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Oil-Collecting structures in Tapinotaspidini: Their diversity, function and probable origin

(Hymenoptera: Apidae)

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Abstract

The fine structure of the oil-collecting organs was studied with SEM in females of 17 species representing six of the nine known genera of the tribe *Tapinotaspidini*. The oil sources of this bee group are surveyed on the basis of the literature and own data. Oil-collecting organs may be situated on the forelegs *(Chalepogenus, Caenonomada, Arhysoceble, Paratetrapedia)*, midlegs *(Tapinotaspis)*, fore- and midlegs *(Monoeca)*, or the metasoma *(Tapinotaspoides)*. Most basal *Tapinotaspidini* are tropical and subtropical and use Iridaceae, Scrophulariaceae and Solanaceae as oil-sources. One species may gather oil from several plant genera. Species of the mostly temperate and subtropical *Chalepogenus, Lanthanomelissa* and *Tapinotaspis* are apparently more specialized and seem to be mostly depending on one or few species of a single plant genus *(Calceolaria, Nierembergia* or *Sisyrinchium)*. *Chalepogenus* species that depend only on *Calceolaria (Ch. rasmusseni, Ch. rufipes* and *Ch. vogeli)* have a particular and derived type of oil-collecting structure. They also have relatively long midlegs, though without oil-collecting structures, probably suited to grab the broad lower flower lip. The midlegs of *Tapinotaspis* are elongated due to longer femora, basitarsi and meditarsi. Thus the oil-collecting organs, located on the more distal of these segments, can sweep on an extended elaiophore surface such as that of *Nierembergia*. The alliance *Monoeca-Trigonopedia-Paratetrapedia* contains tropical bees reportedly or putatively associated with Malpighiaceae and Orchidaceae.

Introduction

In addition to collecting nectar and pollen, oil-collecting bees have specialized in obtaining floral oils, a third flower attractant after pollen and nectar. For this activity these bees are equipped with elaborate setal combs and pads which are situated on the legs or the metasoma. Oil-collecting bees are mutualistically associated with a disparate array of Monocots and Dicots which produce floral oils in glands termed elaiophores (Buchmann 1987; Vogel 1974, 1986, 1988, 1990a, 1990b). The polyphyletic origin of elaiophores results in a morphological and anatomical diversity which may in turn have influenced the morphology and behavior of oil-collecting bees.

The biota of the Holarctic, Paleotropical, Neotropical and Capensic regions each hold their own sets of endemic oil-based flower-bee relationships (Vogel 1988). The Neotropical region harbors the richest array of oil-collecting bees and oil flowers. Oil-collecting bees in this region belong to the apid tribes Tetrapediini, Centridini and Tapinotaspidini. About 280 to 320 species of oil-collecting bees are known, most of them (about 200) belonging to the Centridini (Vogel 1989).

Basitarsal combs of specialized setae are predominantly found in Centridini (Vogel 1974; Neff & Simpson 1981) whose combs may be located either on the front and midlegs or on the forelegs only. Species with collectors on four legs represent the most widespread type in the tribe and are mainly associated with Malpighiaceae with four sets of elaiophores (Vogel 1990a). The comb structure is mainly adapted to collecting oil from the so-called epithelial elaiophores of this plant family (Vogel 1974). However, some *Centris* species have different types of collecting structures matching other kinds of elaiophores (Simpson et al. 1990).

The oil-collecting structures of the Tapinotaspidini may be situated either on the front legs, the middle legs or the metasoma (Neff & Simpson 1981). These bees are characterized by combs of unbranched setae

Fig. 1: *Chalepogenus luciane.* **A:** posterior view of right leg. **B:** margin of the oil-collector.

and setal pads of finely branched hairs, furthermore scraping structures formed by specialized setae are also present. In several genera the front tarsus has rows or areas of flattened, apically curved setae. Strikingly specialized setae are present on the midleg oil-collectors of *Tapinotaspis*, and on the metasomal sternal fringes of *Tapinotaspoides*.

The study of oil-collecting structures was pioneered by Vogel (1974) in his broad-scope study of oil flowers and their bees. He described oil-collecting structures for the two genera of Centridini, and for species from three genera of Tapinotaspidini (then included in Exomalopsini). This work was followed by an extensive study by Neff & Simpson (1981), which showed the amazing diversity of the oil-collecting structures present in the Neotropical Apidae. Though they focused their observations on the Centridines, the variability within the Tapinotaspidini was recognized. However, a more detailed study remained to be undertaken. Studies of oil-collecting structures have been completed for the Palaeotropical Ctenoplectrini and the Holarctic Melittidae by Vogel (1986, 1990b).

By surveying the collection of bees we have obtained from oil flowers of several plant families, we are here extending knowledge on the oil-collecting structures of the Tapinotaspidini. In addition, we review the known oil sources of this group. We hope these data will help better understand the origin and evolution of the Tapinotaspidini and their oil flowers. In addition, it is also necessary to integrate previous information with a new classification of Tapinotaspidini accomplished by one of us (Roig-Alsina 1997, 1999).

Fig. 2: *Chalepogenus rasmusseni.* **A:** posterior view of the oil-collector pad on the left leg. **B:** anterior view of the same leg. **C:** detail of A. **D:** oil-collector on the meditarsus.

