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„Form and function of the mouthparts of adult wasps *Paravespula vulgaris* and *Paravespula germanica*“

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1 Acknowledgement

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2 Introduction

Insect mouthparts are composed of a set of homologous organs that are derived from appendages of head segments. In the plesiomorphic morphology of Pterygota, the mouthparts are composed of an unpaired plate in front of the mouth, paired mandibles and maxillae as well as an unpaired labium extending from the last head segment (Krenn, 2007). The mouthparts of adult Hymenoptera are characterized by the labio-maxillary complex, which is a functional unit formed by the labium and the maxillae (Krenn et al., 2005). The terminology to describe the labium introduced by Seifert (1995) will be used in this paper. Additionally mouthpart features are seen as autapomorphies such as the four-segmented labial palpus and the ventral margins of the clypeus being inflected and overlapping the proximal part of the labrum (Krenn, 2007). In general the mouthparts of Hymenoptera are complex in form and function. They are functionally versatile allowing their use in various kinds of tasks in many taxa. Often the mouthparts are modified according to specific food preferences (Aspöck & Krenn, 2012).

The family of Vespidae is ascribed to the suborder Apocrita (order Hymenoptera), that comprises well known insects such as wasps, bees and ants. Wasps belong to the infraorder Aculeata. Aculeata are characterized by the formation of a sting in females (Bellmann, 1995). The subfamily of Vespinae (Vespidae) is divided into the five genera *Vespa, Provespa, Dolichovespula, Vespula* and *Paravespula* (Archer, 1989). Since the study on phylogeny and taxonomy of the subfamily Vespinae by Persson (2015), which was based on molecular markers, strongly supports the allocation of both the german wasp and the common wasp to the genus *Paravespula*, this classification will be favored in this paper. Due to these new insights the nomenclature *Paravespula vulgaris* (Fabricius, 1793) and *Paravespula germanica* (Linnaeus, 1758) seem to be more accurate than the allocation to the genus *Vespula.* Additionally the authors of a recently published paper about the structures of the antenna in *Paravespula vulgaris* also used the genus *Paravespula* (Agmon et al., 2006).

Both *Paravespula vulgaris* (Fabricius, 1793) and *Paravespula germanica* (Linnaeus, 1758) (Gusenleitner, 1981) are eusocial vespids. Both species tend to use subterranean nesting sites, mostly mammal made holes (Schenck, 1854). When enlarging the underground cavities wasps pick up small pieces of soil and small stones with their mandibles. In close proximity to humans both *Paravespula germanica* and *Paravespula vulgaris* also use nesting sites above ground, e.g. hollow trees, attics or cavity walls (Schremmer, 1962). The nests consist of paperlike material, which wasps produce out of weathered wood mixed with their saliva. Both species use their mandibles to scrape off wood fibers to construct their nests. After a new nest has been initiated the queens bring up the first generation of larvae. The development from the egg to the adult wasp takes approximately five weeks (Friese, 1926). The queens are henceforth concerned with reproduction and the female workers are in charge of growing the nest and feeding the new larvae. In August the new queens and males are born (Ripberger et al., 1992). After mating the new queens overwinter in a sheltered location whereas the old queens, the workers and the males die around October, depending on the weather (Friese, 1926).

Vespinae collect two classes of food. Adults feed on liquid carbohydrates obtained from honeydew secreted by aphids, ripe fruits, flower nectar and sometimes tree sap (Matsuura & Yamane, 1990). Wasps belonging to the genus *Paravespula* have relatively broad heads and short licking apparatuses and are therefore not appropriately equipped to feed on flower nectar, which makes their dependency on nectar obtained from flowers rather low. If nectar is obtained, wasps tend to visit flowers with freely accessible nectaries such as *Heracleum sphondyleum, Archangelica silvestris* or *Peucedanum cervaria* (Schremmer, 1962). The larvae are fed with protein rich meat. Therefore wasps prey on other insects and sometimes spiders, 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). Matsuura & Yamane (1990) state that *Paravespula vulgaris* and *Paravespula germanica* not only prey on insects but they also use the muscles of dead vertebrates like frogs or snakes. They also tend to carry away pieces of either grilled fish or meat.

Since wasps are widely distributed in the northern hemisphere they have been research objects for behavioral research during the last decades. Interestingly wasps display far more diversity in their social biology than any other group ascribed to the annual eusocial insects (Greene, 1991). Even so, only very few researchers have concerned themselves with the mouthparts in wasps and only two of them, namely Kirmayer (1909) and Spradbery (1973) have specifically looked into the mouthpart structures of *Paravespula vulgaris*. Both Seifert (1995) and Schremmer (1962) have concerned themselves with the mouthparts of *Vespa crabro* (hornet). Duncan (1939) released an extensive work containing a detailed analysis of the mouthparts of *Vespula pensylvanica.*

These studies used light microscopes to investigate the morphology of the mouthparts but scanning electron microscopes haven't been used so far.

Although wasps can often be seen to feed on nectar of various flowers, their mouthparts are not elongated like in many other flower-visiting Hymenopterans like honey bees or bumble bees. However similar to these eusocial Hymenoptera, the principal composition is similar since the mouthparts show well developed biting mandibles and a labio-maxillary complex, which primarily is used to take up nectar and other kinds of sugary fluids. In other flower-visiting Hymenoptera modifications concerning the mouthparts are obvious, such as the formation of a proboscis in Masarinae (pollen wasps). Due to the presence of a very long tongue, pollen wasps have shifted to pure suction feeding. (Borrell & Krenn, 2006) Since *Paravespula germanica* and *Paravespula vulgaris* have short mouthparts, the uptake of liquids is accomplished in large part by adhesion, like in other short tongued flower-visiting insects (Krenn et al., 2002).

Female wasps use their mouthparts for many different tasks. They are used for cutting and scraping off vegetable fibers during nest building, for picking up soil and stones when colonizing underground cavities, for the uptake of liquid food, for the manipulation of solid food and for feeding the larvae. Hence the mouthparts could be compared to a swiss army knife; they are looked upon as microtools for different kinds of tasks. Male wasps were never studied and detailed information about mouthpart use is missing.

The primary goal of this diploma thesis is a description of the morphology of the mouthparts in the genus *Paravespula* using SEM-techniques and to conclude on the functional morphology of the various parts. Special emphasis is laid on the differences between female workers and males. Since male wasps feed only on sugary fluids and neither hunt insects nor participate in nest building procedures or brood care it seems possible, that their mouthparts differ from those of the female workers and queens.

3 Material and Methods

3.1 Light Microscopy

The 15 individuals of *Paravespula germanica* (Fabricius, 1793) and *Paravespula vulgaris* (Linnaeus, 1758) used for light microscopy were taken from the collection of the Department of Integrative Zoology (University of Vienna, Austria). The wasps were being stored in 70% ethanol.

The dissections were performed with the use of a stereomicroscope Nikon SMZ 10. The heads were removed and the mouthparts extracted using a pair of scissors, two forceps and dissecting needles. The labio-maxillary complex was then further trenched into the two maxillae and the labium.

For the removal of the musculature two different methods were applied. To start with the removed and disaggregated parts were put in 70% ethanol. Afterwards the labium and the maxillae were rinsed with deionized water for 10 minutes. Then the mouthparts were transferred to glass tubes that contained lactic acid (30%). After 120 hours on the vibrating unit at room temperature the musculature had dissolved. The mouthparts were rinsed again with deionized water for ten minutes before being transferred into 30% ethanol. Ultimately the labium and the two maxillae were put onto a hollow object slide with a drop of polyvinyl-lactophenol and a cover glass.

As the above described procedure took relatively long, the removal of the musculature was afterwards performed manually using two forceps. This technique has proven to be as effective as the method requiring lactic acid and it was quicker. The mouthparts were then placed on a hollow object slide with a drop of glycerine and a cover glass. The cover glass was then fixed with nail polish.

Photos were taken using a light microscope (Nikon Eclipse E 800) with an attached camera (Nikon DS-Fi2 U3). Additionally pictures of the whole head were taken using a stereomicroscope (Nikon SMZ 25). Several photos were combined using Helicon Focus software to produce a focused image.

3.2 Scanning Electron Microscopy

The specimens for the scanning electron microscope were prepared and observed at the Core Facility of Cell Imaging and Ultrastructure Research at the University of Vienna.

The wasps were stored in 70% ethanol. The mouthparts were prepared in three different ways for observation in the scanning electron microscope. On the one hand entire heads were used. Secondly the labio-maxillary complex, which had been taken out of the head, was used after the removal of the musculature. Thirdly the labio-maxillary complex was trenched into two maxillae and the labium and the musculature was removed under a stereomicroscope Nikon SMZ 10 using two forceps.

