were not studied in detail.

The present study used various morphological methods including scanning electron microscopy and micro CT to investigate the micromorphology of the mouthparts in two species of the genus *Vespula*. Detailed examination of the cuticle structures including the sensilla allowed conclusions on the functional morphology of the various parts. Special emphasis is laid on the differences between females (workers and queens) and male wasps. Fundamental sex-specific differences in mouthpart morphology can be expected because of characteristic differences in behaviour of each sex.

Methods

Specimen sampling

8 individuals (2 queens, 4 female workers, 2 males) of *Vespula germanica* (Fabricius, 1793) and 7 individuals (3 queens, 4 female workers) of *Vespula vulgaris* (Linnaeus, 1758) were used for light microscopy. Eighteen individuals of *V. germanica* were measured including nine female workers and nine males. 4 individuals of *V. germanica* (1 queen, 1 female worker, 2 males) and 8 individuals of *V. vulgaris* (5 female workers, 3 males) were used for scanning electron microscopy. 1 female worker and 1 male individual of *V. germanica* were used for micro CT to compare the musculature of the mandibles in different sexes.

Light microscopy (LM)

The mouthpart components were extracted from the head using a pair of scissors, forceps and dissecting needles. The disaggregated mouthparts were rinsed with deionized water for 10 minutes and were subsequently transferred into 30 % lactic acid. The musculature dissolved after 120 hours on the vibrating unit at room temperature. The mouthparts were rinsed for 10 minutes, transferred to 30 % ethanol for several minutes and put into a drop of polyvinyl-lactophenol on a hollow microscopic slide which was covered with coverslip. The slides were dried in a fume hood for several days before examination with a light microscope (Nikon Laborphot 2) and a stereomicroscope (Nikon SMZ 10). Micrographs were taken using a light microscope (Nikon Eclipse E 800) with an attached camera (Nikon DS-Fi2 U3) and NIS-elements software.

Morphometry

The heads were placed in a small watch glass filled with sand, arranged under the stereomicroscope (Nikon SMZ 10) and imaged with an attached Samsung Digimax V50 camera. Length measurements of the mandibles and other parts of the head were conducted in both sexes (N=18). For the comparison of mandible size to head size three different measurements were performed using ImageJ (US National Institutes of Health, Bethesda, USA): (1) Mandible length measured from the anterior articulation to the tip of the third tooth; (2) Length from the basis of the scapus of one antenna to the distal ridge of the clypeus; (3) Length of the head from the vertex to the distal ridge of the clypeus (Fig. 1A). Data were analysed using a Mann-Whitney U-Test (SPSS Statistics 23.0, IBM Corporation, New York, USA). The significance level was set at $p = 0.05$.

Scanning electron microscopy (SEM)

Wasp heads and mouthparts were dehydrated in an ascending ethanol series, subsequently submerged in 100% acetone for 90 minutes and transferred to hexamethyldisilazane for 60 minutes. The samples were taken out and left to air-dry under the fume hood overnight. Samples were mounted on aluminium stubs using carbon foils and conductive silver and were subsequently sputtered with gold using a JEOL JFC-2300HR Sputter Coater for 120 seconds. SEM micrographs were taken using a Philips XL 30 ESEM and JEOL IT 300 with an acceleration voltage of 20 kV.

