

## Why males of leafcutter bees hold the females' antennae with their front legs during mating

D Wittmann<sup>1</sup>, B Blochtein<sup>2</sup>

<sup>1</sup> *Laboratório de Pesquisas Biológicas da Universidade de Tübingen, PUC/RS, Av Ipiranga 6681, 90620 Pôrto Alegre, Brazil;*

<sup>2</sup> *Zoologisches Institut, LS Entwicklungsphysiologie, Universität Tübingen, Auf der Morgenstelle 28, 72076 Tübingen, Germany*

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**Summary** — Epidermal odor glands were found in the front leg basitarsi of males of various subgenera of leafcutter bees from the Old and New World. In these males, the legs, the mandibles and the head capsules are modified. During mating these structures are used by the male to grasp the female and bring the antennae of the female in close contact with the openings of the basitarsal odor glands of the front legs. Odor glands and analogous modifications of associated body structures were also found in xylocopine bees and in a sphecid wasp.

**Megachilidae / Xylocopini / Sphecidae / odor gland / mating**

### INTRODUCTION

A conspicuous sexual dimorphism in legs is common in all taxa of bees in which females have corbiculae or scopae on their hind legs to transport pollen. In floral oil collecting bees (Anthophoridae: Centridini, Exomalopsini, Tetrapediini; Ctenoplectridae: *Ctenoplectra* Smith 1857; Melittidae: *Macropis* Klug 1809, *Rediviva* Friese 1911), the front and/or middle legs bear scraping and oil-collecting structures (Vogel, 1966, 1974; Neff and Simpson, 1981). However, modified legs are also found in males. Males

of orchid bees (Euglossini) are the only example where structurally modified legs serve to collect materials. With dense tufts of branched hairs on their front legs (Moure, 1950), these males scrape fragrances from flowers (mainly orchids) and transfer them into pouches of their inflated hind legs (Dressler, 1982). The front and/or middle legs of males of some oil-collecting bees, namely those of *Monoeca* Lepeletier 1828 and *Paratetrapedia* Moure 1941 bear combs and scrapers which closely resemble the oil-collecting structures of the females. The function of these modifications is unknown.

Well known are the adhesive and clasper organs on the hind legs of *Apis* drones which serve to hold the female during copula in flight (Ruttner, 1975; Koeniger and Koeniger, 1991).

The function of the dilated front legs of males of some species of carpenter bees (eg, *Xylocopa* (*Platynopoda*) *tenuiscapa* Westwood 1840, *X* (*Platynopoda*) *magnifica* (Cockerell 1929), *X* (*Platynopoda*) *latipes* (Drury 1773), *X* (*Platynopoda*) *perforator* Smith 1861) is only partially understood. For carpenter bees, Anzenberger (1978) and Osten (1989) found the following function of the modified legs during copula in flight: males grasp the females in flight and place their front or middle legs, which have fringes of long setae, over the compound eyes of their mate. Very little is known about the function of the modified legs in some species of *Nomada* Scopoli 1770 and in various genera and subgenera of *Megachile* (eg, *Eumegachile* Friese 1899, *Pseudocentron* Mitchell 1934, *Sayapis* Titus 1905, *Melanosarus* Mitchell 1934, *Acentron* Mitchell 1934) *Chalicodoma* Lapeletier 1841 and *Fidelia* Friese 1899. Mitchell (1930, 1980), Batra (1978) and Osten (1989) assume that the modified front legs in *Megachile* Latreille 1802 play a role during mating. The few ethological observations on copula of megachilid bees with modified front legs (Batra, 1978) indicate that the males also cover the compound eyes of the female with fringes of setae located at their front leg tarsi.

Modifications that resemble those found in megachilid and xylocopine males are also known from sphecids wasps. As a conspicuous feature, the front leg tibia of many males is widely dilated, forming a concave shield. During mating, the male places these shields over the compound eyes of the female (Matthews *et al*, 1979; Low and Wcislo, 1992). Little attention has been paid to the use of the front leg tarsal segments, the mandibles and the head capsule in mating.

The purpose of this study was to elucidate the function of some structural modifications in front legs and other body parts of megachilid bees and to compare them with similar structures in carpenter bees and sphecids wasps. Preliminary reports on our findings have been published elsewhere (Wittmann *et al*, 1992; Blochtein and Wittmann, 1993).

## MATERIALS AND METHODS

This study was initiated with a survey of modified body parts in males of megachilid bees from the Old and New World. As a working hypothesis, a general pattern of the function of these structures during mating was developed and predictions were made on the presence of odor glands in the modified legs of megachilid and xylocopine bees and a sphecids wasp.

The external morphology of preserved males of about 150 New and Old World megachilid species, 2 xylocopine bee species from India and Africa (*X* (*Platynopoda*) *tenuiscapa*, *X* (*Mesotrichia*) *torrida* Westwood 1838 and 3 species from Brazil (*X* (*Megaxylocopa*) *frontalis* (Oliver 1789), *X* (*Dasyxylocopa*) *bimaculata* Friese 1903, *X* (*Neoxylocopa*) *nigrocincta* Smith 1854) and 1 European sphecids wasp species (*Crabro cribrarius* (Linnaeus, 1758)) was studied under a stereomicroscope at 40–60x. Dry museum specimens were placed in boiling water for 10 min to make them flexible during spreading of the legs and thus facilitate access to the otherwise hidden structures.