The mouthparts and the entire heads were dehydrated through an ascending ethanol series (80%, 90%, 100%) for half an hour at each concentration. Then the mouthparts and heads were submerged into 100% acetone for 90 minutes. During these 90 minutes the ethanol was changed every 30 minutes. Finally the heads and mouthparts were put in hexamethyldisilazane for 60 minutes. The hexamethyldisilazane was changed after 30 minutes. The samples were taken out and left to air-dry under the fume hood over night.

The dry parts were mounted on aluminium stubs using carbon foils and conductive silver and were left to dry for one hour before being covered with a thin layer of gold within the Sputter Coater (JEOL JFC-2300HR, 120 seconds).

SEM-Images were taken using a Philips XL 30 ESEM and JEOL IT 300 with an acceleration voltage of 20 kV. Contrast enhancements and brightness adjustments were performed in several pictures using GIMP 2.8.

3.3 Morphometric measurements

Eighteen individuals of wasps were measured in total including nine female workers and nine males. Both the nine female workers and the nine male wasps belonged to

Paravespula germanica. The female workers were taken from the collection of the Department of Integrative Zoology. The male wasps were kindly provided by Dr. Volker Mauss (Germany).

The heads of the wasps were cut off using a pair of scissors and a stereomicroscope Nikon SMZ 10. The heads were placed in a small watch glass filled with sand, arranged under the stereomicroscope and pictures were taken using an attached Samsung Digimax V50 camera.

Length measurements of the mandibles and other parts of the head were conducted in both sexes (n=18) and the results were compared. Measurements of three different parts of the head were taken in total. The length of one mandible was measured from the joint to the tip of the third tooth. Mostly the right mandible of each wasp was measured and only in those cases, where the left mandible was folded over the right one, the left mandible had to be measured since the right mandible was not fully observable. Secondly the length of the head from behind the antenna to the distal ridge of the clypeus was measured. The third measurement taken was the length from the basis of the scapus of one antenna to the distal ridge of the Clypeus (Fig. 3).

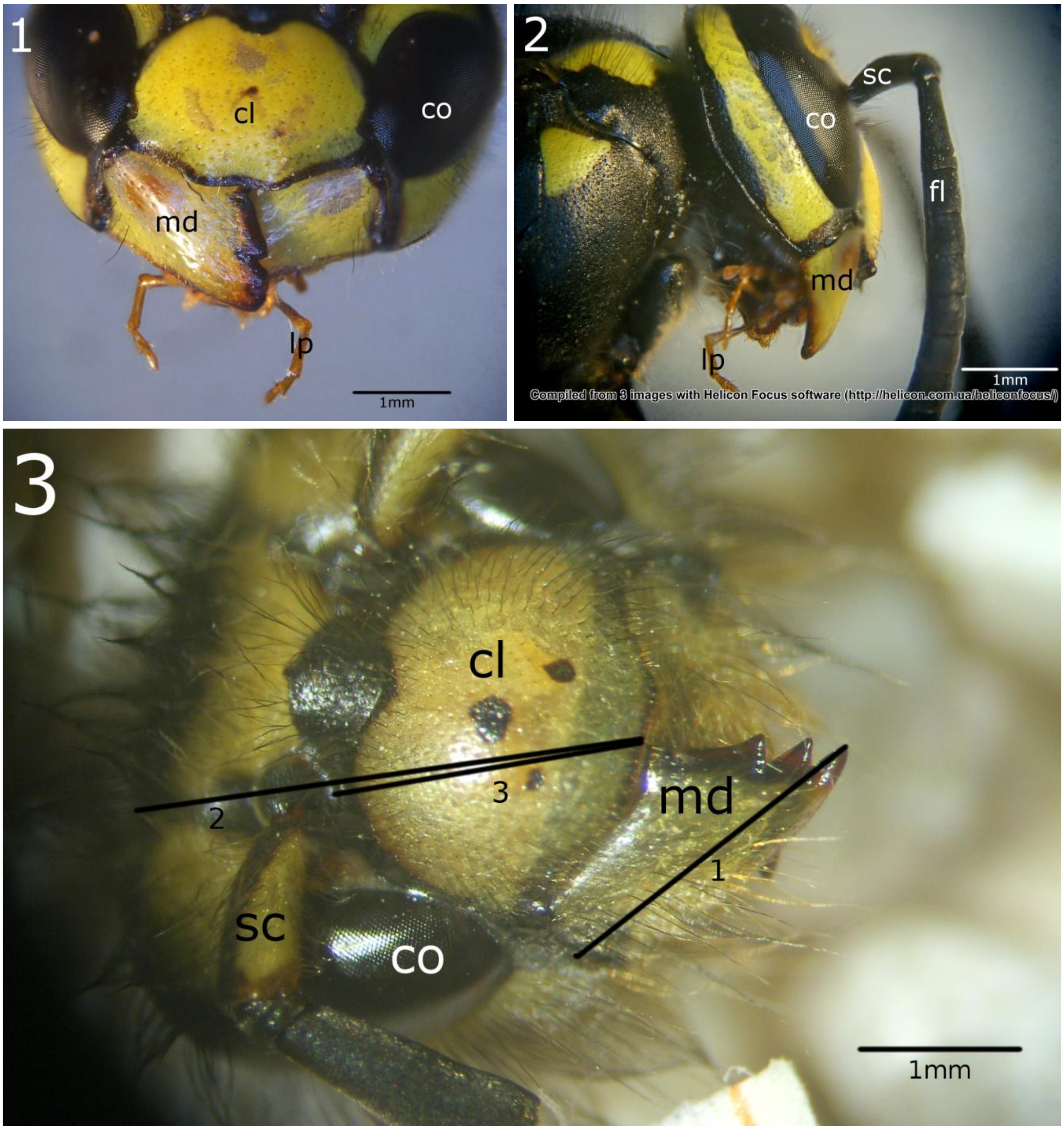
ImageJ was used to measure the length of the mandibles and other parts of the head. GIMP 2.8 was used for adjustments concerning brightness and contrast. The analysis of the gathered data was performed applying the Mann-Whitney U test.

4 Results

The head of *Paravespula vulgaris* and *Paravespula germanica* is of the hypognathous type and the mouthparts are directed downwards (Figs. 1, 2). The mouthparts consist of the concealed labrum, the big mandibles and the labio-maxillary complex. The labio-maxillary complex can further be subdivided into the paired maxillae, each bearing one maxillary palpus and the labium, bearing paired labial palpi. No differences in morphology of the mouthparts could be found between the two species *Paravespula vulgaris* and *Paravespula germanica*. Various types of sensilla located on the mouthparts were observed in females and males of both studied species. Sexual dimorphism was observed since the mouthparts in males bear a higher number and longer sensilla than the mouthparts in female workers. Additionally the mandibles in males are shorter than in female workers although the heads of the male wasps are on average longer than those of the female workers. The morphology of the mouthparts of the queens is similar to the morphology of the mouthparts of the female workers, except that the mouthparts of the queens are bigger. Higher numbers and an increased length of the sensilla could only be found in males.

4.1 Labrum

In repose one mandible is folded over the other in front of the labrum (Figs. 1, 4). The labrum is largely concealed behind the clypeus and can only be observed when the mandibles are opened (Fig. 5). If the mandibles are opened, the bottom part of the labrum is visible. This bottom part is heavily sclerotized and well endowed with sensilla trichodea (Fig. 5). The upper part of the labrum is entirely concealed behind the clypeus. Behind the labrum lies the membranous epipharynx, which plays an important part in forming the cibarium, a cavity anterior to the mouth. This passageway for food is only formed temporarily and the epipharynx constitutes the roof.