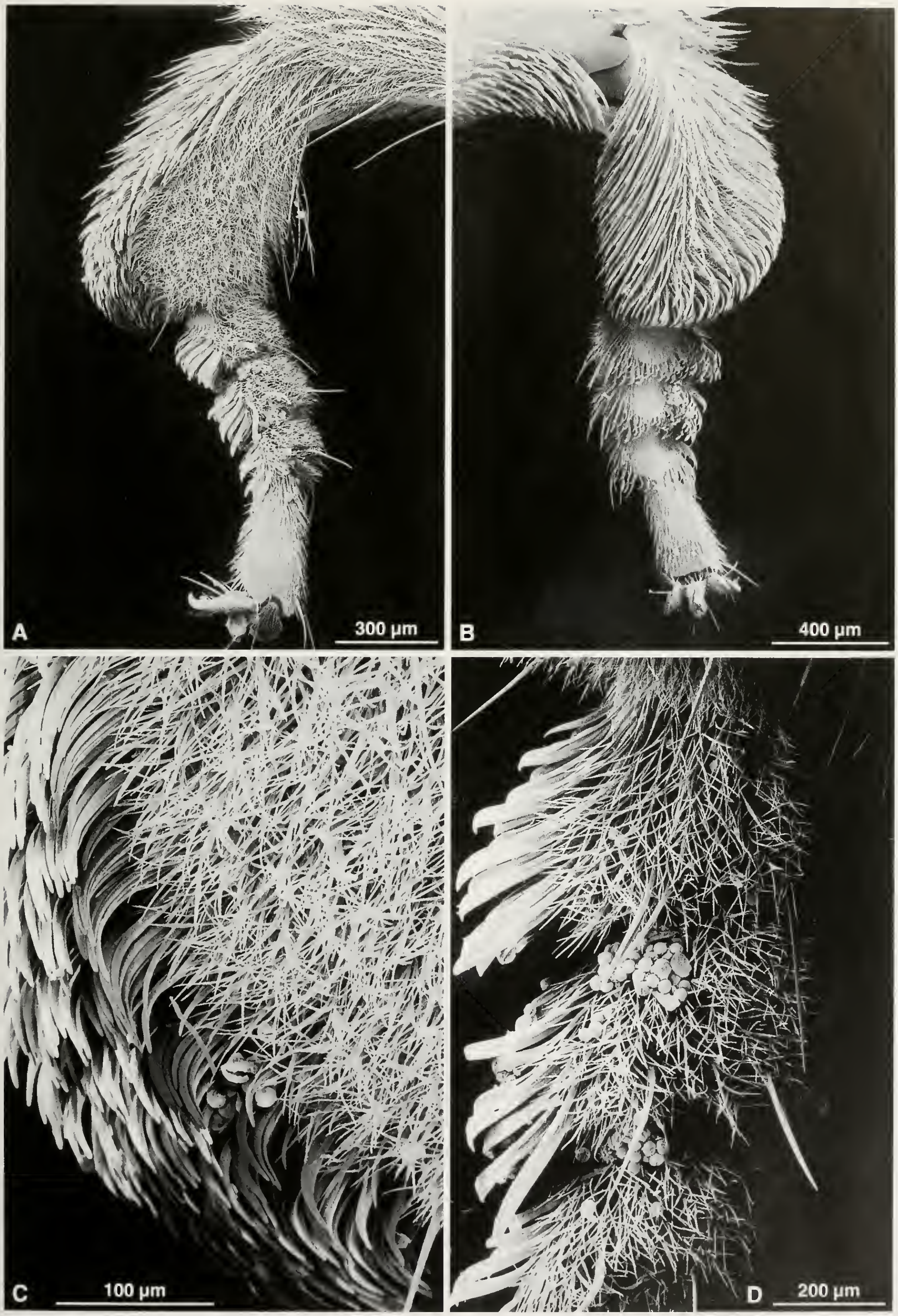
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Fig. 3: *Chalepogenus caeruleus.* **A:** posterior view of the oil-collector on the tibia, basitarsus and meditarsus of the left foreleg. **B:** margin of the oil-collecor.

Material and Methods

We studied females of a total of 17 species from six genera of the tribe Tapinotaspidini: *Tapinotaspis, Tapinotaspoides, Chalepogenus, Lanthanomelissa, Monoeca,* and *Caenonomada.* Not included in the study are only three genera of the tribe: *Paratetrapedia, Trigonopedia,* and *Arhysoceble.* The oil-collecting structures of *Arhysoceble* have received sufficient attention (Neff & Simpson 1981; Vogel 1974; Vogel & Cocucci 1995). Names and voucher specimens are as follows, the number of species known for each of the genera is given in brackets:

Chalepogenus (21)

1. *C. caeruleus* (Friese, 1906). Argentina. Río Negro. El Bolsón. Jan. 1994. Leg. Cocucci & Sérsic
2. *C. cocuccii* Roig-Alsina, 1999. Argentina. Tucumán. Tafí del Valle. Dec. 1989. Leg. Cocucci & Sérsic
3. *C. herbsti* (Friese, 1906). Chile. Peñuelas, Valparaíso. Dec. 1969, Leg. Toro
4. *C. luciane* (Urban, 1996). Argentina. Córdoba. Santa María. Nov. 1987. Leg. Cocucci & Sérsic
5. *C. muelleri* (Friese, 1899). Argentina. Buenos Aires, Delta del Paraná, Dec. 1976.
6. *C. nigripes* (Friese, 1899). Argentina. Córdoba. Copina. Nov. 1983. Córdoba. Río Primero. Nov. 1987. Leg. Cocucci
7. *C. parvus* Roig-Alsina, 1997. Argentina. Córdoba, San Roque. Nov. 1983. Leg. Cocucci.
8. *C. rasmusseni* Roig-Alsina, 1999. Perú. Huánuco. Apr. 1983. Leg. Molau.
9. *C. rufipes* Roig-Alsina, 1999. Argentina. Tucumán. Tafí del Valle. Febr. 1988. Leg. Cocucci & Sérsic.
10. *C. vogeli* Roig-Alsina, 1999. Argentina. Tucumán. Tafí del Valle. Dec. 1989. Leg. Cocucci & Sérsic.