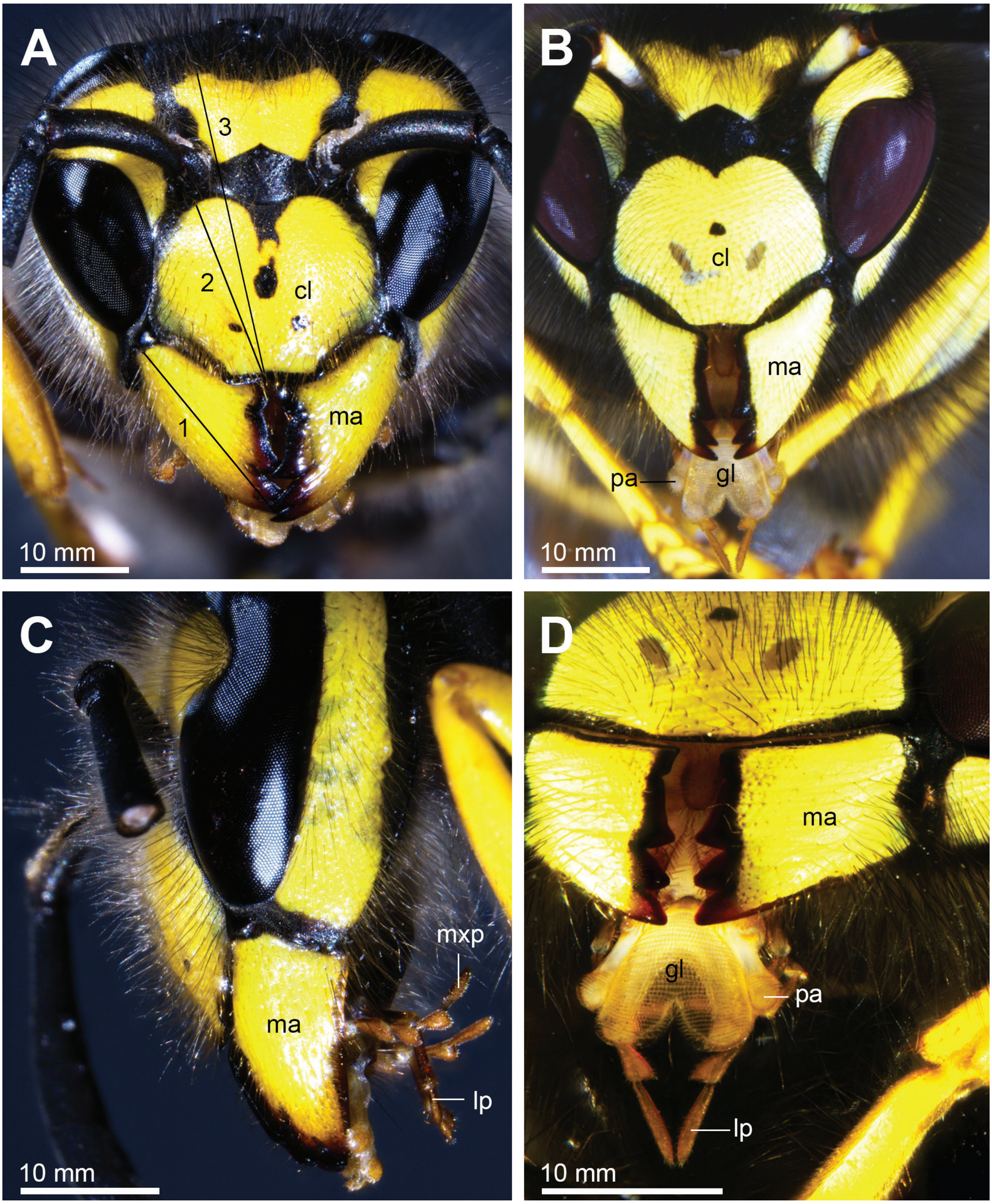

Figure 1. Head of *Vespula germanica* (LM). **A.** Female worker in frontal view; 1, 2, 3 measuments taken to compare head size. **B.** Male in frontal view. **C.** Female worker in lateral view. **D.** Male in ventral view; **cl** – clypeus, **gl** – glossa, **lp** – labial palpus, **ma** – mandible, **mxp** – maxillary palpus, **pa** – paraglossa.

Microcomputed tomography (Micro CT)

Wasps were fixed in Dubosq-Brazil solution (alcoholic Bouin solution), stored in 70 % ethanol and stained with 1 % Iodine in ethanol (Metscher 2009). An Xradia MicroXCT system was used for scanning. The photo stacks (.tiff files) were prepared using Xradia software. The stacks were reconstructed using Amira 6.0 and 6.1 (FEI comp., Hillsborow, USA). The musculature of the mandibles was reconstructed for each individual. Photoshop CC (Adobe Systems Inc., San Jose, California, USA) was used for composing the plates and contrast enhancing of the pictures.

Results

No differences in head and mouthpart morphology were found between *V. vulgaris* and *V. germanica* (Fig. 1). The heads of male wasps were slightly larger (males: 3.23 ± 0.38 mm, N = 9; females: 3.08 ± 0.21 mm, N = 9), but no significant differences between sexes were found (Z = - 0.97, p = 0.33, N = 18). Female workers had significantly longer mandibles than males (males: 1.88 ± 0.11 mm, N = 9; females: 2.07 ± 0.13 mm, N = 9; Z = - 2.87, p = 0.003, N = 18). The distance between the scapus and the distal ridge of the clypeus was similar in males and females (males: 1.85 ± 0.16 mm, N = 9; females: 1.79 ± 0.13 mm, N = 9; Z = - 0.88, p = 0.38, N = 18).

The mouthparts of both sexes in *V. vulgaris* and *V. germanica* are characterized by large toothed mandibles and the labio-maxillary complex which is folded posteriorly under the head behind the mandibles (Fig. 1C). The labrum can only be observed when the mandibles are open. The proximal part of the labrum is entirely concealed behind the clypeus; the distal part of the labrum is well equipped with sensilla trichodea (Fig. 2B).

The dentate mandibles are heavily sclerotized and shaped like a gouge in both sexes (Fig. 2C, D). The mandibles have sharp distal margins; they are slightly convex on their lateral sides and concave on the medial sides. In repose, one mandible is folded over the other (Fig. 2A). The right mandible folds over the left in 11 (including 5 males) out of 18 wasps, whereas 7 wasps (including 4 males) fold the left mandible over their right one. The cutting edge of the incisive part bears three frontal teeth and a curved proximal cutting edge (Fig. 2C, D). In female workers and queens, two additional teeth and edges with stout bristles are present on the median side of the mandible that is not visible from frontal side (Fig. 2C). In comparison to the incisive part the molar region of the mandible is rather small in females and reduced in male wasps (Fig. 2C, D).

The mandibles bear bristle-shaped sensilla and sensilla campaniformia towards the teeth on the frontal side (Fig. 2). The mandibles of males are almost entirely covered with long sensilla trichodea (Fig. 2B). Their sensory bristles are rough and some are as long as the mandible. Mandibles of female workers show a lower number of sensilla. Their bristles are smooth and shorter, measuring