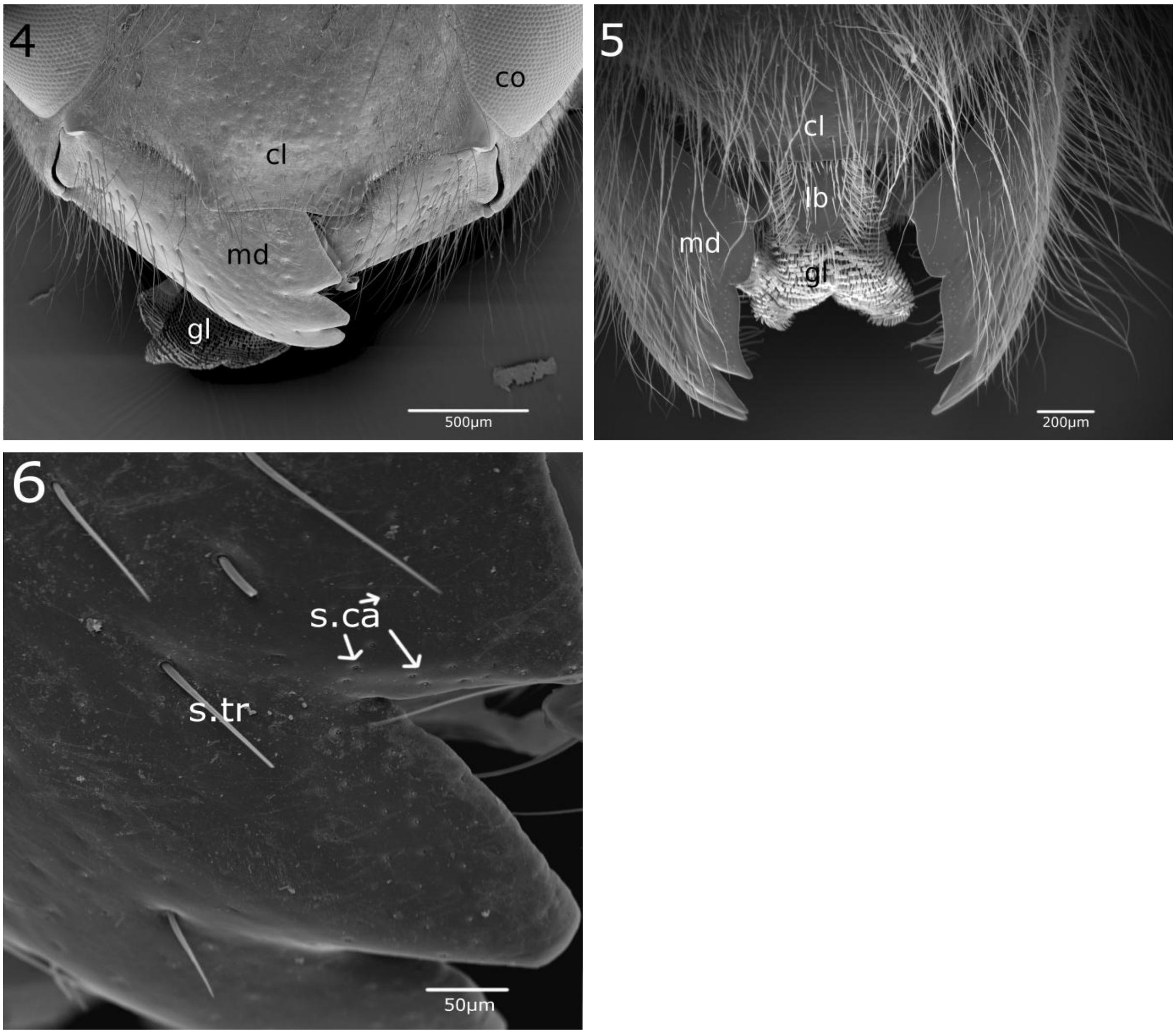


Figures 1-3: Head of *Paravespula germanica*; pictures taken using a stereomicroscope; **Fig. 1** Frontal view of the head of a female worker; *md* mandible, *cl* clypeus, *co* compound eye, *lp* labial palpus; **Fig. 2** Lateral view of the head of a female worker; *sc* scapus, *fl* flagellum, *co* compound eye, *md* mandible, *lp* labial palpus; **Fig. 3** Head of male wasp; numbers (*1-3*) indicating the three measurements taken, *cl* clypeus, *co* compound eye, *sc* scapus, *md* mandible

4.2 Mandibles

The mandibles appear roughly triangular in shape when viewed laterally or head-on (Figs. 1, 2). They are slightly convex and heavily sclerotized. When the mandibles are being used they meet in a vertical line whereas in repose one mandible is folded over the other (Fig. 4). Considering the wasps that were observed in the course of taking measurements 11 out of 18 wasps folded the right mandible over the left one whereas 7 wasps folded the left mandible over their right one. In males 5 individuals folded their right mandible over their left mandible and 4 individuals folded their left mandible over their right whereas in females 6 wasps folded their right mandible over their left one and 3 female wasps folded their left mandible over their right.

The cutting edge of the incisive part bears three frontal teeth and above the teeth an emargination is apparent (Fig. 5). Behind the three visible teeth two secondary teeth are hidden. The molar region is distinguishable but it is not very sophisticated. The molar region is rather small in comparison to the incisive part of the mandibles. The mandibles are, like the labrum, well covered with sensilla trichodea. Towards the cutting edge on the frontal side, where the teeth are located, sensilla campaniformia can be found (Fig. 6).



Figures 4-6: SEM-images of the head of *Paravespula* sp.; **Fig. 4** Frontal view of the head of female worker, mandibles in closed position; *co* compound eye, *cl* clypeus, *md* mandible, *gl* glossae; **Fig. 5** Frontal view of male, mandibles in open position; *cl* clypeus, *lb* labrum, *md* mandible, *gl* glossae; **Fig. 6** Detailed view of the incisive region of the mandible; *s.ca* sensilla campaniformia (arrow), *s.tr* sensilla trichodea

The sexual dimorphism relating to coverage with sensilla is observable on the mandibles. The mandibles of the males (Fig. 5) are almost entirely covered with long sensilla trichodea whereas the mandibles of the female workers (Fig. 4) show a reduced number of sensilla trichodea and the sensilla are shorter in comparison to those of the males.

The length of the mandibles, the length of the whole head from behind one antenna to the distal edge of the clypeus and the distance between the basis of the scapus of one antenna to the edge of the clypeus were measured and compared in female workers and males (n=18) (Fig. 3). The comparison of the length of the mandibles between female workers and male wasps showed that workers have longer mandibles than males although the distance between the scapus and the distal ridge of the clypeus is greater in males than in females (Tab. 1). Additionally the whole head is bigger in males than in females (Tab. 1). The applied Mann-Whitney U test indicated significant differences in mandible length between workers and male wasps (n=9). Considering the length of the heads in females and males the heads of male wasps are on average bigger but no significant differences between workers and males could be found (Tab. 1).

Table 1: Measurements of parts of the head in female and male wasps; *n* sample size; *SD* Standard deviation

	Mean +/- SD (mm)		
	Females (n=9)	*Males (n=9)*	*Sign. difference p<0,05*
Mandible	2,07 +/- 0,13	1,88 +/- 0,11	Sign. diff. (z= -2,87)
Length of the head	3,08 +/- 0,21	3,23 +/- 0,38	No sign. diff. (z= -0,97)
Antenna base to clypeus	1,79 +/- 0,13	1,85 +/- 0,16	No sign. diff. (z= -0,88)

4.3 Labio-maxillary complex

The posterior view of the head shows the labio-maxillary complex. The basal sclerite of the labium with the labial palps is embraced by the two stipites bearing the maxillary palps (Fig. 7). After separation from the head the labio-maxillary complex shows the two cardines, which connect the complex to the head (Fig. 8). The labio-maxillary complex is located in an oval depression on the posterior part of the head. The connection to the cranium is established by the two cardines, a pair of small sclerites and membranous cuticle. This coadunate complex is quite firmly connected by membranous cuticle to ensure that the complex extends and retracts as a unit. Additionally, two small sclerites, one on either side of the labium, connect the two maxillae and the labium (Fig. 23).

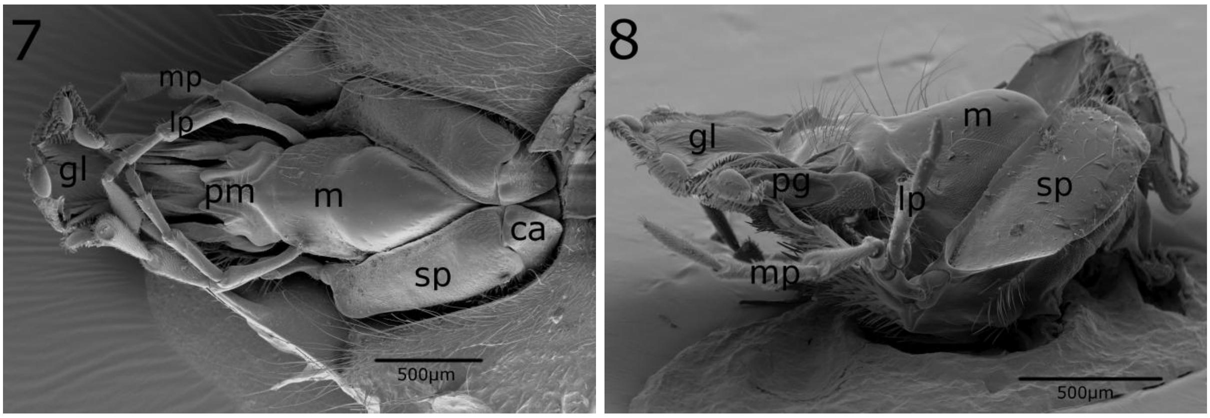


Figure 7-8: Fig. 7 Ventral view of the head; *sp* stipes, *ca* cardo, *mp* maxillary palpus, *m* mentum, *pm* prementum, *lp* labial palpus, *gl* glossae; **Fig. 8** Labio-maxillary complex after removal from the head; *sp* stipes, *mp* maxillary palpus, *m* mentum, *lp* labial palpus, *pg* paraglossae, *gl* glossae

4.3.1 Labium

The labium can be divided into the submentum, forming the lateral connection to the cardines, the roofshaped mentum and the prementum (Fig. 9). The mentum is stable and heavily sclerotized and has the shape of a trough whereas the prementum is moderately sclerotized and the submentum is even less sclerotized. The mentum is internally equipped with muscles. Median the prementum is beset with a small number of sensilla of the type trichodea (Fig. 10). In males (Fig. 11) these sensilla are represented in a higher number and they are longer than in female workers (Fig. 10). The two labial palps are attached to the prementum, one on each side. Each palpus consists of four segments bearing numerous sensilla trichodea and fewer sensilla basiconica.