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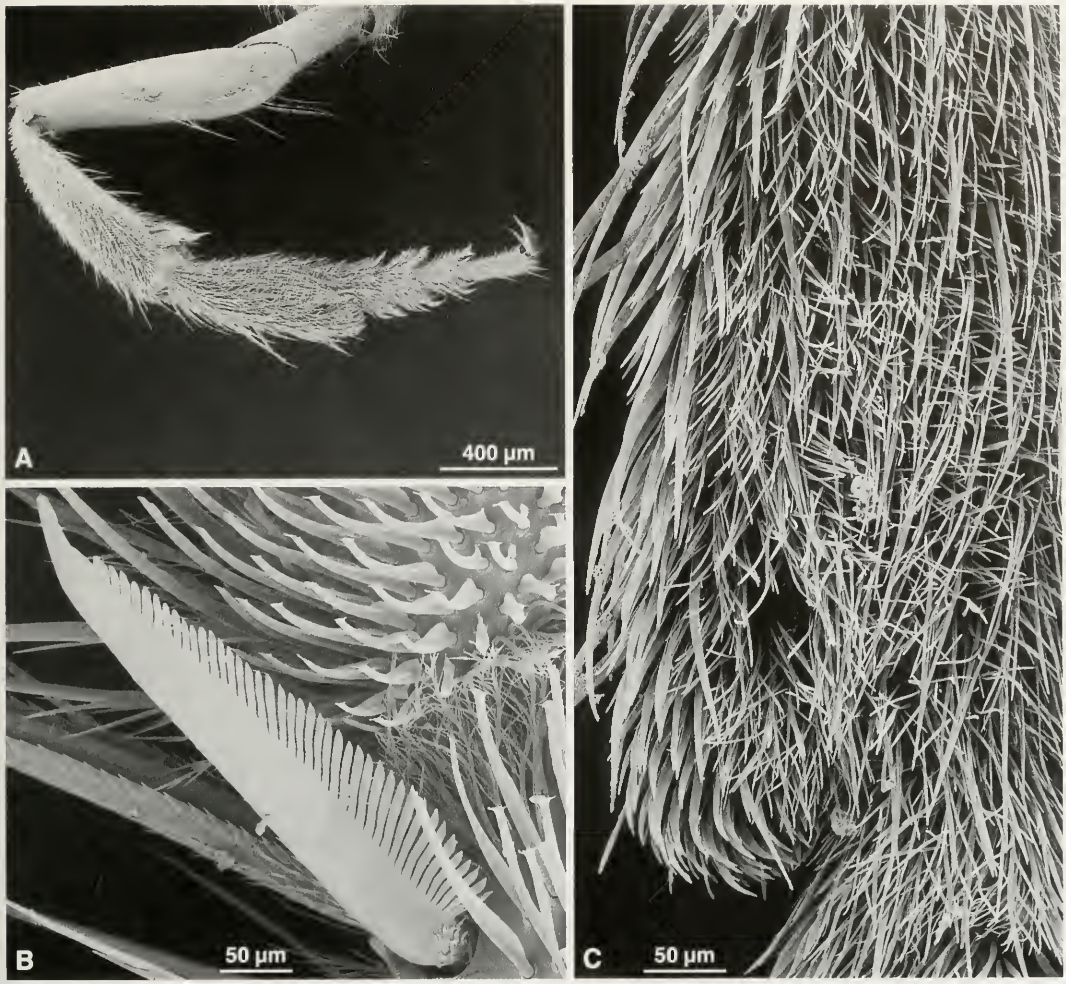

Fig. 4: *Chalepogenus parvus*. **A:** posterior view of left foreleg. **B:** detail of oil-collector of the same leg. **C:** spurs on left hind leg.

Caenonomada (1)
11. *C. brunerii* Ashmead, 1899. Argentina. Corrientes, Perichón, Mar. 1995. Leg. Cocucci.

Lanthanomelissa (5)
12. *L. discrepans* Holmberg, 1903. Argentina. Córdoba. Copina. Dec. 1987. Leg. Cocucci & Sérsic.
13. *L. betinae* Urban, 1995. Brasil. Parana. Curitiba. Leg. Bustos-Singer.

Monoeca (6)
14. *M. schrottkyi* Friese, 1902. Brazil. Parana. Manançias da Serra. nov. 1966.

Tapinotaspis (2)
15. *T. chalybaea* (Friese, 1899). Argentina. Córdoba. El Cóndor. Jan. 1988. Leg. Cocucci & Sérsic.
16. *T. latitarsis* (*Friese*, 1899). Argentina. Buenos Aires. Punta Lara.

Tapinotaspoides (4)
17. *T. tucumana* (*Vachal*, 1904). Argentina. Tucumán.

Study of the fine structure of the oil-collecting organs was carried out with a Scanning Electron Microscope (SEM), Cambridge Stereoscan Mark II. Cleaning of the specimens was performed according to the method developed by Neff & Simpson (1981) especially for oil-collecting structures. Each entire pinned specimen