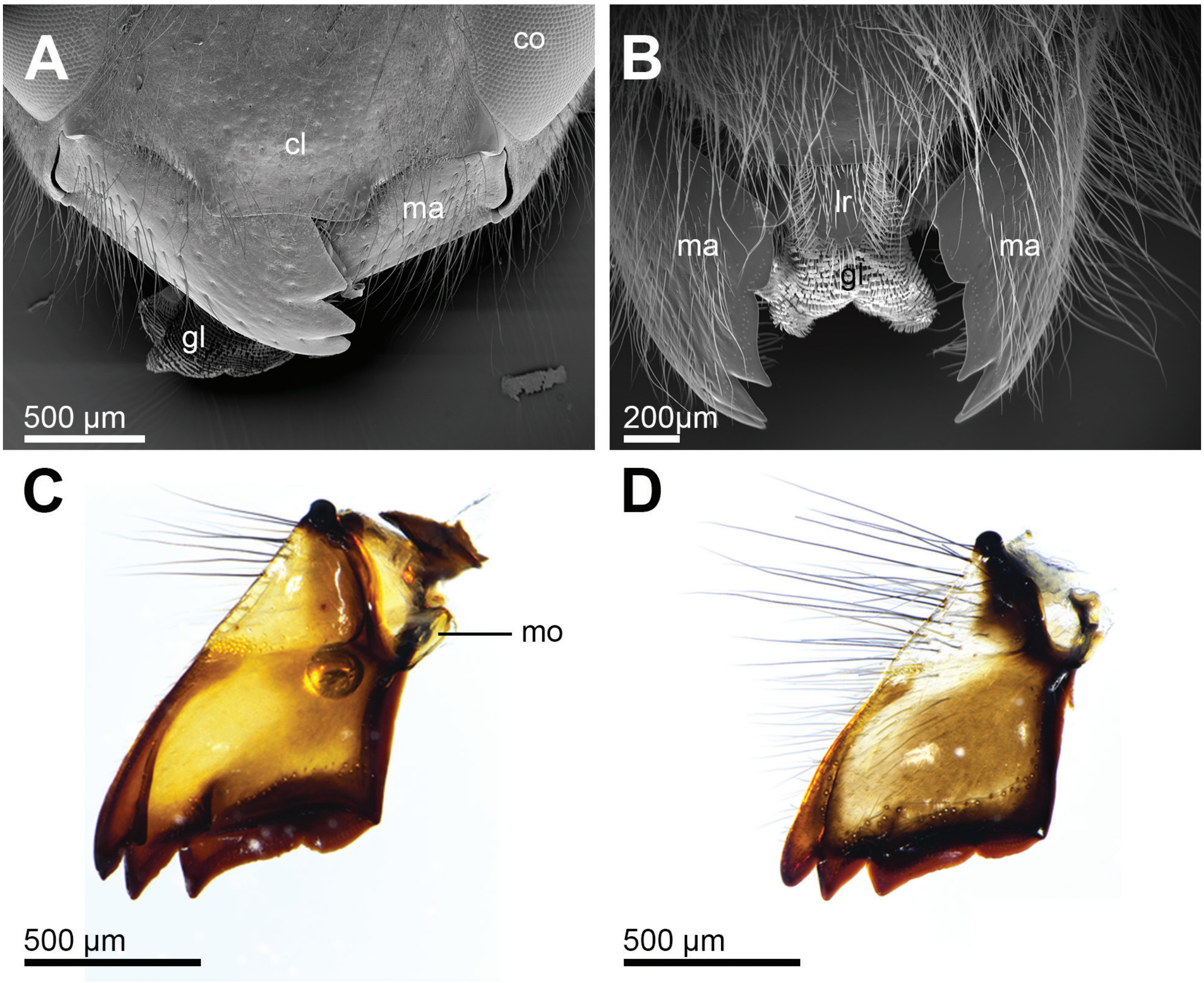

Figure 2. Mandibles and labrum (SEM, LM). **A.** Mandibles (**ma**) overlapping in repose in front of the clypeus (**cl**); **co** – compound eye, **gl** – glossa. **B.** Open mandibles (**ma**), labrum (**lr**) and glossa (**gl**) underneath (male wasp). **C.** Mandible of female (LM), short bristles and mola (**mo**). **D.** Mandible of male (LM), long bristles and inconspicuous inner teeth.