In search of glandular structures, we studied the inner morphology of tarsal segments in some megachilid bees (*M ericetorum* Lapeletier 1841, *M willughbiella* (Kirby 1802), *M rotundata* (Fabricius 1784), *M* (*Acentrina*) *anthidioides* Radoszkowski 1874, *M lagopoda* (Linnaeus 1761), *M* (*Acentron*) spp, *M* (*Pseudocentron*) spp). Furthermore, we searched for glandular structures in the front legs of *X* (*Platynopoda*) *perforator* and *X* (*Mesotrichia*) *torrida*, and the sphecids wasp *C cribrarius* Linnaeus. For the scanning electron microscopic studies (SEM), specimens were mounted on aluminium stubs and coated with gold and palladium. To study the interior surface of the tarsal segments, they were cut open, macerated in 5% KOH for 12–24 h, de-

hydrated in 70, 80, 90 and 100% acetone, and dried at 30°C.

To test our hypothesis on the use of modified body structures during mating, the behavior in *M willughbiella* was studied at the Botanical Garden of the University of Tübingen from June to August 1992 and 1993. We also analysed the copulation behavior of laboratory reared, newly emerged *M rotundata* using video recordings. These matings occurred in glass boxes measuring 7 x 2 x 2 cm.

Males of megachilid species (*M (Acentrina) apicipennis* Schrottky 1902, *M (Pseudocentron) terrestris* Schrottky 1902) collected in Brazil, and the European *M willughbiella*, captured on flowers in Germany, had their heads and front legs removed, washed and extracted in pentane. Gas chromatographic and mass spectroscopic analyses were carried out at the Institute of Organic Chemistry and Biochemistry, University Hamburg, on a Varian MAT 311. A coupling system using a 50 m x 0.25 mm (id) fused silica column with a FFAP-CB as a stationary phase was employed.

## RESULTS

Although our focus in this paper is on the functional morphology of modified body parts, a short description of the positioning of the male during copulation in *M willughbiella*, is also presented. Subsequently, we compare it with the positioning of males in *M rotundata*. A more detailed description of the mating and territorial behavior in *M willughbiella* has previously been reported by Blochtein and Wittmann (1993).

### **Case study: overview of the copulation behavior in *M willughbiella***

In *M willughbiella*, the male mounts the female in such a position that his head is above and in front of the female's head. He then places his dilated front leg basitarsi over the flagella of the female's antennae and presses them downwards to the fronts.

By doing so, the concave fan of long setae covers the compound eyes of the female. With his middle legs, he presses the female's wings downward and thus prevents her from taking off. The hind legs are positioned under the female's abdomen and pulled slightly upwards. A closer look at the morphology of these body parts gives us a better understanding of their positioning and function during copulation (fig 1).

### **Modified structures of the mandibles and the head capsule of *M willughbiella***

Below their articulation, the mandibles protrude into a 'basal' or 'inferior process' according to Moure (1943) and Mitchell (1980). These structures have their counterpart in the head capsule immediately beneath the articulation of each mandible. That is, the head capsule is deeply excavated and projects ventrally into a pointed protuberance (fig 2).

*Function:* When the male has mounted the female, he pushes her antennae into the wide buccal space by grasping the scapi with the mandibular basal processes. By widely opening the mandibles, the male presses the flagellum of each antennae into the excavations of the head capsule. In this position, one can see the female's flagella sticking out on either side through the gap between the male's mandibles and the head capsule.

### **Modified structures of the male's front leg coxa of *M willughbiella***

The coxae of the front legs protrude into long spines which are curved anteriorly. At their tip and their margins, these coxal spines have patches of sensory receptors (fig 3).

*Function:* When the male has mounted the female, he places his coxal spines behind the head capsule of the female. This not

only allows the male to tightly hold the head of the female, but also forces the head slightly downwards and thus prevents any roll and pitch movements.

### **Modified structures of the front leg tarsus of *M willughbiella***

The basitarsi, and tarsi 2, 3 and 4, bear fringes of branched setae which form an elongated and slightly concave fan. This fan has the curvature and almost the size of the female's compound eye. The anterior-ventral side of the basitarsus is strongly expanded and deeply excavated into a 'U'-shaped groove (fig 4). This 'marginal excavation' (Mitchell, 1980) is elongated and reaches the distal tip of the second tarsal segment. Furthermore, a hairless black spot is found on the dilated second and third segment of the tarsus. The surface of these spots appears smooth when viewed with the SEM.

*Function:* When the male has grasped the female's antennae between the basal processes of the mandibles and head capsule, he inserts her flagella into the marginal excavation of the basitarsi and presses them onto the fronts of the female. Since the flagella are slightly longer than the marginal excavation, their tips can be seen extending beyond the male's basitarsi. In this position, the concave fans cover the female's eyes and serve as blindfolds. The black dots

cover a very small number of ommatidia of the compound eyes of the female.

### **Modifications of the middle and the hind legs of *M willughbiella***

The tibiae of the middle and the hind leg are slightly inflated and curved ventrally. They bear long setae, but do not form fan-like fringes.

*Function:* The males clasp the wings of the females with their middle legs and press them down and towards her body. With his hind legs, the male clasps the abdomen of the female and pulls it upwards.