At its distal end the prementum develops four lobes. The two central lobes, the glossae, are heart-like in shape and largely grown together (Fig. 10). The slimmer and shorter paraglossae lay laterally on each side of the central glossae (Fig. 12).

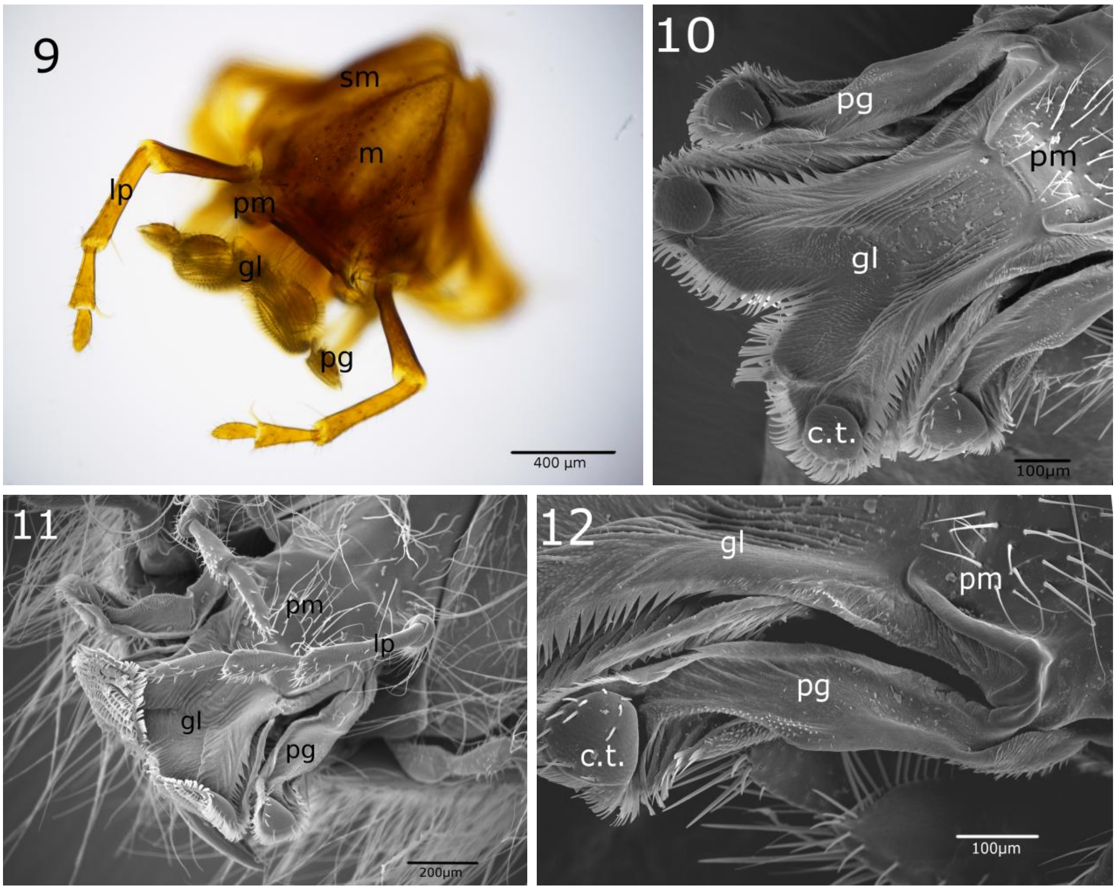
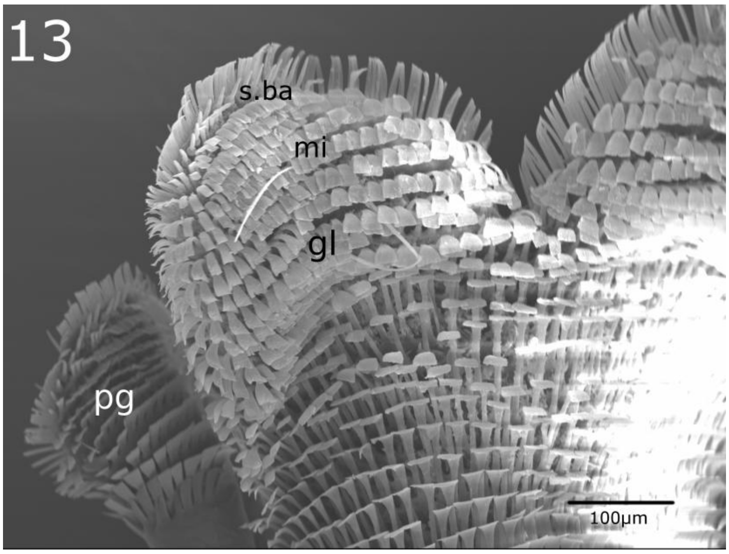


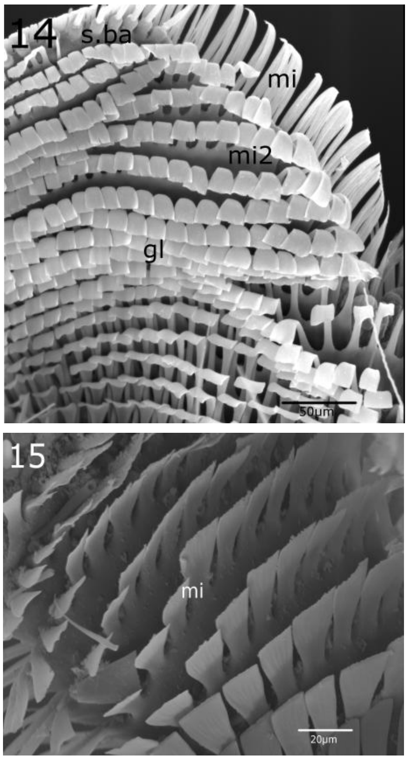
Figure 9-12: Ventral side of the labium; **Fig. 9** Picture taken with a light microscope showing different parts of the labium; *sm* submentum, *m* mentum, *pm* prementum, *lp* labial palpus, *gl* glossae, *pg* paraglossa; **Fig. 10** SEM-image showing a female wasp, detailed view of the labium; *pm* prementum, *gl* glossae, *pg* paraglossae, *c.t.* cuticular thickening; **Fig. 11** Male wasp, detailed view of the labium; *pm* prementum, *gl* glossae, *pg* paraglossae, *lp* labial palpus; **Fig. 12** Detailed view of the paraglossa; *pm* prementum, *gl* glossae, *pg* paraglossae, *c.t.* cuticular thickening

The whole complex of the glossae and paraglossae can either be folded up or elongated. In extended position, the dorsal and the ventral surfaces of the glossae and paraglossae show obvious differences in structure.

The dorsal surface of the glossae and paraglossae is covered with numerous microtrichia. The microtrichia on the glossae look slightly different than those located on the paraglossae (Fig. 13). The cuticle structures that cover the dorsal side of the glossae are relatively thin at the bottom but expand towards the tips. The structures located near the tips are curved and they appear hook-shaped. The tips are broad and the borders slightly waved. These spatula-shaped microtrichia are arranged in several rows and partially overlay each other to form a large-scale surface (Fig. 14).

Considering the wasps examined for this paper, 25 to 30 of these rows of microtrichia were counted. The microtrichia on the paraglossae however have a basis almost as broad as the tips. The borders of the tips are slightly waved (Fig. 15).