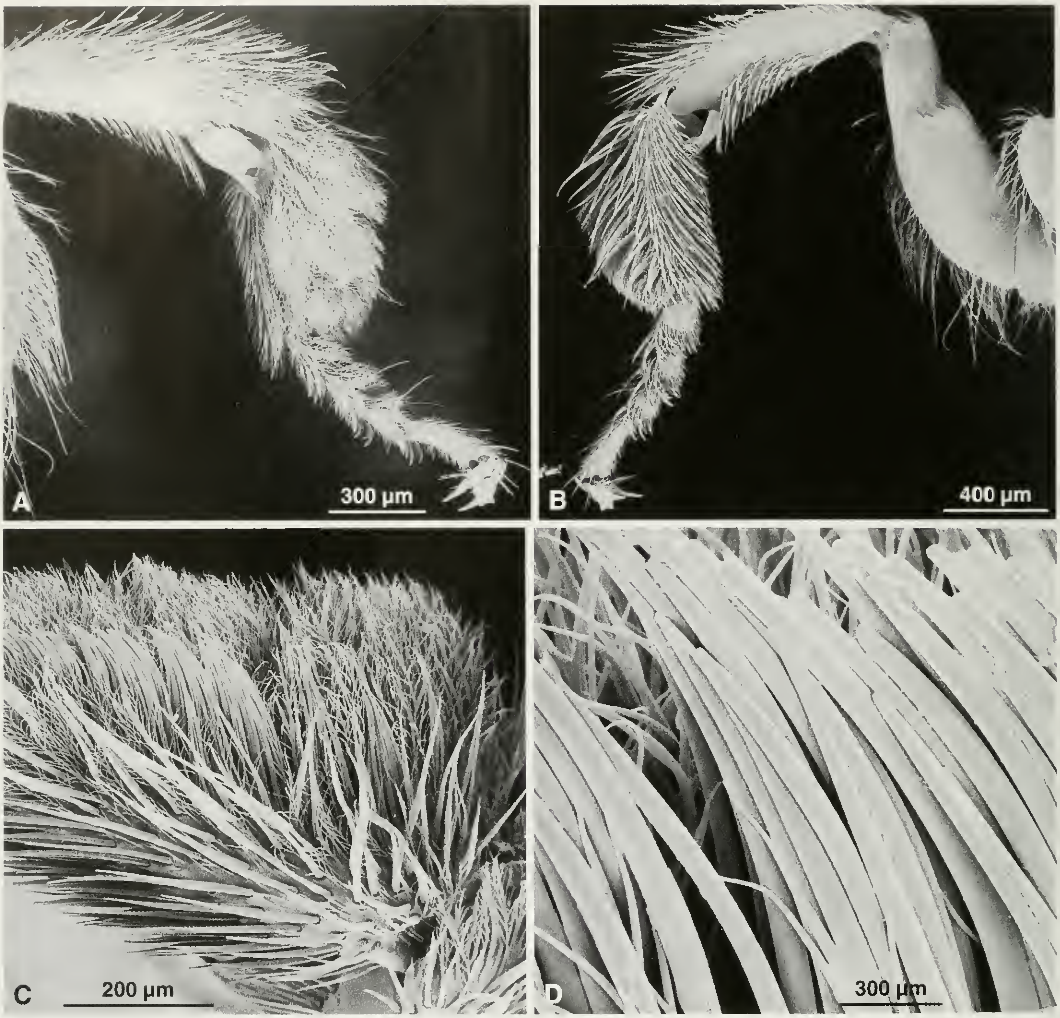

Fig. 5: *Chalepogenus vogeli.* **A:** oil-collector on the posterior surface of right foreleg. **B:** stiff and unbranched setae on anterior surface of the same leg. **C:** detail of different types of setae on the oil-collector. **D:** detail of C.

was soaked in the solvent series given by Neff & Simpson (1981) and sonicated. After drying at room temperature the legs were removed and mounted with nail enamel on metal SEM stubs. The mounted specimens were coated with gold.

The length relations of the leg segments were analyzed in *Chalepogenus caeruleus, Ch. luciane, Ch. nigripes, Ch. parvus, Ch. rufipes, Ch. vogeli, Tapinotaspis chalybaea,* and *Tapinotaspoides tucumana.* For one individual of each species the legs of one side were removed and soaked in EtOH 95 %, cleared with diluted chlorine, dehydrated in a graded series (50, 95, 100 % EtOH, xylene), and mounted in balsam. Measurements were made on drawings obtained with a camera lucida. To make the measurements comparable, lengths of the legs and leg segments are standardized by expressing them as percent of the intertegular distance.

We adopted the descriptive terminology proposed by Neff & Simpson (1981), according to which the legs are imagined to be extended at right angles to the body. It is thus possible to identify anterior, posterior, dorsal and ventral surfaces.

The cladogram in Fig. 15 was constructed by hand on the assumption that *Chalepogenus* is monophyletic (Roig-Alsina 1997), and taking into account the nested sets of apomorphies listed by Roig-Alsina (1999) for the several species groups of *Chalepogenus.*

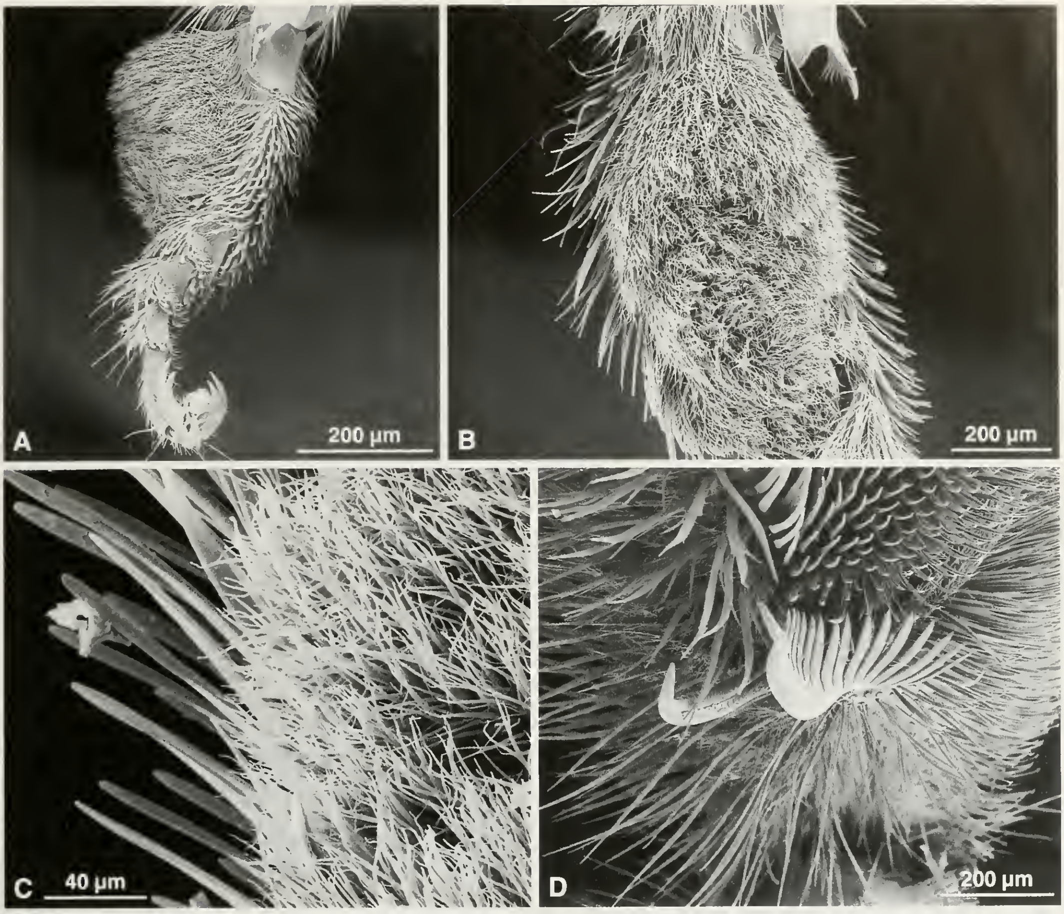

Fig. 6: *Chalepogenus rufipes*. **A:** ventral view of left foretarsus. **B:** posterior view of the same leg. **C:** detail of B. **D:** spurs of left hind leg.