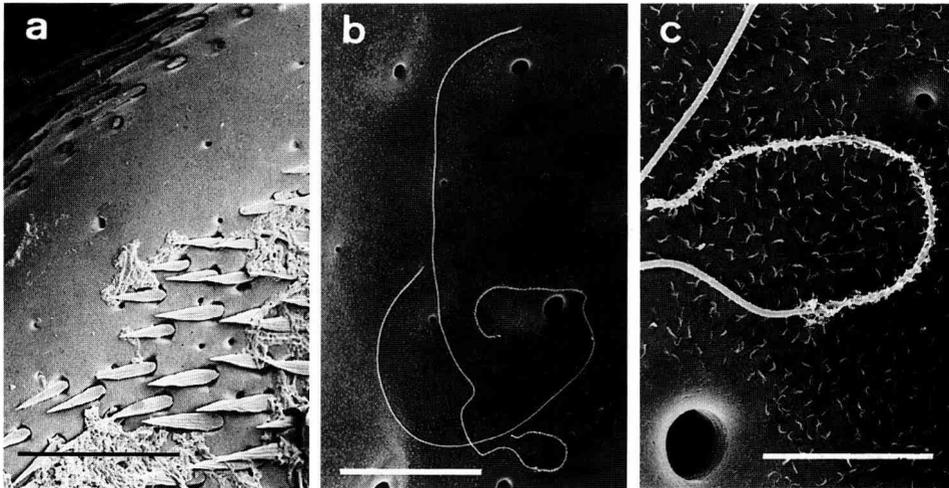
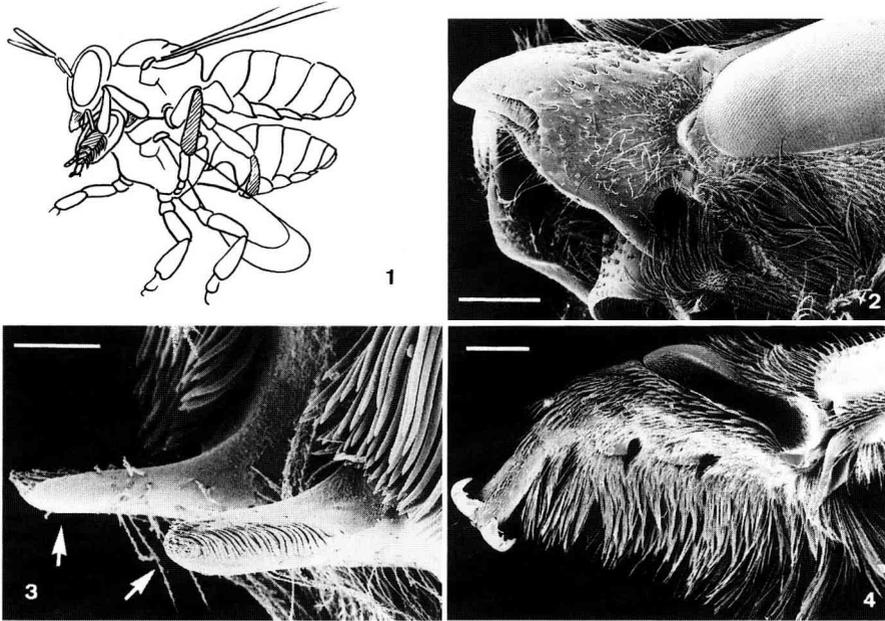
We should now ask the question as to the purpose of the clasping structures of the mandibles, the coxal spines and the lateral excavation on the front legs' basitarsi. Clearly, the male stabilizes his position on the female by grasping her antennae with his mandibles and by pushing the coxal spines against her head. By immobilizing the head and capturing the antennae with the mandibles, the male can readily push the flagella into the lateral excavation of the basitarsi. However, holding onto the flagella, the loose ends of the antennae, cannot provide the male with a firm hold. Therefore, we hypothesize that the marginal excavation serves to keep the female's flagella closely attached to the basitarsus of the male. If so, this would suggest that chemical

**Fig 1.** Schematic drawing of the copula position in *M willughbiella*. Hatched body parts are modified to assist in mating.

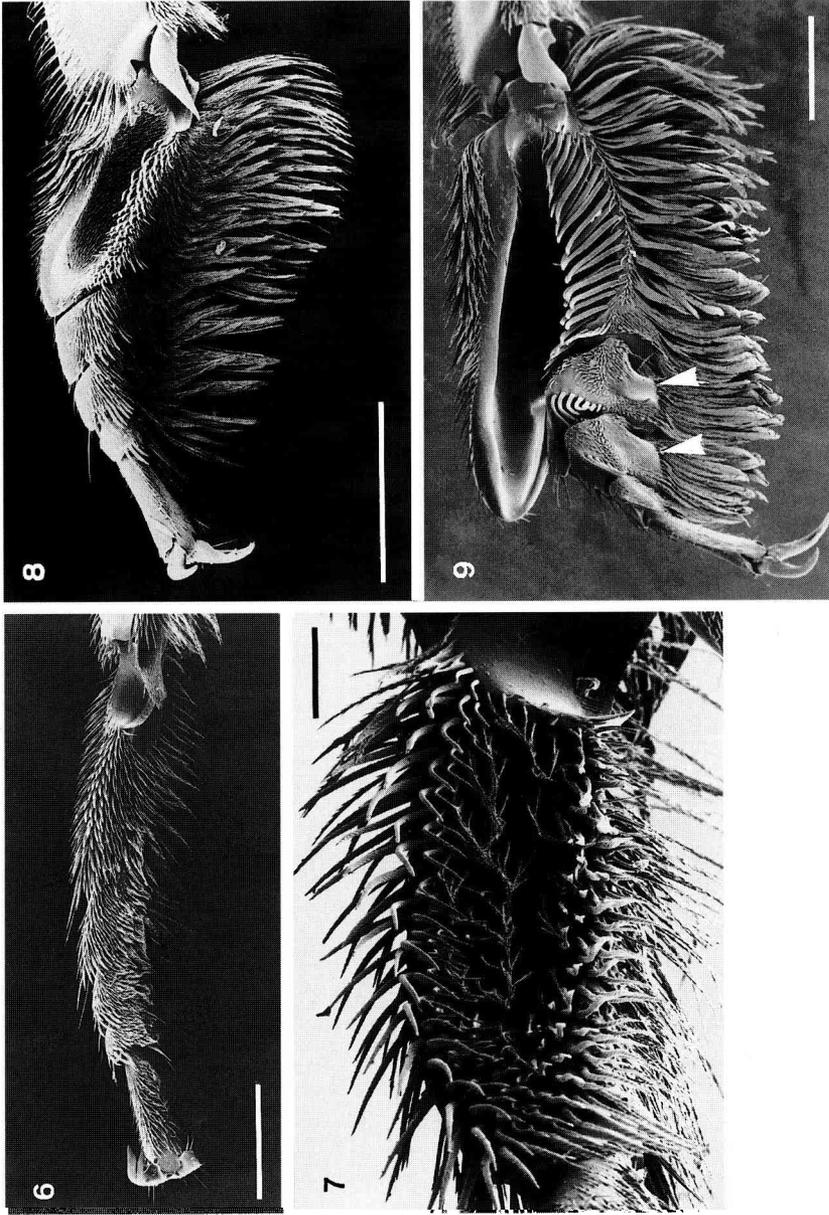
**Fig 2.** Lateral view of the male head of *M willughbiella* showing the inferior process of the left mandible and the excavation of the subocular area. Both structures serve as a clamp to hold the scape of the female's antenna. Bar: 0.5 mm.