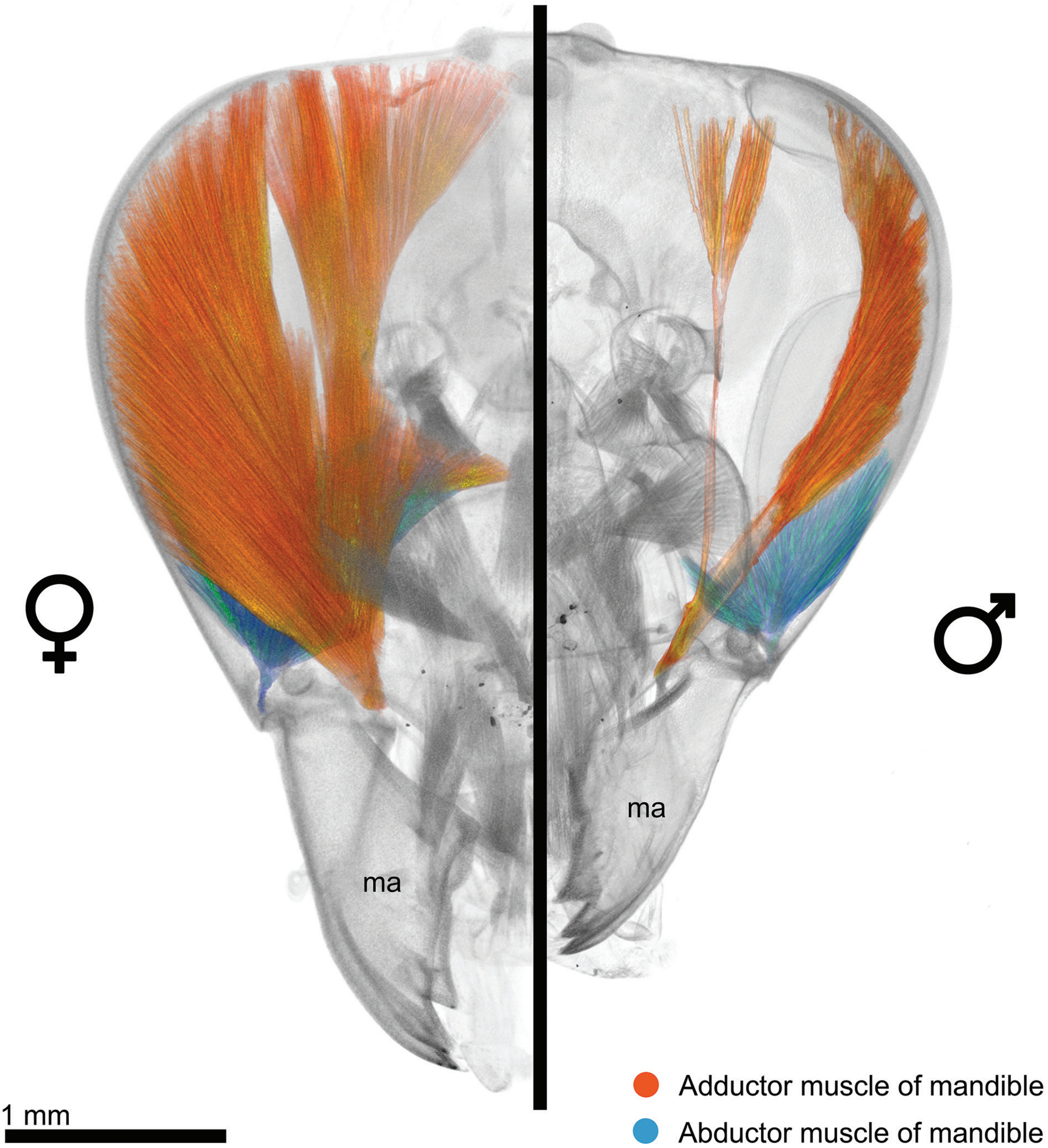

Figure 3. Head anatomy of a female worker (left) and a male individual (right) of *V. germanica* (micro CT). Adductor of the mandible (red) is much bigger in females than in males; abductor muscle (blue) is slightly bigger in females; **ma** – mandible.

only half of the mandible length (Fig. 2C) in contrast to males (Fig. 2D).

The comparison of the head anatomy in female workers and males showed that the muscles of the mandibles were remarkably smaller in males (Fig 3). Despite both portions of the adductor of the mandible (Musculus craniomandibularis internus) had the same origin and attachment sites, the volume of both was much smaller in males than in females. Especially the median portion of the adductor muscle was very small in males. The volume of the abductor muscle (Musculus craniomandibularis externus) was slightly smaller in male wasps than in workers (Fig. 3).

The labio-maxillary complex of both sexes is retracted in an oval depression on the posterior part of the head capsule in repose (Fig. 4). The components of this functional unit are firmly connected to ensure that the complex extends and retracts as a unit. In the extended position, the ligula (i.e., glossa plus paraglossae) is longer than the mandibles (Fig. 1B, D). In retracted position, the glossa and paraglossae are folded backwards under the head (Figs 1C, 4A).