Results

Oil-collectors and oil-collection

Chalepogenus

Location and structure of the oil-collector. The oil-collecting structure is situated mainly on the forebasitarsus, but it may extend to the meditarsus, particularly in *Ch. luciane* (Fig. 1 A) and *Ch. rasmusseni* (Fig. 2 A & D). Most species of *Chalepogenus* have in addition a small area with fine branched hairs on the apex of the tibia, contiguous with the foretarsal pad; this area is notably extended in *Ch. caeruleus* to nearly half of the length of the tibia (Fig. 3 A). The meditarsus is covered, at least on the two proximal segments, with fine branched hairs (Fig. 1 A, 2 A & D, 3 A, 5 A & B, 8 A). The oil-collector is normally located on the posterior surface of the forebasitarsus, but it is slightly rotated to a dorsal position in *Ch. rasmusseni* (Fig. 2 A & B), and *Ch. vogeli* (Fig. 5 A & B).

The pad consists, in the middle of the absorbing surface, of densely set, woolly, slender, flexible, branched setae. This pad is fringed in a comb-like fashion along the dorsal margin by rows of longer, relatively stiff and unbranched setae. The comb and the pad agree in structure and position with the compound comb found in species of *Arhysoceble*, *Trigonopedia* and *Paratetrapedia* (Neff & Simpson 1981, Vogel & Cocucci 1995).

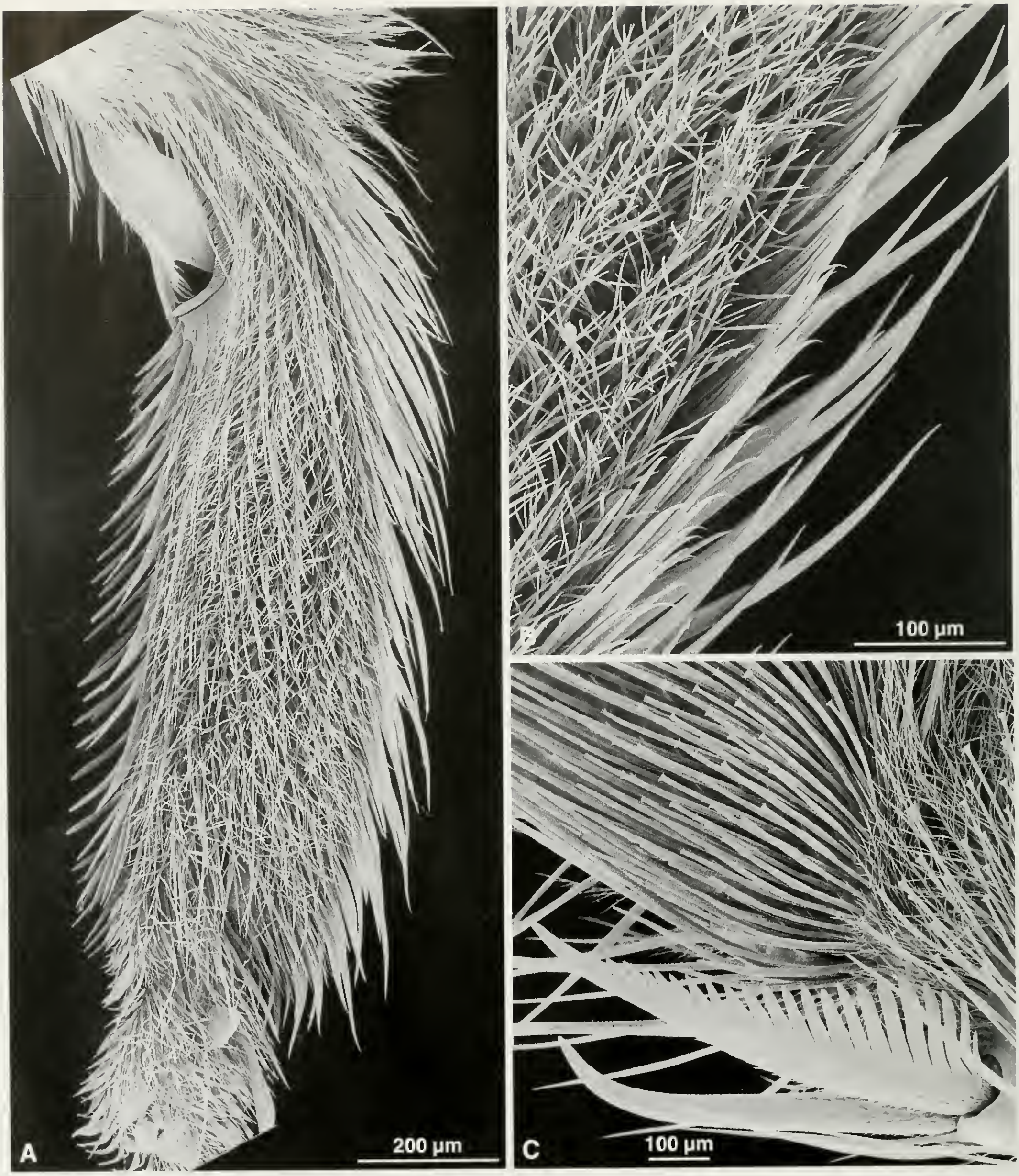

Fig. 7: *Chalepogenus nigripes*. **A:** oil-collector on the posterior surface of the right forebasitarsus. **B:** posterior margin of the oil-collector on the left leg. **C:** spurs of left hind leg.

Fig. 8: *Chalepogenus herbsti*: **A:** oil-collector on the posterior surface of the foreleg. **B:** detail of the oil-collector. **C:** basitarsus of left midleg. **D:** spurs of left hind leg.