Figures 13-15: Dorsal view of the glossae and paraglossae; **Fig. 13** Comparison of the microtrichia on the glossae and paraglossa; *gl* glossae, *pg* paraglossa, *s.ba* sensilla basiconica, *mi* microtrichia that are spatula-shaped and enlarge the surface; **Fig. 14** Detailed view of the glossae; *gl* glossae, *mi 2* spatula-shaped microtrichia, *mi* hair-shaped microtrichia, *s.ba* sensilla basiconica; **Fig. 15** Detailed view of the paraglossae; *mi* microtrichia

Ventrally the surface is wavy and cuticular developments can be observed. The glossae and paraglossae each bear apical a brownish cuticular thickening (Fig. 10). These thickenings have an entire different surface than the glossae and paraglossae and are roundish in shape. From the brinks of these thickenings of the cuticle that are located on the glossae, a few sensilla basiconica emerge (Fig. 19). On the paraglossae the same type of sensilla can be found but they emerge all over the cuticular thickening (Fig. 18). Posterior to these cuticular thickenings the glossae and paraglossae terminate in a row of long, flat hair. These hairs are microtrichia, which are emergences of the cuticle (Figs. 18, 19).

Not only the distal regions of the glossae but also the tips of the paraglossae terminate in one row of sensilla basiconica (Fig. 17). These sensilla basiconica have a small socket and a terminal pore can be observed (Fig. 16). The sensilla basiconica can only be found close by the above described cuticular thickenings, where sensilla basiconica are located as well. The sensilla basiconica found on the cuticular thickenings lack a socket and no terminal pore could be observed (Fig. 16).

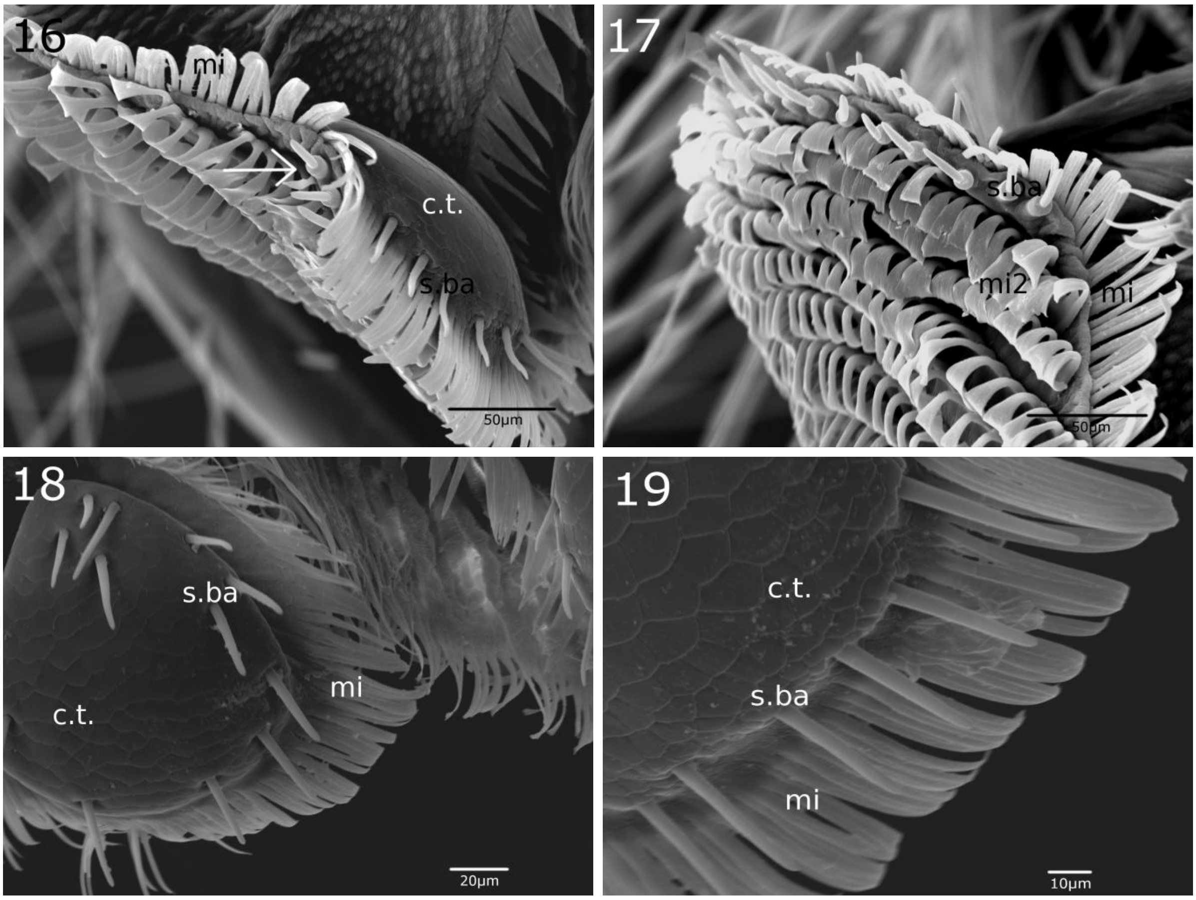
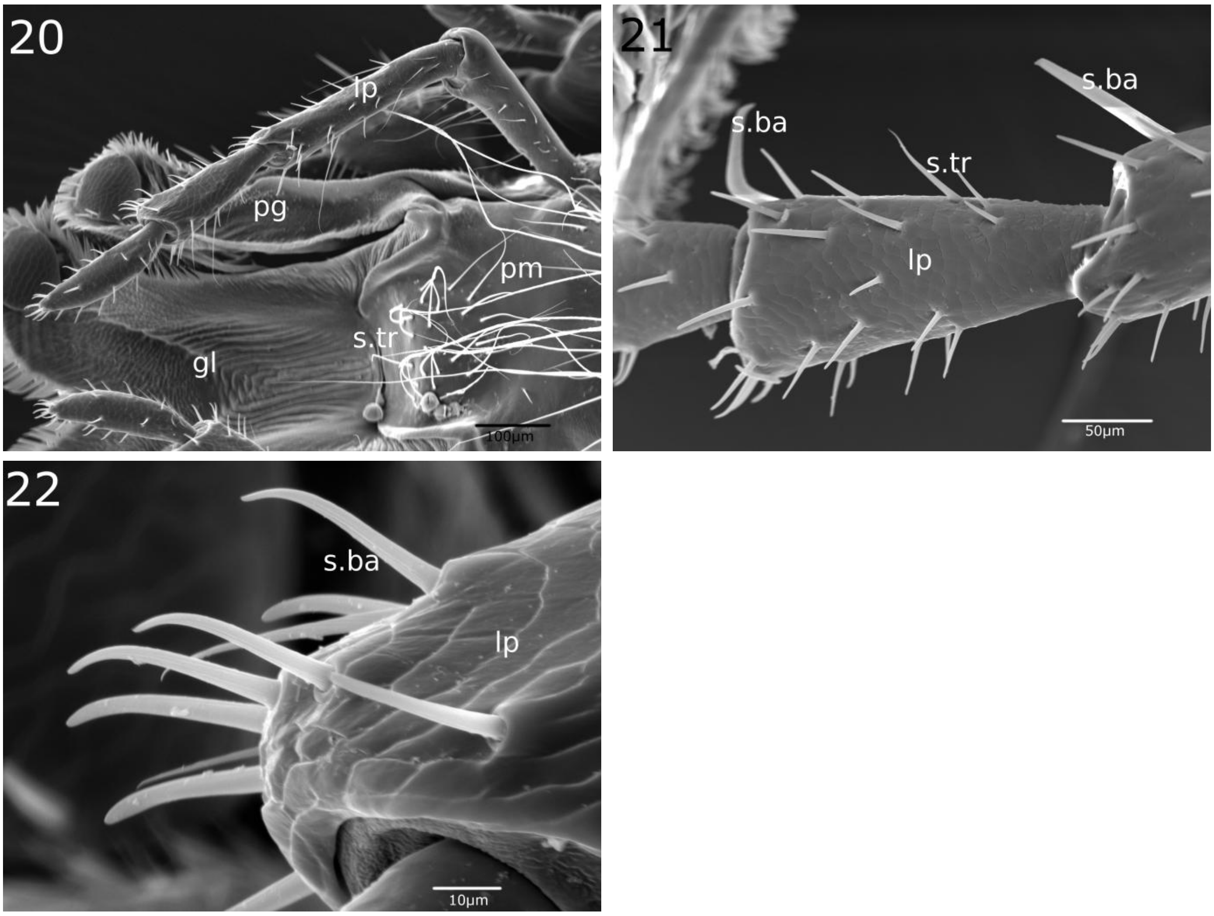


Figure 16-19: Detailed view of the tips of the glossae and paraglossae; **Fig. 16** Glossa; *c.t.* cuticular thickening, *s.ba* sensilla basiconica, *mi* hair-shaped microtrichia, additionally different shaped sensilla basiconica with a socket and a terminal pore are perceptible (arrow); **Fig. 17** Terminal region of the glossa, dorsal side; two types of microtrichia are distinguishable, *mi* hair-shaped microtrichia and *mi 2* unfoldings of the cuticle, *s.ba* sensilla basiconica; **Fig. 18** Detailed view of the ventral tip of the paraglossa; *c.t.* cuticular thickening, *s.ba* sensilla basiconica emerge all over the thickening of the cuticle, *mi* hair-shaped microtrichia on the edge of the paraglossa; **Fig. 19** Detailed view of the ventral tip of the glossa; *c.t.* cuticular thickening, *s.ba* sensilla basiconica emerge only on the edge of the thickening, *mi* hair-shaped microtrichia on the edge of the glossa

4.3.2 Labial palpi

The two labial palps insert at the anterior side of the prementum where it borders the mentum. Each labial palpus is composed of four segments (Fig. 20). Numerous sensilla trichodea can be found on each segment (Fig. 21). Both the second and the third segment additionally show one prickle-shaped thorn each. These thorns are sensilla of the type basiconica (Fig. 21). Female wasps have one sensillum basiconicum both on the second and third segment of the labial palpus (Fig. 21). Male wasps however have more sensilla basiconica developed on the end of the third segment (Fig. 22). Considering the male wasps examined, the number of sensilla basiconica present on the third segment of each labial palpus ranged from 6 to 8 sensilla basiconica.