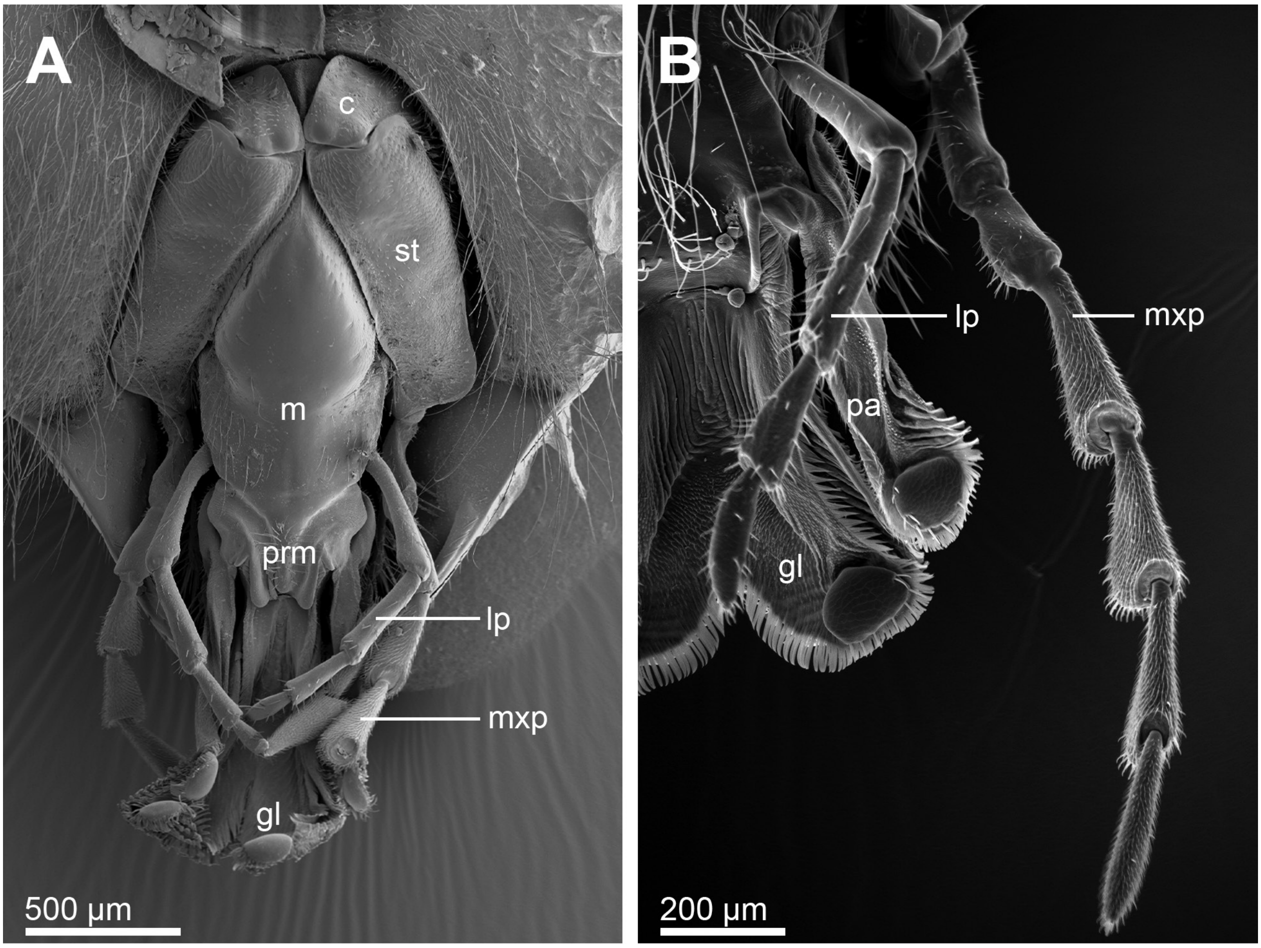

Figure 4. Labio-maxillary complex (SEM), head in posterior view. **A**. Maxilla and labium in resting position, ligula (**gl** – glossa and paraglossa) folded, female worker; **c** – cardo, **lp** – labial palpus, **m** – mentum, **mxp** – maxillary palpus, **prm** – prementum, **st** – stipes. **B.** Extended ligula, labial palpus (**lp)** and maxillary palpus (**mxp**), male; **gl** – glossa, **pa** – paraglossa.

The cardo is a roughly triangular sclerite that connects the rest of the labio-maxillary complex with the head. The flat stipes is medially uplifted with the median side next to the labium (Fig. 4A). A few bristle-shaped sensilla are distributed over the lateral surface of the stipes. Lacinia and galea are weakly sclerotized and bear a high number of sensory bristles in both sexes (Fig. 5A). The lacinia is a short lobe positioned medially and covered by the larger flat galea from the lateral and ventral sides. The lacinia shows long bristle-shaped sensilla on the ridge that borders the galea. The galea is subdivided and bears a high number of long bristle-shaped sensilla on the edge and shorter ones over the entire outer surface; sensilla campaniformia occur medially (Fig. 5C).

All six segments of the maxillary palpus vary with respect to length and distribution of sensory bristles (Fig. 4B). The first two segments are cylindrical in shape and possess a few bristle-shaped sensilla. Segments three to six are club-shaped and have smaller diameters proximally than distally. In comparison to segments one and two, the number of bristle-shaped sensilla increases distinctly in segments three to six including an increasing number of sensilla basiconica (Fig. 5B). The maxillary palpi bear a much higher number of sensilla than the labial palpi, although the types of sensilla are the same (Fig. 4B).

The basal sclerites of the labium are embraced laterally by the well sclerotized two stipites and cardines (Fig. 4A). The mentum is heavily sclerotized and has the shape of a trough, whereas the prementum and the submentum are less sclerotized. The prementum is beset with a small number of bristle-shaped sensilla on the median surface (Fig. 4A). At its distal end the prementum bears the four-lobed ligula composed of the central bilobed glossa as well as the two slimmer and shorter paraglossae laterally on each sides (Figs 1D, 6A). The whole complex of the glossae and paraglossae is folded up behind the mandibles in resting position or extended in the feeding position in males and females (Figs 1B, D; 4). While the ventral cuticle is more or less smooth, the dorsal surface of the glossae and paraglossae is covered with numerous spatula-shaped microtrichia (Fig. 6A–C). Each microtrichium is relatively thin at the base but broadens towards its tip, which is curved backwards and appears hook-shaped (Fig. 6B, C). These spatula-shaped microtrichia are arranged in 25–30 rows and form a large cuticular surface. The microtrichia on the paraglossae are similar but their basis is almost as broad as the tip.