**Fig 3.** Lateral view of the male front leg coxae of *M willughbiella*. The arrows point at spine-like protrusion extending from each coxa. During the copula these spines are placed behind the female's head. Bar: 200  $\mu$ m.

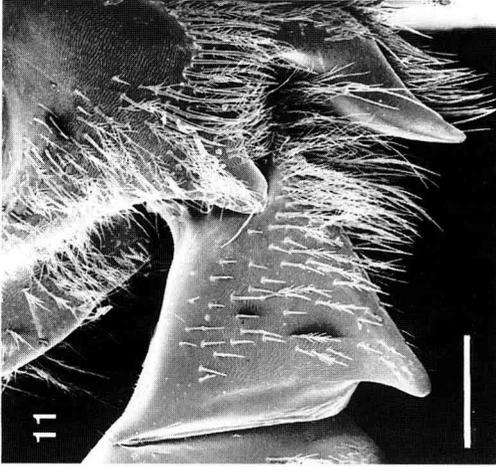
**Fig 4.** Ventral view of the right front leg tarsus of *M willughbiella* male. The basitarsus is elongated laterally. Hairs on the posterior margin of the tarsal segments form a concave fan. The fan functions as a blindfold. The lateral excavation serves to hold the female's flagellum. Bar: 400  $\mu$ m.



**Fig 5.** **a)** Distal end of marginal excavation (right basitarsus, *M willughbiella* male) with pores of odor glands. Bar: 50  $\mu\text{m}$ . **b)** Interior surface of a front leg basitarsus (*M willughbiella* male). A cuticular duct of the glands is seen to enter near on the upper margin and near the center. Bar: 40  $\mu\text{m}$ . **c)** Details of the distal part of the cuticular duct showing branches of the tubules of the end apparatus. Bar: 10  $\mu\text{m}$ .