▷


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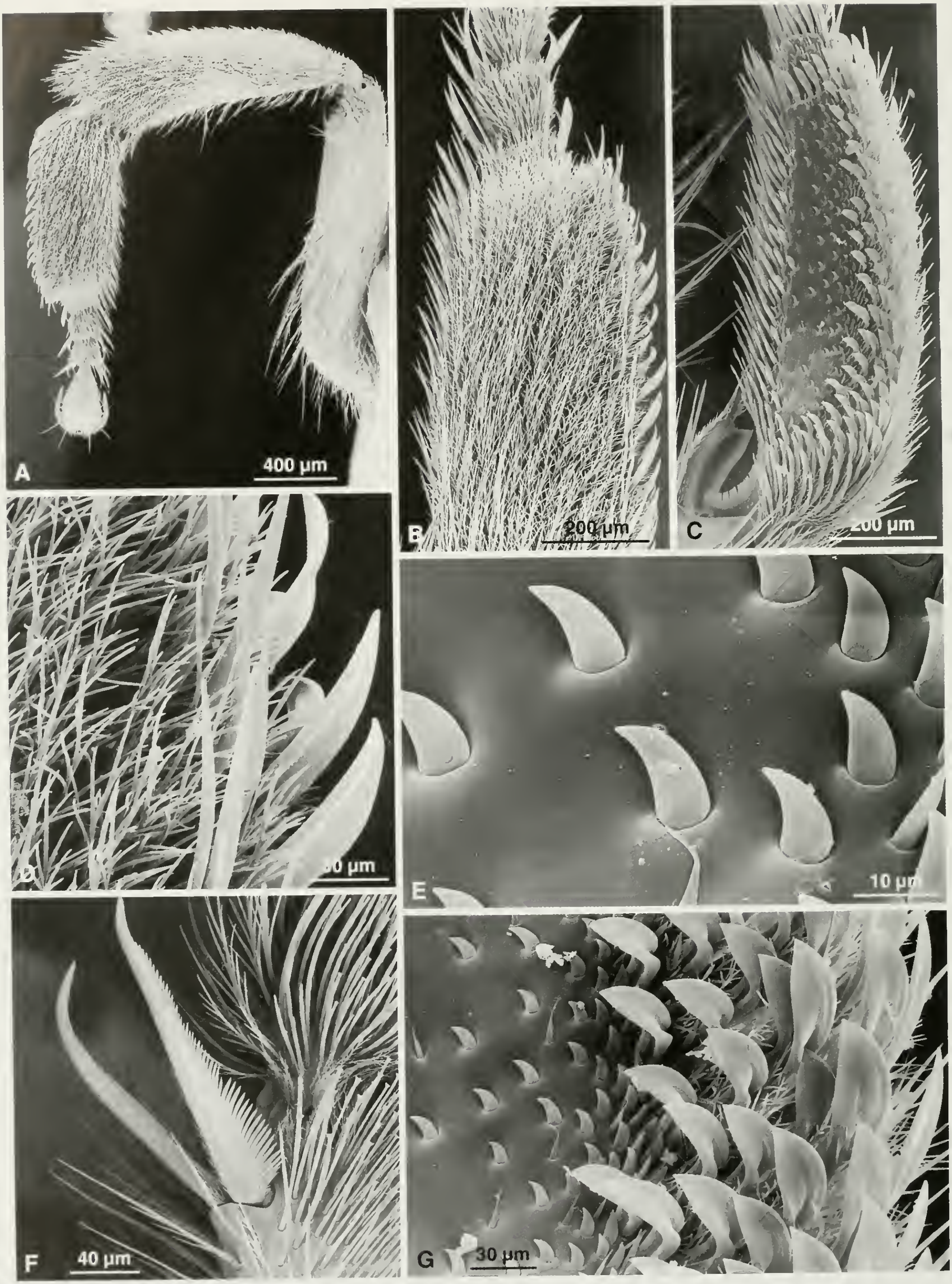


Fig. 9: A, B, D, F: *Lanthanomelissa discrepans*. A: oil-collector on the posterior surface of left foreleg. B and D: detail of oil-collector on the basitarsus. F: spurs of left hind leg. C, E, G: *L. betinae*. C: anterior view of oil-collector. E: detail of short hairs in C. G: margin of the oil-collector.

On this main pattern, the structure of the oil-collecting pads of *Chalepogenus* shows interspecific variation. Two kinds of pads can be distinguished. The pads of *Ch. rasmusseni*, *Ch. rufipes*, and *Ch. vogeli* are strongly protuberant from the forebasitarsus either at their distal end *(Ch. rasmusseni)* or at their proximal end *(Ch. rufipes* and *Ch. vogeli)*. Their absorbing surface is roughly circular or drop shaped and fringed by several series of stout and closely appressed unbranched setae (Figs. 2 A-C, 6 B-C and 5 C-D, respectively). The fringing setae are especially well developed on the dorsal margin of the pad. This margin is oriented to the front of the bee when the front legs are flexed to collect oils.

In the remaining species *(Ch. caeruleus, Ch. cocuccii, Ch. herbsti, Ch. luciane, Ch. nigripes,* and *Ch. parvus)* the pad is not bulging (Figs. 1 A, 3 A, 4 A, 7 A and 8 A). In posterior view, its elongate absorbing surface has a roughly rectangular shape covering the whole basitarsus (Fig. 7 A). The dorsal fringe of stout unbranched setae is formed by a single or few rows of closely set setae. Other unbranched setae do not form dense rows. Most species of *Chalepogenus* have on the lateral margins of the front meditarsus rows of flattened, apically curved setae. In *Ch. rasmusseni* these are markedly larger on the posterior margin (Figs. 2 A & D). In some species, notably in *Ch. luciane* and *Ch. rasmusseni*, also each meditarsus segment is apically fringed by these setae on the anterior surface, forming what could be a scraping structure (Figs. 1 A and 2 B).

Ch. parvus is particular in having a clump of unbranched setae projecting distally on the dorsal margin of the forebasitarsus (Fig. 4 A & B).