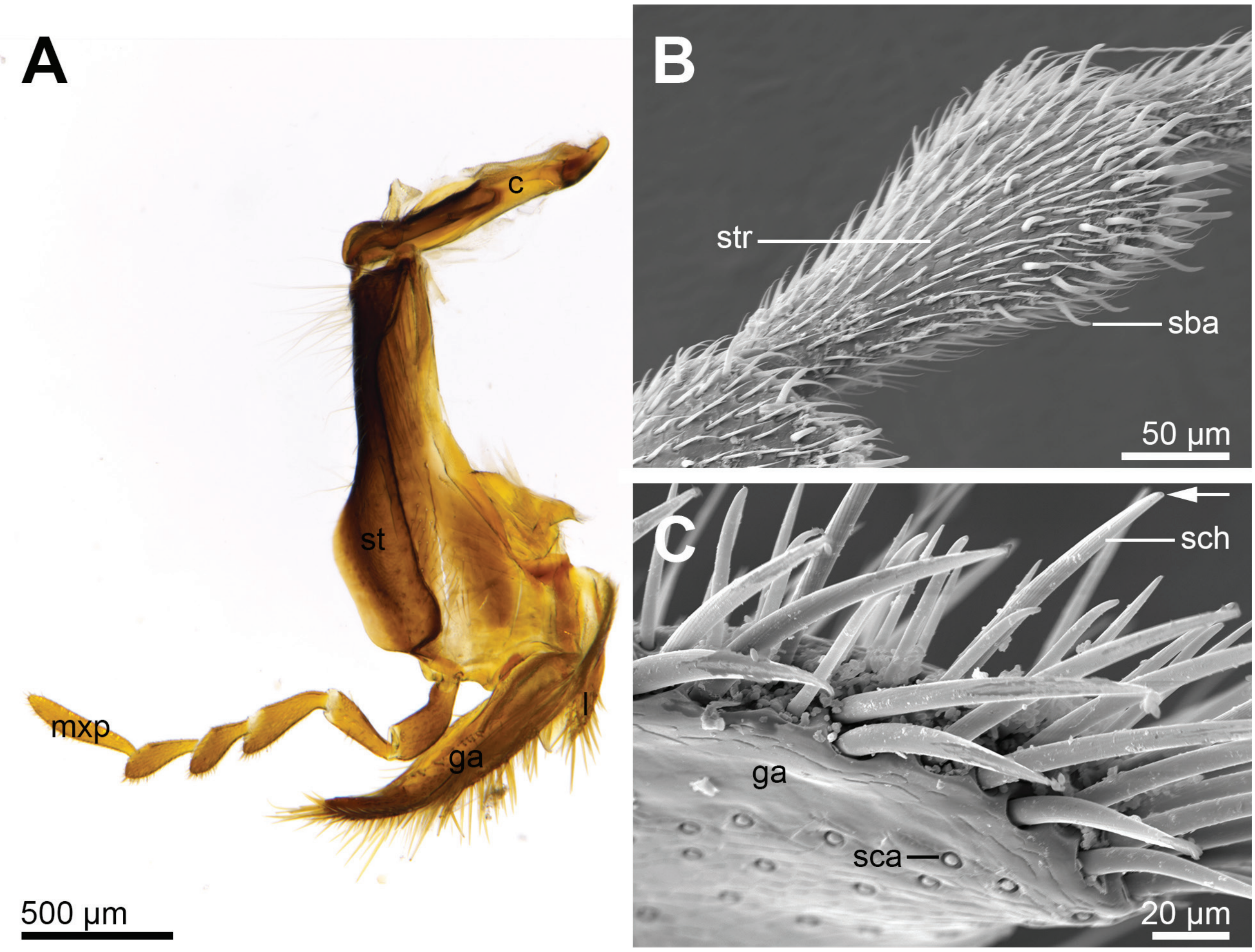

Figure 5. A. Maxilla (LM); **c** – cardo, **ga** – galea, **l** – lacinia, **mxp** – maxillary palpus, **st** – stipes. **B.** Fifth segment of maxillary palpus equipped with various sensilla (SEM); **sba** – sensillum basiconicum, **str** – sensillum trichodeum. **C.** Sensilla at the distal edge of galea (**ga**) (SEM); arrow indicates terminal pore; **sca** – sensillum campaniformium, **sch** – sensillum chaeticum.

Ventrally the glossae and paraglossae each bear an apical brownish cuticular thickening, termed the acroglossal button (Duncan 1939), which has a smooth surface in both sexes (Figs 4B, 5A). On the distal and lateral sides of the acroglossal buttons, a single row of sensilla basiconica is situated (Fig. 6C). In addition, a row of long, flat cuticle structures are present. These microtrichia extend from the edges of the glossae and paraglossae (Fig. 6A–C). The distal rim of the glossae and the tips of the paraglossae bear one row of sensilla basiconica (Fig. 6B). These sensilla basiconica which are positioned close to the acroglossal button have a small socket and a terminal pore whereas the sensilla basiconica found on the acroglossal button lack a socket and a terminal pore (Fig. 6C).

The two labial palpi insert at the prementum where it borders the mentum (Fig. 4). Each palpus consists of four segments bearing some bristle-shaped sensilla and few sensilla basiconica (Fig. 4B). Both the second and the third segment additionally have a large thorn-shaped bristle in females (Fig. 6D), which is less conspicuous in males. Female wasps have one sensillum basiconicum both on the second and third segment of the labial palpus whereas male wasps have 6 to 8 sensilla basiconica at the end of the third segment.

Discussion

Mouthpart dimorphism in female and male wasps

Mouthparts of social wasps are complex in form and function and show particular adaptations to both biting and fluid feeding. Our results confirm those of Spradbery (1973) who reported that the mouthpart morphology is similar in female workers and queens. The comparison of female workers and male *Vespula* individuals showed that the mandibles were significantly smaller in male wasps. In female wasps the mandibles are stout and heavily sclerotized since they primarily serve as cutting tools. They are applied to cut plant fibers from wood surfaces and also function as weapons for snatching prey (Duncan 1939). The mandibles are also used for scraping earth loose and picking up stones and debris in with the context of nest building (Spradbery 1973, Matsuura and Yamane 1990, Mauss 2007). Additionally, the mandibles are used by emerging wasps to cut through the cocoon of the pupae (Schremmer 1962). For all those tasks the mandibles bear three frontal teeth and a cutting edge. In repose, one mandible is folded over the other, which indicates a scissor-like function in action in both sexes.