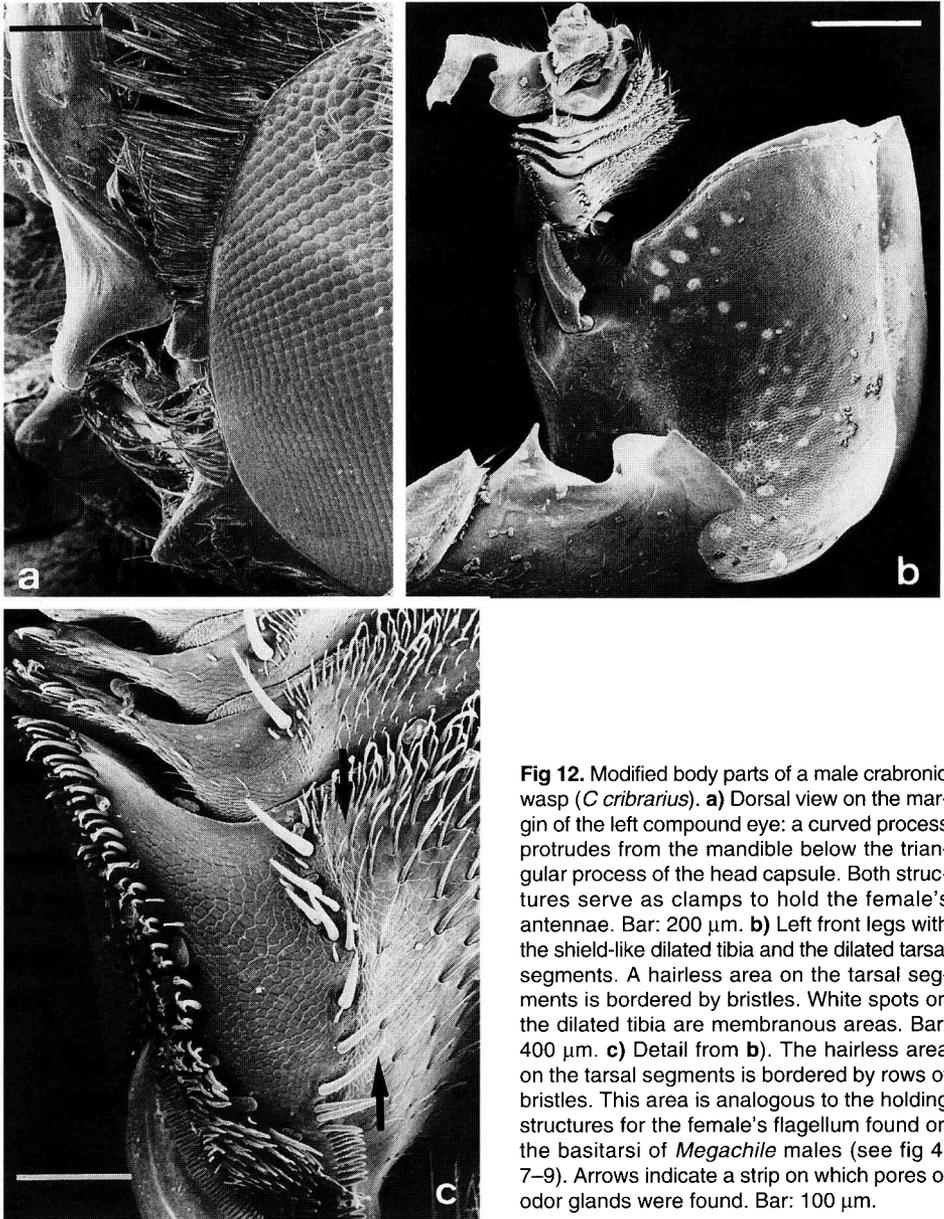


**Fig 6.** Ventral surface of the right front leg tarsal segments (*M. rotundata* male). Bar: 100 µm.  
**Fig 7.** Ventral view of the right front leg basitarsus (*M. Acentrina anthracoides* male). The basitarsus is slightly expanded. Bar: 100 µm.  
**Fig 8.** Antero-ventral view of the right front leg tarsus (*M. maritima* male). The basitarsus is deeply excavated on its long axis. This marginal excavation is bordered by curved bristles. Hairs on the posterior margin of the tarsal segments form a concave fan. Bar: 1 mm.  
**Fig 9.** Ventral view of the right front leg tarsus (*M. Pseudocentron curvipes* male). Tarsal segments 1–4 are dilated and the posterior margin is bordered with a fan. The basitarsus is elongated laterally and extends beyond segment 4. Arrows indicate areas of black dots. Bar: 0.5 mm.



**Fig 10.** Right front leg tarsus of a male *X (Platynopoda) perforator* with a prolonged, dilated and curved basitarsus. All segments are bordered by a fringe of hairs. The arrow points to an area where pores of odor glands are situated. Bar: 1 mm.

**Fig 11.** Lateral view of 3 spines on the front leg coxa and trochanter of *X nigrocincta* male. Bar: 0.5 mm.



**Fig 12.** Modified body parts of a male crabronid wasp (*C. cribrarius*). **a)** Dorsal view on the margin of the left compound eye: a curved process protrudes from the mandible below the triangular process of the head capsule. Both structures serve as clamps to hold the female's antennae. Bar: 200  $\mu\text{m}$ . **b)** Left front legs with the shield-like dilated tibia and the dilated tarsal segments. A hairless area on the tarsal segments is bordered by bristles. White spots on the dilated tibia are membranous areas. Bar: 400  $\mu\text{m}$ . **c)** Detail from **b)**. The hairless area on the tarsal segments is bordered by rows of bristles. This area is analogous to the holding structures for the female's flagellum found on the basitarsi of *Megachile* males (see fig 4, 7–9). Arrows indicate a strip on which pores of odor glands were found. Bar: 100  $\mu\text{m}$ .

signals are emitted by basitarsal glands. Indeed such glands were detected.

### Odor glands in the front, the middle and the hind legs of *M willughbiella*

SEM analyses of the front legs revealed the presence of pores ( $d = 2 \mu\text{m}$ ) on the surface of the marginal excavation of the basitarsi (fig 5a). This is exactly the location in which the female's antennae come in contact with the basitarsi. From the inner surface of the front legs basitarsi, these pores lead into cuticular ducts ( $d = 2 \mu\text{m}$ ;  $l = 120 \mu\text{m}$ ) which end in branched tubules (fig 5b,c). These tubules are located within the secretory cell. The main compounds found in the basitarsal glands of the front legs are carbohydrates and esters. Of all species analyzed, 7-pentacosen and pentacosan were the dominating components. Furthermore, we found pores of odor glands on the tibia of the middle leg and on the basitarsi of the hind legs. On the inner surface of these segments, the pores also lead into long chitinous ducts ( $d = 2 \mu\text{m}$ ,  $l = 40\text{--}100 \mu\text{m}$ ). The list of compounds, and the histology of the basitarsal odor gland units, and other epidermal odor glands, will be described elsewhere (Blochtein *et al*, unpublished data).

*Function:* When the male holds the female's flagella in the lateral excavation of his front legs basitarsi, the pores of the odor glands are in close contact with the flagella. This facilitates close range chemical communication during courtship and/or mating. Studies are in progress on the function of the odor glands of the middle and hind legs during territorial marking and the post-mating behavioral period.

### Megachilid bees

To test whether our explanations of the functional properties of the modified body parts

found in *M willughbiella* can be extended to other megachilid bees, and some xylocopine bees and a sphecoid wasp, we examined the modifications of the body parts of other bee species. In general, our examination of the coxal spines, the basal processes at the mandibles and the lateral excavations of the front legs basitarsi has revealed that most of the species with lateral excavations on the basitarsi also have coxal spines and modified mandibles. There are, however, species in which the males have either 1 or 2 modified body parts. These body parts are lateral excavation and basal processes of the mandibles without its counterpart on the head capsule (*eg*, *M (Acentrina) anthid-ioides*), or mandibular processes in combination with coxal spines, but without a lateral excavation of the front leg basitarsus (*eg*, *M rotundata*, *M ericetorum*). On many modified front legs, black dots (see fig 9 below) are found on the ventral side of tarsal segment 2. In some species, the black dots are found on tarsal segments 2, 3 and/or 4. In rare cases, such as *M (Stelodides) euzona* Perez 1899, males have black dots on the basitarsus, or as in *M (Dactylomegachile) sp* Mitchell 1934, on the tip of the mushroom-shaped spine of the strigillum. In some species with modified legs (*eg*, *M lagopoda* and *M (Tylomegachile) orba* Schrottky 1913), the black dots are lacking.