Taking into account the nature and extension of the pad and the degree of development of the comb on the dorsal margin of the basitarsus, several types of oil-collecting apparatus can be distinguished:

1. Compound comb, consisting of a row of simple, flattened setae, clearly differentiated on the dorsal margin; pad not bulging, weak on meditarsus (*Ch. muelleri*)
2. Compound comb on dorsal margin poorly differentiated; pad not bulging and well developed on the posterior margin of the basitarsus,
    - 2.1. Pad well developed on the meditarsus and present on the apex of the tibia (*Ch. cocuccii, Ch. herbsti, Ch. luciane* and *Ch. nigripes*, Figs. 1, 7 A & B and 8 A & B)
    - 2.2. Pad very dense on the basitarsus and well extended over distal tibia and meditarsus (*Ch. caeruleus*, Fig. 3)
    - 2.3. Pad restricted to basitarsus (*Ch. parvus*, Fig. 4 A & B)
3. Compound comb not differentiated, setae on dorsal margin as long as those of anterior surface; pad of basitarsus extremely dense, bulging (*Ch. rasmusseni, Ch. rufipes, Ch. vogeli*, Figs. 2 A-C, 5 and 6 A-C)

Associated structures of the mid- and hind legs. No oil-collecting structures are found on the midbasitarsi. On the midbasitarsi there is a ventral brush-like structure next to the well developed midtibial spur (Fig. 8 C). On the midtibiae and basitarsi fine, branched setae partially cover the posterior surfaces. The latter areas are implicated in oil transfer from the fore to the hind leg (VOGEL 1974).

In the hind tibia the anterior spur (Figs. 4 C, 6 D, 7 C and 8 C & D) is doubly serrate and the posterior one is pectinate and sometimes contorted (e.g. *Ch. rufipes*). The teeth of the pectinate spur may be short as in *Ch. parvus* where they are at most as long as the diameter of the shaft (their length ranging from 20 to 50 μm), or comparatively long as in *Ch. rufipes* where they are up to four times as long as the diameter of the shaft (their length ranging from 100 to 200 μm).

Oil-collection. Species of *Chalepogenus* have been observed collecting oils from *Calceolaria* (Scrophulariaceae), *Nierembergia* (Solanaceae) and various Iridaceae *(Cypella, Herbertia,* and *Sisyrinchium)* (see Table I and Fig. 15). For oil-collection on a horizontal surface, the legs have to be flexed inward and rotated to the front. The effective motion of oil-collection is towards the body. The oil-collected is transferred ipsilaterally to the middle leg and from the middle leg to the hind leg. This action is performed while the bee sits on the flower, between intervals of oil-collection or just before leaving the flower. Since *Ch. rasmusseni*, *Ch. rufipes* and *Ch. vogeli* have been found almost exclusively on *Calceolaria*, their oil-collecting structures are probably adapted for collection on this particular plant genus where oil is secreted by very dense and small pads of glandular trichomes (VOGEL 1974; SÉRSIC 1994). The oil-collector of these species, described above as type 3, undoubtedly represents a derived type within *Chalepogenus* (Fig. 15). The secreted oils soak the trichome pad, wetting it completely. During the oil-collection the forelegs reach the gland, and by touching it rhythmically the oil is mopped up by capillarity, as was already described by VOGEL (1974) for *Ch. caeruleus*. The other species *(Ch. parvus, Ch. nigripes, Ch. cocuccii* and *Ch. luciane)* rhythmically sweep out the oil from the elaiophore surface.

Lanthanomelissa

Location and structure of the oil-collector. The oil-collector is located on the forebasitarsus. Its anterior surface is concave with a rectangular outline (Fig. 9 C). The dorsal third of this surface, and also the base and apex, have several (4-5) series of simple flattened setae hooked inwards (Fig. 9 C & G). The centre of this surface is nearly bare, bearing only some very short, simple and stout hairs (Fig. 9 C, E & G). A similar, but smaller surface with short setae is located on the apical portion of the adjacent meditarsus (Fig. 9 C). The posterior surface of the basitarsus bears a relatively dense cushion of branched hairs partially covered by long simple and slender setae (Fig. 9 A, B & D). The surface of fine branched setae extends to the apical part of the foretibia (Fig. 9 A). The cushion of branched setae resembles the oil-collecting pad present in other genera.

Associated structures of the mid- and hind legs. The midlegs have no oil-collecting structures, but branched setae are particularly dense on the posterior surface of the tibia. A pectinate and apically curved spur is well developed on the midtibia. On the hind legs the posterior (inner) tibial spur is pectinate with short teeth about as long as the shaft. The anterior (outer) hind tibial spur is not pectinate but is curved at the apex (Fig. 9 F).

Oil-collection. *Lanthanomelissa* so far has been observed collecting oils only from the trichome elaiophores of *Sisyrinchium* (Cocucci & Vogel, unpublished). The concave depression and the specialized area of setae of the basitarsus scrape the oil-bearing surface, while the posterior pad absorbs the collected oil by capillarity. The short, stout hairs of the concave part of the collector probably damage the individual trichome elaiophores. The oil is transferred ipsilaterally to the hind legs after leaving the flower.