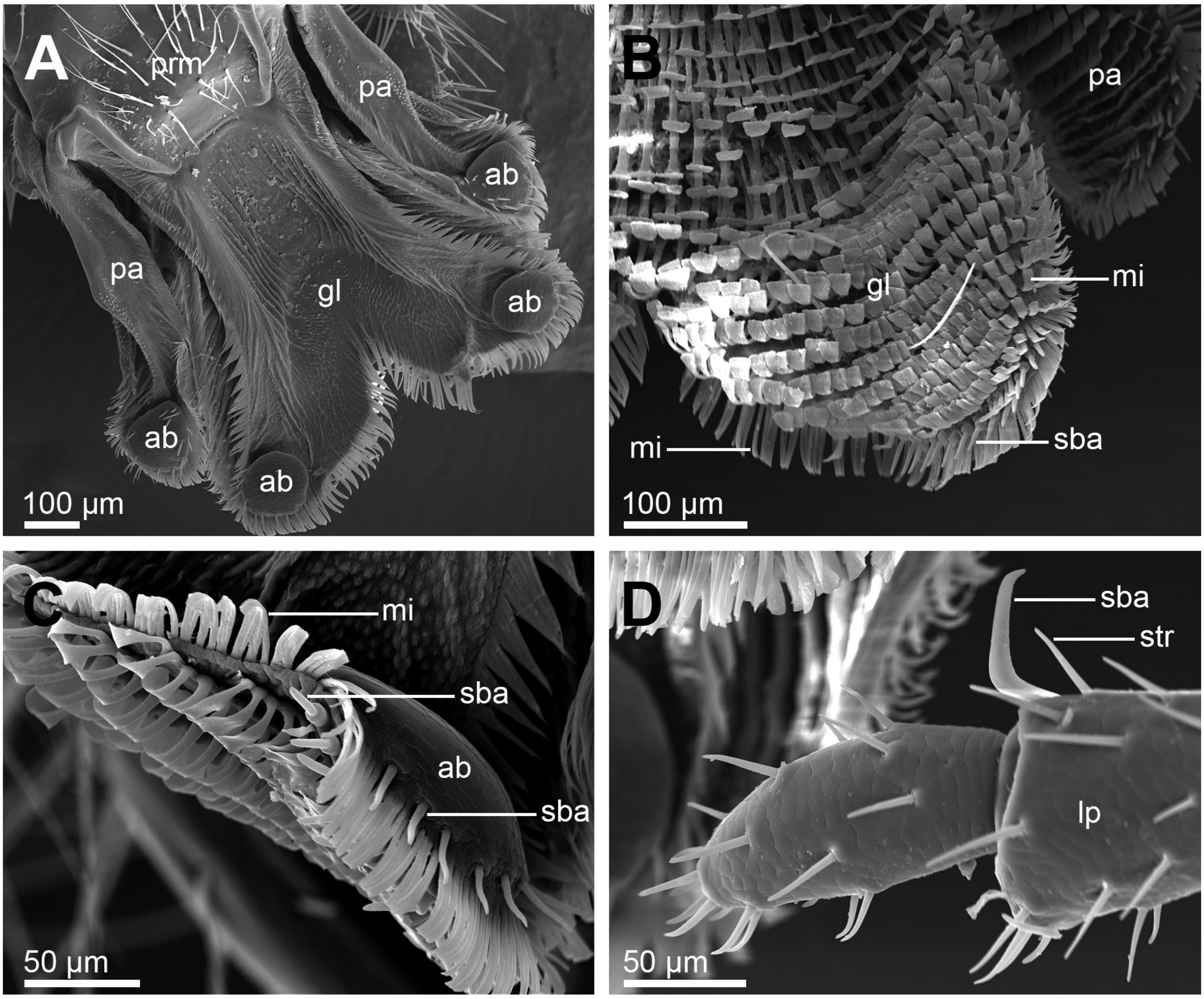

Figure 6. Labium (SEM). **A.** Extended ligula (**gl** – glossa, **pa** – paraglossa) in posterior view, acrosomal buttons (**ab**) at the apex; **prm** – prementum. **B.** Apex of glossa (**gl**), spatula shaped microtrichia (**mi**) of the dorsal side; **pa** – paraglossa, **sba** – sensillum basiconicum. **C.** Distal edge of the paraglossa with rows of microtrichia (**mi**) and sensilla basiconica (**sba**); **ab** – acrosomal button. **D.** Third segment of labial palpus (**lp**), female with thorn-shaped sensillum basiconicum (**sba**) and sensilla trichodea (**str**).

However, our results showed that the smaller size of the mandibles in male wasps is associated with inconspicuous median teeth and mola as well as reduced musculature in *Vespula*. Micro CT investigations showed that especially the adductor muscles are conspicuously smaller in males. From this dimorphism of head anatomy, it can be expected that the biting force is smaller in males than in females. The different morphology is explained by the fact that male wasps do not use their mandibles for larval provisioning (Spradbery 1973, Matsuura and Yamane 1990). In male wasps, the mandibles are only used to bite open the pupae during emerging (Schremmer 1962).

The labio-maxillary complex is capable of operating completely independent from the mandibles (Jervis 1998). In adult wasps of both sexes the labio-maxillary complex is extensible and almost solely concerned with the uptake of liquid food. The lobe-shaped distal parts of the labium act like a tongue where the surface of the glossa and paraglossa is used for fluid uptake. Both components are characterized by the dense endowment with microtrichia on the dorsal/frontal side. The high number of spatula-shaped microtrichia forms a large surface on the ligula. The particular shape of the microtrichia creates a space underneath and between the cuticular structures. Under the assumption that the cuticle is wettable, it can be supposed that this arrangement and the specific micromorphology of the structures are crucial to upload fluids and the ligula serves as an adhesive device (López-Cubillos and Sarmiento 2013). Schremmer (1962) suggested that these structures are no sensory bristles but chitin emergences, enabling the wasps to lap up liquids. Alternatively, the microtrichia of the glossa and paraglossae were interpreted to serve as a rasping device (Duncan 1939). This function should be considered in addition, since wasps feed from soft ripe fruits by rasping over the surface to gain more fruit juice.