Our examination of the fine structures of pores and ducts of the odor glands in the basitarsi has shown that pores are also present in species like *M (Acentrina) anthid-ioides*, *M (Acentron) sp*, *M lagopoda*, *M (Pseudocentron) sp* and *Anthidium manicatum* (Linnaeus 1758). We also found odor glands in *M ericetorum*, *M maritima* (Kirby 1802), *M (Pseudocentron) curvipes* Smith 1853, *M rotundata* and *M willughbiella*.

In our studies of the front leg tarsal segments, different patterns of modifications were found within various species of *Megachile*. We recognize a morphological series of modifications of male basitarsal

holding structures for the antennae of the female. This is best illustrated by some examples:

– In *M ericetorum* and *M rotundata*, the males' front legs do not possess a holding structure for the female's antennae. Some tarsal segments have elongated setae, but they do not form a fan (fig 6).

– In *M (Acentrina) anthidioides* and in *M (Pseudocentron) sidalceae* Cockerell 1897, the front leg basitarsi are slightly thickened and 2 distinct rows of curved bristles border an elongated area which is covered by a few branched hairs. The width of this area corresponds to the diameter of the female's antennae. No conspicuous blindfold is present (fig 7).

– In *M (Tylomegachile) orba*, *M (Pseudocentron) framea* Schrottky 1913, *M (Acentrina) squalens* Haliday 1836, *M (Acentrina) brunneriella* Cockerell 1917, *M willughbiella* and *M maritima*, the basitarsus is excavated in its long axis. Both sides of the excavation are bordered with bristles, a fan-like blindfold is present (fig 8).

– In *M (Pseudocentron) curvipes*, the tarsal segments 1–4 are dilated and bear a fan-like blindfold. The basitarsus is elongated laterally. This elongated part forms a conspicuous lateral excavation and is bordered on both sides by rows of bristles (figs 4, 9).

### **Exceptions in the pattern of modified body parts**

In *M (Chrysosarus) bella* Mitchell 1930, *M (Chrysosarus) melanopyga* Costa 1863 and *M (Chrysosarus) inermis* Provancher 1888, the mandible, at its point of articulation, does not protrude into a basal process but instead has a bundle of stiff bristles which serves to hold the female's antennae. We also found an exception in the basic pattern of the basitarsal holding structures: in males of *M (Chelostomegachile) otomita* Cresson

1878, the front leg basitarsus, and the second and third tarsal segments, are folded in such a manner that the 3 segments almost form a tube. This tube has a diameter corresponding in size to that of the female's antennae. These modifications strongly suggest that they also serve to hold the female's antennae. Furthermore, it should be noted that males of *M (Pseudocentron)* spp have false, hook-like spurs which protrude from the anterior surface of the middle leg tibia. Their shape and position strongly suggest that they serve to press the female's wings downward during mating.

### **Case study: overview of the copulation behavior in *M rotundata***

For our second case study, we selected *M rotundata* as a representative of species in which males have no holding structures for the female's flagella on the front leg tarsal segments. Males, in this instance, have coxal spines and basal mandibular processes. However, odor glands are also present in their basitarsi. In *M rotundata*, the male mounts the female and pushes his coxal spines behind the female's head and with his middle legs he presses the female's wings downward. He then grasps the scapi of the female's antennae with the basal processes of his mandibles. The flagella now protrude on both sides below the head of the male. He then grasps the female's flagella with his front leg tarsi. Subsequently, he pins the flagella with his tarsi to the frons of the female. To fix the flagella in this position, he hooks the claws of his front legs to the inferior margin of the female's mandibles. While the female is held down and thus motionless, the basitarsi are in direct contact with the proximal part of the flagella. This clearly shows that even males, without a holding structure for the female's antennae on their front legs basitarsi, can

use their modified body parts in such a manner that the openings of their basitarsal odor glands come in direct contact with the flagella of the female.

### **Modified structures and odor glands in the front legs of xylocopine bees**

In males of some Old World species, for instance in *X (Platynopoda) tenuiscapa*, *X (Platynopoda) latipes* and *X (Platynopoda) perforator*, the front legs basitarsi are 'S'-shaped, dilated and bordered by dense hairy fans (fig 10). Although we found spines on the coxae of the front legs, the clasping structures on the mandibles and the marginal excavations on the basitarsus are lacking. In our studies of the inner surface of the front legs basitarsi in males of *X (Platynopoda) perforator*, we found odor glands in the dorsal parts. The pores, ducts and the end apparatus of these glands are similar to those found in megachilid bees (fig 5). In males of some New World xylocopine species (eg, *X frontalis*, *X nigrocincta*, *X bimaculata*), the front leg tarsal segments are not dilated, but bear blindfolds of long hairs at their posterior side. On the anterior-ventral margin of the basitarsus of *X bimaculata*, we found an elongated almost hairless area which is bordered by long bristles suitable for holding the female's flagella. More importantly, at the basal part of this holding structure are pores ( $d = 2 \mu\text{m}$ ) similar to those found in megachilid bees. Spines, are present on the coxa and the trochanter of the front legs (fig 11).