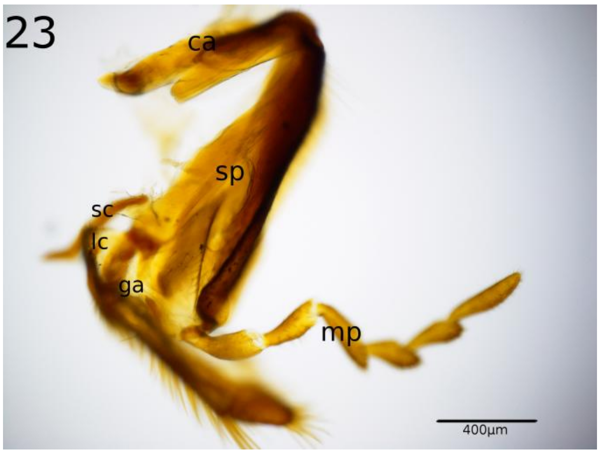
Figures 20-22: The labial palpus; **Fig. 20** Male wasps, location of the labial palpus; *pm* prementum, *s.tr* sensilla trichodea, *gl* glossae, *pg* paraglossa, *lp* labial palpus; **Fig. 21** Female wasp, detailed view of the third segment of the labial palpus, right image border: second segment, left image border: fourth segment; *lp* labial palpus, *s.ba* sensilla basiconica, *s.tr* sensilla trichodea; **Fig. 22** Male wasp, detailed view of the third segment of the labial palpus; *lp* labial palpus, *s.ba* sensilla basiconica

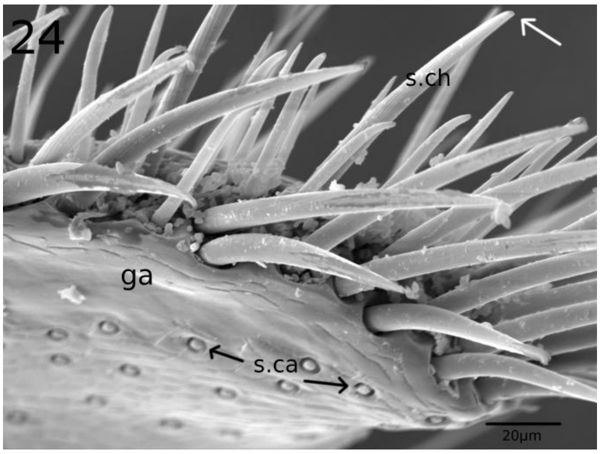
4.3.3 Maxillae

The basal sclerites of the maxillae border the labium one on each side. One maxilla consists of the cardo, the big stipes, the small lacinia, the elongate galea and the maxillary palpus (Fig. 23).

The cardo is a roughly triangular club-like sclerite that forms the joint from the labio-maxillary complex to the head. The flat stipes-sclerite is medially uplifted and lies next to the labium. A few sensilla trichodea, distributed over the surface of the stipes, are perceptible. The labium and the two stipites are connected through membranous cuticle and two small sclerites (Fig. 23). Both cardo and stipes are well sclerotized.

The stipes further bears a reduced lacinia and a relatively broad galea that is defined in two segments. Both structures are beset with a high number of sensory bristles and both parts can be described as weakly sclerotized. The galea has a high number of long sensilla chaetica on the edge and sensilla trichodea distributed over the entire outer surface. The sensilla chaetica show one terminal porus. Sensilla campaniformia can also be observed (Fig. 24). The lacinia shows long sensilla chaetica on the ridge that borders the galea. The remaining region is also beset with sensilla trichodea that are shorter and thinner. Both the lacinia and the galea serve as parts of the passageway through which food may be sucked into the mouth.



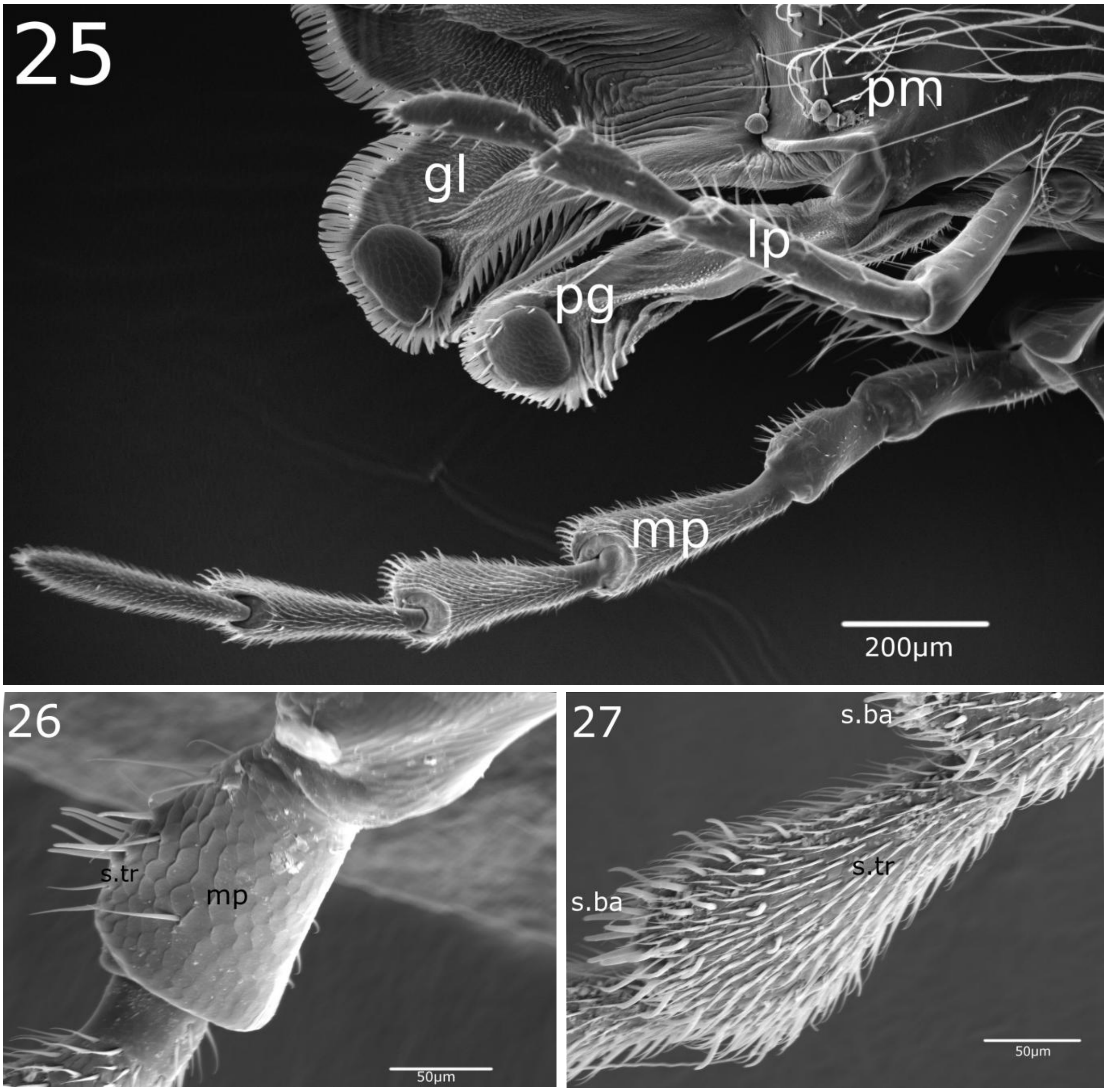


Figures 23-24: The maxilla; **Fig. 23** LM-image showing one maxilla; *ca* cardo, *sp* stipes, *sc* sclerite, *lc* lacinia, *ga* galea, *mp* maxillary palpus; **Fig. 24** SEM-image providing a detailed view of the galea; *ga* galea, *s.ca* sensilla campaniformia, *s.ch* sensilla chaetica with a terminal porus (white arrow)

4.3.4 Maxillary palpi

Each maxillary palpus consists of six segments. All six segments vary in respect to length and distribution of sensory hairs (Fig. 25). The first two segments are cylindrical in shape and few sensilla trichodea can be located (Fig. 26). Segments three to six are club-shaped and have smaller diameters at the proximal end than distally. From segment three to six the coverage with sensory hairs changes. In comparison to segments one and two the number of sensilla increases dramatically in segments three to six (Fig. 27). Additionally another type of sensilla, sensilla basiconica can be observed on segments three to six (Fig. 27).