Fluid feeding in wasps

Adult Vespinae of both sexes feed exclusively on liquid food such as the juice of ripe fruits, honeydew or nectar since larger particles of food are prevented from travelling down the narrow esophagus (Spradbery 1973). Since wasps are not equipped with a closed tubular proboscis, feeding of fluid has to be accomplished in a different way than suction. A short food canal for the uptake of liquid food is temporally formed by parts of the labio-maxillary complex and the labrum/epipharynx. The labium constitutes the bottom, the stipites including the laciniae and galeae form the sides and the labrum/epipharynx composes the roof of this short temporary food tube (Duncan 1939) which was termed "Wespenrüssel" (Kirmayer 1909) or "wasp proboscis". The glossae and paraglossae produce lapping motions, similar to the "licking cycle" in honey bees (Snodgrass 1956, Wu et al. 2015). In the extended position of the ligula, liquid adheres to the spatula-shaped microtrichia that is thus transported into the food canal when the glossae and paraglossae are retracted towards the mouth (Seifert 1995).

Imagines of *V. germanica* and *V. vulgaris* may feed only on flowers with easily accessible nectar (Schremmer 1962, Mauss 2007). Likewise, many adult Hymenoptera feed on flowers with freely accessible nectar using rather short feeding organs (e.g., Osten 1982, Jervis 1998, Jervis and Vilhelmsen 2000, Mauss 2007). The fluids adhering to the mouthpart structures are brought into the food canal by retraction of the distal parts of the labium. The liquids are conveyed further by suction force from the muscular cibarial or pharyngeal pumps (Krenn et al. 2005). Likewise in ants, insects devoid of elongated mouthparts, employ the labium for the uptake of liquid food by capillarity (Paul et al. 2003). Like in social wasps, the distal components of the labium are prime organs for the uptake of liquid food by capillarity. By contrast, many representatives of pollen wasps (Masarinae) are able to feed from concealed nectaries in spurred and resupinate flowers using their elongated labio-maxillary complex (Gess and Gess 1989, Gess 1996, Mauss and Müller 2000, Mauss et al. 2010). These pollen wasps possess an elongate suctorial proboscis which is composed primarily of the particularly long glossa. The cuticle structures of the glossa form a closed food tube and a specialized apex for nectar uptake (Krenn et al. 2002).

Sensilla equipment of mouthparts

Compared to the female workers, male wasps have a higher number of long bristle-shaped sensilla on the mandibles, whereas the sensilla equipment of the labio-maxillary complex is nearly identical except for the higher number of sensilla basiconica and the lack of the thorn-shaped sensillum on the labial palpi of males. The reason for the higher numbers of mandibular sensilla of male wasps is unknown. Although it can be expected that the sensilla on the palpi mainly provide information about food, the differences in sensilla equipment cannot be interpreted since the external morphology of sensilla gives only rough estimates about their sensory functions (Zacharuk 1985).

Various types of sensilla are located on the labio-maxillary complex that could give information about food uptake and transport as well as position of the mouthpart components. Both the lacinia and the galea serve as lateral parts of the passageway through which food may be ingested (Kirmayer 1909). SEM analyses of the sensilla located on the galea revealed sensilla with a terminal pore in addition to thin sensory bristles and sensilla campaniformia. The observed porus at the sensillum tip of galeal sensilla suggests a chemosensitive function rather than a bare tactile one (Zacharuk 1985). Likewise, the sensilla of galea and lacinia could provide information about the status of extension of the labio-maxillary complex. In addition, the lobes of the lacinia and galea serve a secondary function as cleaning organs for the antennae, maxillary and labial palpi and the forelegs (Spradbery 1973), where sensilla are expected to play a role in behavioral control.

In spite of the similar putative function of the palpi in feeding, the coverage with sensilla is much higher on the maxillary palpi than on the labial palps. In addition to many sensory bristles having a putative tactile function, the labial palpi just show one to three sensilla basiconica whereas the number of sensilla basiconica is much higher on the maxillary palpi. This distribution of sensilla would suggest that the maxillary palpi are rather used for testing the consistence of food substances. Detailed analysis of the movements of both maxillary palpi and labial palpi during feeding could provide insight into the possible different tasks.

It can be expected that the sensilla at the distal edges of the ligula and the acroglossal buttons detect sugar. The acroglossal buttons are developed in this typical form only in Vespidae (Duncan 1939). The thickenings of the cuticle located on the ventral/posterior side of both the glossae and paraglossae were assumed to have a protective function (Kirmayer 1909). However, the fact that the acroglossal buttons are beset with sensilla basiconica suggests that they serve to taste food. Sensilla basiconica could either be mechanosensitive, both mechano- and chemosensitive, thermosensitive, hygrosensitive, olfactory or combinations of these functions (Zacharuk 1985). Either one of these possible functions would make sense at this specific location. Instead, we suggest that the wasps taste composition and quality of liquids with the sensilla basiconica on the acroglossal buttons before they lap up the fluids. These sensilla basiconica, which lay close to the acroglossal buttons, show a socket and a terminal pore. This porus suggests that the sensillum could react chemosensitively and could be helpful in tasting substances (Altner 1977). The arrangement of sensilla is in line with other nectar feeding insects, i.e. butterflies, flies or bees that exhibit sugar detecting sensilla at the apex of the proboscis where nectar adheres to the mouthpart surface (Galić 1971, Krenn 1998, Krenn et al. 2005, Bauder et al. 2013, Krenn and Bauder 2017, Düster et al. 2018).

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