### **Modified structures of the front legs and the head capsule in *C cribrarius* (Sphecoidae)**

In males of *C cribrarius*, the mandibles have at the upper part of their articulation a hook-shaped process (fig 12a). In contrast, near

the lower margin of the compound eye, a pyramid-like structure protrudes (fig 12a). The shield-like blindfold on the front leg however is formed by the tibia (fig 12b). On the ventral side of the strongly dilated basitarsus, as well as on the other tarsal segments, we find 2 conspicuous rows of bristles, which border an elongated area (fig 12b,c). Similar to what occurs in some megachilid and carpenter bees, these structures are suitable to hold the female's flagella. Moreover, we found pores and ducts of odor glands on the inner surface of the basitarsus.

## **DISCUSSION**

The conclusions drawn from our morphological, functional and behavioral studies on the general positioning of the modified body parts during copula in megachilid bees are confirmed for other species by a photograph of *Chalicodoma spissula* (Batra, 1978) and an unpublished photograph by F Amiet of *M argentata* Friese 1899. Batra (1978) and Sihag (1986) give interesting descriptions of the courtship and copulation behavior and its effect on the female. We are now aware that basitarsal odor glands are involved in copulation behavior in various megachilid bees, and thus their descriptions are subject to a different interpretation.

Sihag (1986) studied the mating and copulating behavior in 4 Indian megachilid species (*M nana* Bingham 1897, *M cephalotes* Smith 1853, *M flavipes* Spinola 1838, *M lanata* Fabricius 1775). We examined his material and found coxal spines and a marginal excavation in *M cephalotes*, but only coxal spines in *M lanata*. The other 2 species had no modified body parts. For all 4 species Sihag states: "In the dorsal mounting position in the beginning, the head of the male projects ahead of the female. The fore-legs grapple the head of the female. The male, then, in this position strikes his antennae vigorously on the forehead/anten-

nae of the female ... after this the female becomes motionless and her antennae are directed downwards." Batra (1978) reports on *C spissula*: "then the male placed the wide, flattened, pale, hairy tarsi of his front legs over the upper part of the female's compound eyes and presses her wings down with his other legs. If she began to move, he rubbed her eyes with these tarsal brushes, which calmed her." The observations of both authors further corroborate our findings in regard to the general pattern in the positioning of the male's legs on the female. Most importantly, in all the cases so far reported, the male's front legs made contact with the head of the female. It is an open question whether the front legs made contact with the antennae. At least in the case of *M cephalotes*, we assumed that this is the case because the front legs of these males have a lateral excavation.

### **Female choice and chemical communication**

At a first glance, the elaborate array of clasping structures make it questionable that there is any possibility for the female to reject a male, once he has mounted her. Sihag (1986) states: "The female's rejection response only appears in the form of offering some resistance by not rising and opening of her genitalia otherwise she, in a true sense, is raped by the male." However, in a large series of conspecific males of *M (Acentrina) apicipennis*, we found pronounced differences in size of these structures. The holding structures of smaller males would hardly fit larger females. Therefore, a female's choice for a male may also be based on his size. Furthermore, the set of holding structures and the possible use of chemical communication, or pheromones, employed by a male during courtship and/or mating, requires finely tuned motor coordination. Holding structures for keeping the

female's antennae in close contact to the odor source suggest that at least some of the semiochemicals from the basitarsal glands are likely to serve as short range signals. We are not sure, whether there are substances involved which could not be detected by our sampling methods and our GC analysis. Moreover, it is not clear, whether the chemical signals emitted from the front leg basitarsal glands are only used for species recognition, or if they also function in mate acceptance. Virgin females of *M rotundata* rejected some conspecific males in mating box tests, but copulated with other individuals under identical conditions. *M willughbiella*, under natural conditions, was also observed to reject males. These females literally throw off males by using rapid abdominal jerks. Thus, a female is clearly able to escape or reject a male.

The elucidation of the overall effects of chemical communication in *M willughbiella* is further complicated by the fact that males have also odor glands on the middle and the hind legs, and in sternite 6. Studies on the function of volatiles in territorial marking and post-mating behavior are in progress (Blochtein and Wittmann, 1993).

### **Convergent modifications in bees and sphecid wasps**

The similarities in the modifications of front legs and functionally related structures in male megachilid and xylocopine bees, and in sphecid wasps, are remarkable. Not only do these structures serve the same mechanical functions, but they are also associated with odor glands. Interestingly, in males of *Xylocopa (Platynopoda)* spp, the modified front legs serve as blindfolds (Hurd and Moure, 1963; Osten, 1989) and bear odor glands, whereas in males of *X (Mesotrichia) torrida* the middle legs bear a blindfold (Anzenberger, 1978) but no odor glands. In xylocopine bees, we were unable to detect

distinct mandibular holding structures for the antennae of females. Holding structures at the mandibles, however, were found in a sphecid wasp. In contrast to megachilid bees, they are formed by lateral and not basal processes of the mandible. When the wasp mandible is opened, it forms a clamp with a pyramid-like structure at the lower margin of the compound eye. In sphecid wasps it is the front leg tibia which forms a shield-like blindfold. As suggested by Matthews *et al* (1979), West Eberhard (1984) and Low and Wcislo (1992), the membranous openings in the blindfold may transmit species-specific patterns of light signals when held over the female's eyes. In this respect, it is noteworthy that the highly modified front legs in megachilid bees are translucent, yellow and, with the exception of a few species, bear black dots. In some megachilid species, without front leg modifications, we found disk-like dilations with black dots on tarsal segments 1 to 4. The presence of the black dots appears to be independent of the modification found on the front legs. This could indicate a highly specialized function of these dots. That is, these dots may serve as visual species specific signals by shading (instead of illuminating) specific groups of ommatidia of females. In males of many species, these dots are located at the margins of rounded indentations between the tarsal segments (fig 9), and thus may augment the light-dark contrast perception when these front legs are held over the eyes of the females.