If the coverage of sensilla on the maxillary palps is compared to those of the labial palps it is evident, that the maxillary palps bear a much higher number of sensilla than the labial palps, although the types of sensilla located are the same (Fig. 25).



Figures 25-27: Fig. 25 Comparison of the labial and the maxillary palpus; *pm* prementum, *gl* glossae, *pg* paraglossae, *lp* labial palpus, *mp* maxillary palpus; **Fig. 26** Detailed view of the second segment of the maxillary palpus; *mp* maxillary palpus, *s.tr* sensilla trichodea; **Fig. 27** Detailed view of the fourth segment of the labial palpus; *s.tr* sensilla trichodea, *s.ba* sensilla basiconica

5 Discussion

5.1 Functional morphology of the mouthparts in wasps

Female wasps feed on carbohydrate-rich fluids, they provide protein-rich food for their larvae and build nests using their mouthparts. Accordingly the mouthparts of the wasps *Paravespula vulgaris* and *Paravespula germanica* have to be suitable for different food sources. Therefore the mouthparts are able to bite solids but also to lick up fluids (Spradbery, 1973). Adult wasps feed on sugary fluids exclusively but nevertheless female wasps are also equipped for hunting insects and converting the hunted prey into small meat balls that are fed to the larvae (Matsuura & Yamane, 1990). Additionally both wasps *Paravespula vulgaris* and *Paravespula germanica* use their mouthparts for activities related to nestbuilding. Consequently the mandibles need to be stable enough to allow cutting and tearing (Spradbery, 1973).

Numerous sensilla belonging to the four different types chaetica, trichodea, basiconica and campaniformia could be found on the mouthparts using SEM techniques. That equates to the expectations of Spradbery (1973) since he has stated that in wasps sense organs are associated with mouthparts. The antennae are often associated to be the smell-organs of wasps while the mouthparts are supposed to be organs of taste (Zacharuk, 1985).

The labrum is small and roughly triangular in shape with an elongated bottom part. The surface is well endowed with sensory setae (Spradbery, 1973). The sensilla observed belong to the type trichodea. Since the labrum is largely concealed behind the clypeus only the bottom part is visible. That bottom part is only observable when the mandibles are opened. The epipharynx, a structure closely related with the pharynx, lies behind the labrum and is largely covered by it. The sides of the epipharynx are wing-like lobes, which cover the angles of the mouth (Duncan, 1939). Since the labrum is concealed partly by the clypeus and by the mandibles it has lost its function of protecting the mandibles and other parts of the mouth (Kirmayer, 1909).

The mandibles primarily serve the function of cutting tools. As they are applied to cut vegetable fibers from wood surfaces and also function as weapons for the snatching of prey, the mandibles are stout and heavily sclerotized (Duncan, 1939). The mandibles are also used for scraping earth loose and picking up stones and debris in connection with nestbuilding (Spradbery, 1973). Additionally, the mandibles are used by the metamorphosed wasps to cut through the cocoon (Schremmer, 1962). For all those tasks the mandibles in both sexes bear on the inner margin three visible teeth and an emargination. That shows concordance with the fact that mandibles are usually 4-5 toothed in Vespinae (Carpenter, 1988). In repose one mandible is folded over the other, which indicates a scissor-like function. The sensilla found on the mandibles are sensilla trichodea and sensilla campaniformia. No pores or openings in the walls of the sensilla trichodea could be found, which indicates that these sensilla serve a function as mechanoreceptors only (McIver, 1975). Sensilla campaniformia are typical mechanosensilla as well (Zacharuk, 1985). These sensilla are cupola-shaped compositions homologous to hair sensilla and peculiar to insects (McIver, 1975).

The functional connection of the remaining mouthparts forms the labio-maxillary complex that is coordinated and featured to move as a unit in Hymenoptera (Duncan, 1939). This complex is capable of operating completely independent from the mandibles (Jervis, 1998).

In adult wasps of both sexes the labio-maxillary complex in contrast to the mandibles is almost solely concerned with alimentation and the uptake of liquid food. The two maxillae and the labium are bound together by cuticular membranes. Additionally two small sclerites, one on either side of the labium, connect the maxillae and the labium. Duncan (1939) referred to the membrane that holds the whole complex together as the oral field. The two small sclerites are called the labio-maxillary jugum (Duncan, 1939). The labium is divided into the trough-shaped mentum, the prementum and the submentum (Seifert, 1995). The prementum is the anterior part of the mentum, which develops the glossae and paraglossae. The submentum is the posterior part that surrounds the mentum. The starting points of the labial palps are located on the end of the prementum, where it borders the mentum. These insertions are referred to as palpigeres. The palpigeres lie quite basal so that they appear to be part of the mentum rather than the prementum (Seifert, 1995).

The paraglossae are shorter and thinner than the median glossae, which appear heart-like in shape (Schenck, 1854). Duncan (1939) named the median lobe lingua and the lateral lobes paraglossae. The whole part in front of the mentum was termed ligula. Spradbery (1973) already used the terms glossae and paraglossae, like it was later done by Seifert (1995). The thickenings of the cuticle located on the ventral side of both the glossae and paraglossae are called acroglossal buttons (Duncan, 1939). Blüthgen (1961) described the acroglossal buttons as elliptical, brownish structure made of chitin. The acroglossal buttons are developed in this typical form only in Vespidae (Duncan, 1939). Kirmayer (1909) thought that these thickenings of the cuticle subserve a protective function. However the fact that the acroglossal buttons are beset with sensilla basiconica suggests that these compositions are designed to taste liquids or solids and their composition and quality. Sensilla basiconica could either be mechanosensitive, dually mechano- and chemosensitive, thermosensitive, hygrosensitive or olfactory (Zacharuk, 1985). Either one of these possible functions would make sense at this specific location. The wasps taste the liquids with the ventrally located sensilla basiconica on the acroglossal buttons before they lap up the liquids. Aspects in this favor are the sensilla basiconica that emerge close to the acroglossal buttons. These sensilla basiconica, which lay close to the acroglossal buttons, show a socket and a terminal pore. This porus suggests that the sensillum reacts chemosensitive and could be helpful in tasting substances (Altner, 1977). Therefore it can be assumed that the acroglossal buttons function as detectors and observers of the quality of nourishment. The spatula-shaped microtrichia, developments of the cuticle, were interpreted by Duncan (1939) to be setae of some kind serving as a rasping device. Already Schremmer (1962) suggested that these developments are no sensory hairs but chitin emergences, enabling the wasps to lap up liquids. The spatula-shaped microtrichia found on the glossae and paraglossae serve as adhesive devices (López-Cubillos & Sarmiento, 2013).

The labial palps consist of four segments and the two palps are operated by a single thin muscle (Duncan, 1939). Sensilla trichodea and a few sensilla basiconica were found on the labial palps. Both types of sensilla match the suggestion of Zacharuk (1985) that the labial palps serve sensorial functions.

The stipes bears the six-segmented maxillary palpus. Next to the maxillary palpus the broad galea is localized and next to the galea the smaller lacinia emerges. The slightly convex outside surface of the galea is implemented with numerous sensilla whereas the inner surface shows sensilla on the ridge only (Kirmayer, 1909). The lacinia and galea are oval, flattened and foliaceous (Duncan, 1939). Both are less sclerotized than the cardo and the stipes and well endowed with sensilla. Duncan (1939) has already noted that numerous long setae are distributed over the surfaces of the lacinia and galea. He concluded that the sensilla found on the galea are allocated to the type sensilla basiconica. Analyses of the sensilla located on the galea using scanning electron microscopes revealed new insights. Sensilla chaetica with a terminal pore were observed on the galea. Additionally the galea also bears sensilla trichodea and sensilla campaniformia. The observed porus at the tip would suggest a chemosensitive function rather than a bare tactile one, according to Zacharuk (1985). In addition, the lobes of the lacinia and galea could serve a secondary function as cleaning organs for the antennae, maxillary and labial palps and the forelegs (Spradbery, 1975). The maxillary palpus can be moved by two slender muscles (Duncan, 1939). The function of the maxillary palps is considered to be primarily sensory just like the labial palps (Zacharuk, 1985).