## CONCLUSIONS

In conclusion, our studies show that in leafcutter bees, carpenter bees and a digger wasp analogous modifications of different body parts function as blindfolds and holding structures for the female's antennae. These structures work together to improve the transmission of chemical signals from

the front leg basitarsal odor glands to the antennae of females.

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**Résumé — Pourquoi les mâles de mégachiles tiennent-ils les antennes des femelles avec leurs pattes antérieures au cours de l'accouplement ?** Jusqu'à présent on ne sait pas pourquoi les pattes antérieures des mâles de plusieurs espèces de mégachiles (Megachilidae), de xylocopes (Xylocopinae) et de sphécidés (Sphecidae) sont modifiées de façon spectaculaire. En étudiant la morphologie des pattes de ces insectes, nous avons trouvé sur les basitarses des glandes odorantes. Ces substances odorantes sont étalées directement sur les antennes de la femelle lors de l'accouplement. Chez les mâles de mégachiles il existe d'autres parties du corps qui sont modifiées en rapport avec le transfert de substances odorantes : sous leur articulation les mandibules portent une excroissance et les coxas des pattes antérieures des protubérances pointues. Les tarse des pattes antérieures sont élargis et bordés de longues soies en forme d'éventail. Chez les mâles de quelques espèces les basitarses sont fortement élargis et creusés d'un sillon (fig 4). Les observations faites sur le com-

portement d'accouplement de *Megachile willughbiella* et de *M rotundata* indiquent que les coxas modifiés servent aux mâles à s'agripper à la femelle au cours de la parade et de la copulation. Le mâle attrape avec ses mandibules les articles basaux de l'antenne de la femelle. Il essaie ensuite de mettre en étroit contact les basitarses de ses pattes antérieures avec le flagelle des antennes de la femelle. Les mâles de *M willughbiella*, par exemple, engagent le flagelle des antennes de la femelle dans le sillon latéral de leurs basitarses. Les antennes viennent alors en contact direct avec les ouvertures des glandes odoriférantes. Lorsque le mâle presse ses pattes antérieures sur le front de la femelle, l'éventail de soies des tarse élargis couvre les yeux composés de la femelle. Les mâles de *M rotundata* possèdent bien, sur les basitarses de leurs pattes antérieures, des glandes odoriférantes mais aucune structure particulière pour maintenir le flagelle de l'antenne. Lors de l'accouplement ils caressent de leurs tarse les antennes de la femelle et pressent le flagelle avec leurs pattes antérieures sur le front, en accrochant leurs griffes sous les mandibules de la femelle. Chez les xylocopes de l'Ancien et du Nouveau Monde et chez les sphécidés on trouve des modifications semblables sur des parties du corps, qui servent à appliquer les substances odorantes des pattes antérieures directement sur les antennes de la femelle.

#### **Megachilidae / Xylocopini / Sphecidae / glande odoriférante / accouplement**

**Zusammenfassung — Warum Männchen von Blattschneider-Bienen bei der Paarung die Antennen der Weibchen mit den Vorderbeinen festhalten.** Bisher war unklar, wo die auffällig modifizierten Vorderbeine der Männchen mehrerer Arten von Blattschneiderbienen (Megachilidae), Holzbienen (Xylocopinae) und Grabwespen

(Sphecidae) dienen. Bei unseren Untersuchungen zur Morphologie dieser Insektenbeine, fanden wir in den Basitarsen Duftstoffdrüsen. Wie sich zeigte, werden die Duftstoffe dieser Drüsen bei der Kopula direkt auf die Antennen des Weibchens aufgetragen. Bei den Männchen der Blattschneiderbienen stehen weitere modifizierte Körperteile in funktionellem Zusammenhang mit der Duftstoffübertragung: Die Mandibeln sind unterhalb des Gelenkes zu Haken ausgezogen und die Coxae der Vorderbeine tragen lange dornförmige Fortsätze. Die Vorderbeintarsen sind verbreitert und von langen Haaren eingesäumt. Bei Männchen einiger Arten sind die Basitarsen stark verbreitert und zu einer Rinne ausgekehlt. Beobachtungen des Paarungsverhaltens bei *Megachile willughbiella* und bei *M rotundata* ergaben, daß die modifizierten Coxae dem Männchen dazu dienen, sich während der Balz und der Kopulation auf dem Weibchen festzuhalten. Dabei fixiert das Männchen mit den Mandibeln die Basalglieder der Antennen des Weibchens. Das Männchen versucht dann seine Vorderbein-Basitarsen in engen Kontakt mit den Antennengeißeln des Weibchens zu bringen. Die Männchen von zB *M willughbiella* führen dazu die Antennengeißeln in die laterale Rinne ihrer Basitarsen ein. Dabei kommen die Antennen in direktem Kontakt mit den Öffnungen der Duftstoffdrüsen. Presst das Männchen seine Vorderbeine auf die Frons des Weibchens, so werden mit dem Haarsaum der verbreiterten Tarsen die Komplexaugen des Weibchens abgedeckt. Die Männchen von *M rotundata* haben in ihren Vorderbein-Basitarsen zwar Duftstoffdrüsen, aber keine spezielle Struktur zum Festhalten der Antennengeißel. Bei der Kopula streichen sie mit ihren Tarsen über die Antennen des Weibchens und pressen die Flagella schließlich mit ihren Vorderbeinen auf die Frons, indem sie ihre Klauen unter den Mandibeln des Weibchens einhaken. Bei Holzbienen der Alten und Neuen Welt und bei Grabwespen fanden wir analoge

Modifikationen von Körperteilen, die der direkten Applikation von Duftstoffen aus den Vorderbeindrüsen auf die Antennen des Weibchens dienen.

### **Megachilidae / Xylocopini / Sphecidae / Duftstoffdrüse / Paarungsverhalten**

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