In spite of the similar function of the two different kinds of palps the coverage with sensilla is much higher on the maxillary palps than on the labial palps. The labial palps just show one to three sensilla basiconica whereas sensilla basiconica are much more prominent on the maxillary palps. This distribution of sensilla would suggest that the maxillary palps are rather used for testing the consistence of substances. To confirm this assumption further morphological but also behavioral studies would be inevitable.

5.2 Dimorphism of the mouthparts

The data gathered in the course of taking measurements suggest that there is a tendency of laying the right mandible over the left one but folding the left mandible over the right one is possible also. No significant differences between male wasps and female workers could be found in relation to folding-behavior of the mandibles. The idea to compare measurements taken from male and female wasps was initiated by a claim made by Spradbery (1973), saying that the mouthparts are modified according to sex or caste. It was further stated that males have proportionally smaller mandibles for their head size than female workers, although details are not reported.

The smaller mandibles in male wasps were explained by the fact that males do not forage and the mandibles are not used for their personal alimentation consisting of fluids only (Spradbery, 1973).

The measurements revealed that the mandibles in male wasps are significantly shorter than those of female workers. The mean length of the head as well as the mean distance from the scapus of one antenna to the ridge of the clypeus both were greater in males than in females. These results support the claims made by Spradbery (1973) although they are surprising, since broad agreement can be found in recent literature that males tend to be slightly bigger than female workers. Ripberger (1992) has listed the sizes of workers, queens and males in the genus *Paravespula germanica* as follows: Workers: 12-16 mm; Queens: 17-20 mm; Males: 13-17 mm. Consequently it was surprising that the length of the head was bigger in males than in females but the mandibles were shorter in males than in female workers. The explanation given by Spradbery (1973) that the mandibles are primarily used as cutting tools for nestbuilding and hunting and since male wasps neither hunt nor engage in nestbuilding suggests, that they do not need their mandibles like the female workers do. That statement seems plausible and was affirmed by the measurements conducted. In this context an investigation of the musculature of the mandibles in males and females could reveal whether mandibles in male wasps function similar to those of females.

Comparisons between the female workers and the male wasps show, that male wasps have a higher number of sensilla basiconica distributed over their labial palps. These sensilla basiconica are mostly located on the terminating region of each palpus. The reason for the higher number of sensilla basiconica on the labial palps of male wasps is currently unknown.

5.3 Fluid-feeding in wasps

Adult wasps of both sexes need to be equipped for the uptake of liquid food like the juice of ripe fruit, honeydew or nectar, since adult wasps are restricted to obtain nourishment in liquid form because larger particles of food are detained from travelling down the narrow esophagus (Spradbery, 1937). A short food canal for the uptake of liquid food is formed by parts of the labio-maxillary complex and the epipharynx. The labium constitutes the bottom, the stipites including the lacinia and galea form the sides and the epipharynx composes the roof of this temporarily constructed food tube (Duncan, 1939). The epipharynx probably serves a function in fluid uptake (Seifert, 1995). Kirmayer (1909) termed that food tube “Wespenrüssel” and since that also other authors referred to this complex as proboscis of wasps. However, it has to be stressed that the mouthpart-formation in *Paravespula* is not nearly as long as in bees or pollen wasps (Krenn et al., 2002). Since wasps of the genus *Paravespula* are not equipped with a proboscis, the uptake of liquids has to be accomplished in a different way. In insects that have short mouthparts, the uptake of liquid food is performed in large part by adhesion (Krenn et al., 2002). The labio-maxillary complex, which allows both licking and sucking, is the actual feeding organ of wasps. The glossae and paraglossae produce a licking motion by repeated extension and retraction (Krenn et al., 2005). In this context the surfaces of the glossae and paraglossae play a major part in the uptake of liquids because the dorsal sides present a large wettable surface. The spatula-shaped microtrichia adhere liquids that are thus transported into the food canal when the glossae and paraglossae are lifted towards the mouth (Seifert, 1995).

Both wasps *Paravespula germanica* and *Paravespula vulgaris* feed on flowers with easily reachable nectar. Many other Hymenoptera that also feed on openly accessible flowers, have short and unspecialized feeding organs. The fluids adhering to the ligula are brought into the food canal by retraction of the ligula. In the food canal the liquids are conveyed further by capillarity and suction force from the muscular cibarial or pharyngeal pumps (Krenn et al., 2005). Ants, also insects devoid of elongated mouthparts, employ the glossae for the uptake of liquid food. Like in wasps, the glossae and paraglossae are particularly important structures for the uptake of liquid food (Paul et al., 2003).

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7 Abstract

This diploma thesis investigates the morphology of the mouthparts in *Paravespula germanica* and *Paravespula vulgaris* with special emphasis on the differences between female workers and males. For the analysis of the mouthparts light microscopes but also scanning electron microscopes have been used. Despite the fact that wasps are so widely known and widespread, the mouthparts are relatively poor investigated. During the last few decades only a small number of researchers have concerned themselves with the morphology of these insects and those researchers that did investigate the mouthparts, focused primarily on the female workers.

The mouthparts of wasps are of particular interest, because they can be regarded as micro-tools that accomplish different kinds of tasks. Alimentation on carbohydrate-rich fluids, nestbuilding, hunting insects for the alimentation of the larvae and brood care are duties accomplished with the aid of the mouthparts. Since male wasps neither hunt insects for the alimentation of the larvae, nor participate in nest building processes and they only feed on sugary fluids it can be supposed that the mouthparts of the male wasps show different morphology than female wasps.

In both sexes the mouthparts consist of the mandibles, the labrum and the labio-maxillary complex, which can further be divided into the labium and the two maxillae. Sexual dimorphism related to the mouthparts was observed. The divergence between the two sexes was restricted to the length and number of the sensilla found but no differences in types of sensilla could be observed. The higher number of sensilla in males when compared to female workers was particularly well observable on the mandibles and on the labial palps. Morphometric measurements showed that the mandibles in males are significantly shorter than those of female wasps even though the head tends to be bigger in male wasps than in female workers.

8 Zusammenfassung

Die vorliegende Arbeit beschäftigt sich mit der Morphologie der Mundwerkzeuge bei *Paravespula germanica* und *Paravespula vulgaris*, wobei speziell auf die Unterschiede zwischen den männlichen Wespen und den Arbeiterinnen eingegangen wird. Im Zuge der Untersuchungen wurden sowohl Aufnahmen mittels Lichtmikroskop als auch einige rasterelektronenmikroskopische Aufnahmen angefertigt. Obwohl Wespen sehr weit verbreitet und durch ihre Lebensweise vielen Menschen vertraut sind, ist sehr wenig über die Anatomie und Morphologie ihrer Mundwerkzeuge bekannt. Sehr wenige Forscher haben den Mundwerkzeugen dieser Wespen ihre Aufmerksamkeit gewidmet und jene, die sich genauer mit der Anatomie der Mundwerkzeuge auseinandergesetzt haben, haben sich primär mit den Arbeiterinnen beschäftigt.

Die Mundwerkzeuge der sozialen Faltenwespen sind von besonderer Bedeutung, da sie im Leben dieser Tiere eine zentrale Rolle übernehmen. Nicht nur die Ernährung der adulten Tiere, sondern auch die Verpflegung der Brut sowie der Nestbau werden mit Hilfe der Mundwerkzeuge durchgeführt. Da sich männliche Wespen weder an der Versorgung der Larven noch am Nestbau beteiligen und sich selbst ausschließlich von flüssiger, kohlenhydratreicher Nahrung ernähren, kann davon ausgegangen werden, dass die Mundwerkzeuge der männlichen Wespen Unterschiede zu jenen der Arbeiterinnen aufweisen.

Die Mundwerkzeuge von *Paravespula germanica* und *Paravespula vulgaris* bestehen aus dem Labrum, den Mandibeln, sowie dem Labiomaxillarkomplex, der wiederum in das Labium und die zwei Maxillen gegliedert wird. Die Mandibeln werden primär als Beißwerkzeuge verwendet, wohingegen Labium und Maxillen der Aufnahme von flüssiger Nahrung dienen. Unterschiede zwischen den Geschlechtern zeigen sich vor allem in der Anzahl und Länge der Sensillen. Die Mundwerkzeuge der männlichen Wespen sind stärker mit Sensillen besetzt als jene der Arbeiterinnen und die Sensillen sind in der Regel auch länger. Besonders deutlich zeigt sich dies an den Mandibeln und an den Labialpalpen. Morphometrische Messungen haben zudem ergeben, dass die Mandibeln der Männchen in der Regel kleiner sind als jene der Weibchen, obwohl der Kopf der Männchen größer ist.