Monoeca

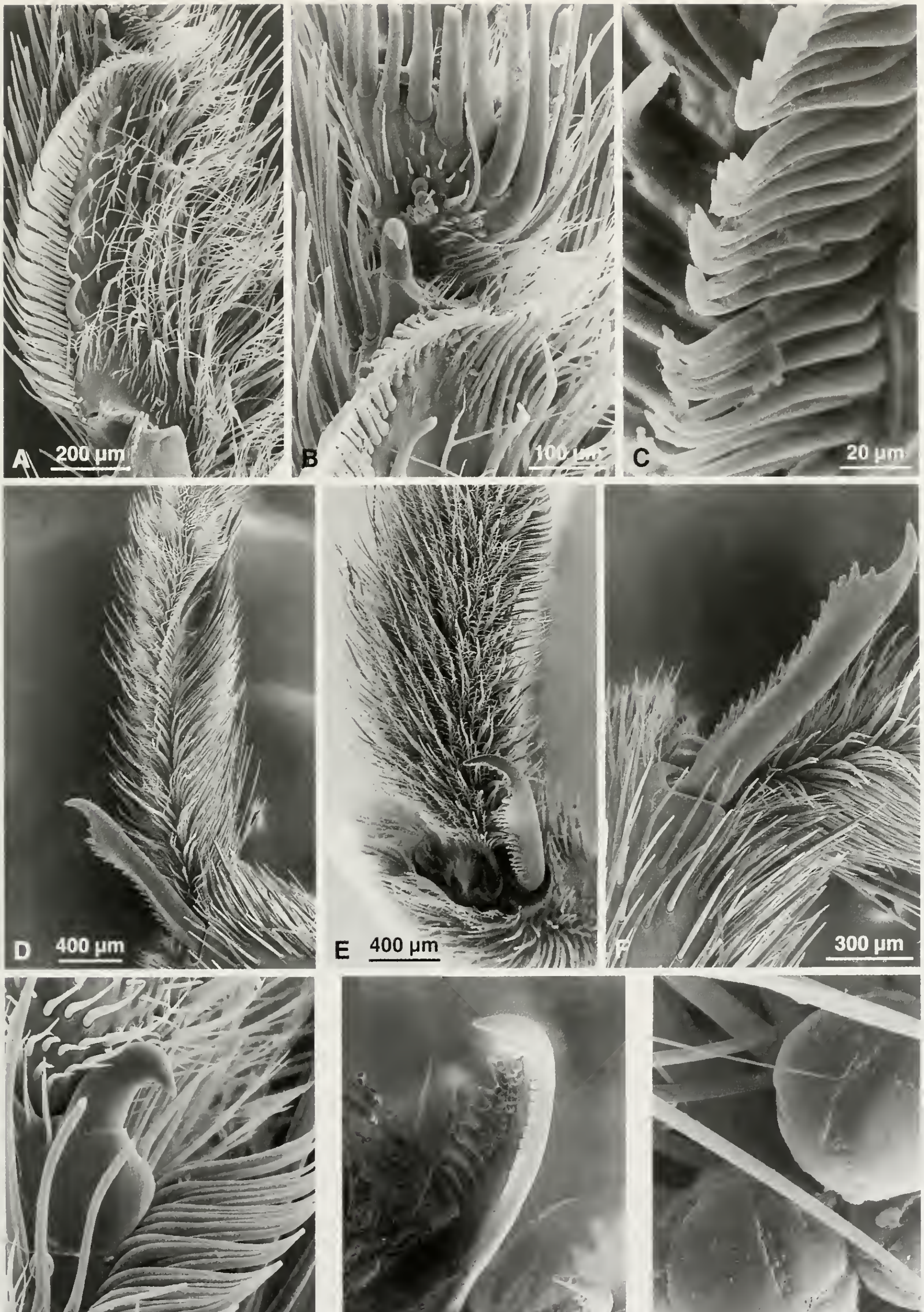
Location and structure of the oil-collectors. The oil-collectors of *Monoeca* are quite different from those of the other members of the tribe, but strikingly similar to those present in *Centris* and *Epicharis* of the tribe Centridini. The oil-collectors are formed by a compound comb that stretches over the ventral margin of the fore and midbasitarsi (Fig. 10 A-D). A detailed description of the collectors has been given by Neff & Simpson (1981). The typical posterior comb, with giant spatulate setae as are characteristic for *Centris* species, is absent on the forelegs of *Monoeca*; in comparable positions there are few little modified setae (Fig. 10 A & B). There is a characteristic large, hooked seta in the distal portion of the forebasitarsus (Fig. 10 A & B), and there are also 3 characteristic curved setae along the posterior side of the compound comb (Fig. 10 A). The first meditarsus shows a distinct comb of setae arranged perpendicular to the main axis of the leg (Fig. 10 B).

The midleg also shows a compound comb located on the ventral margin, but it is especially well developed in the distal part of the basitarsus where it curves posteriorly (Fig. 10 D). A strong, hooked seta is present in the same position as on the foreleg (Fig. 10 D & G). Particularly the antero-dorsal surface of the midbasitarsus is covered with branched setae (Fig. 10 E).

Associated structures of the mid- and hind legs. The midleg spur is well developed and bears a distinct apical hook (Fig. 10). The hind tibial spurs are both doubly serrate. The posterior margin of the posterior spur has longer teeth (Fig. 10 H).

Oil-collection. Species of this genus have never been seen collecting oils. However, the structure and position of the oil-collecting organs suggest that they are associated as are Centridines to Malpighiaceae (Neff & Simpson 1981). Pollen grains of Malpighiaceae (cfr. *Heteropteris*) were found on the hind legs of specimens examined (Fig. 10 I), thus supporting this supposition.

Fig. 10: *Monoeca schrottkyi*. **A:** ventral view of left forebasitarsus. **B:** apical portion of the anterior comb and first meditarsus. **C:** detail of the anterior comb setae. **D:** ventral view of left midbasitarsus. **E:** antero-dorsal view of midbasitarsus. **F:** midtibial spur. **G:** hooked seta of midbasitarsus. **H:** hind tibial spurs. **I:** malpighiaceous pollen grains on a hind leg. ▷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Caenonomada

Location and structure of the oil-collector. The oil-collector, located on the posterior surface of the forebasitarsus, resembles that of *Chalepogenus*. It is composed of a pad of branched, slender setae, which extends to the meditarsus (Fig. 11 A). Several series of stout, flattened and slightly curved setae line the dorsal margin and extend onto the apical dorsal surface of the basitarsus and meditarsus. Since these setae border one margin of the pad, they probably work as scrapers (Fig. 11 A-B).

Associated structures of the mid- and hind legs. Midleg structures are as in *Chalepogenus* (Fig. 11 C & D). The hind leg spurs are similar to those of *Chalepogenus* but with straight shafts (Fig. 11 E).

Metasomal structures. The posterior margins of the metasomal sterna 2, 3, 4 and 5 bear long, branched hairs which form broom-like combs (Fig. G & H).

Oil-collection. The specimen was seen collecting oil on *Cypella gracilis* and pollen of this plant species was recognized on the hind basitarsi (Fig. 11 F). Though the possibility to observe the bees on the flowers was very brief, it could be seen that oil collection is performed with the forelegs by scraping movements. We also suggest that the specialized hairs of the metasoma are involved in the collection of oils, since oil was seen sticking to the tips of the clumped setae (Fig. 11 G-H). However, further observations are needed to confirm if the oil is also actively obtained with these metasomal structures or if it is transferred to this position from other parts of the body.

Tapinotaspis

Location and structure of the oil-collector. Neither combs nor pads are present on the forelegs. Oil-collecting structures are present only on the midlegs. In *T. chalybaea* the midbasitarsi and midmeditarsi are densely covered on the dorsal parts with an unusual kind of long, flattened seta with deeply serrate margins (Fig. 12 A & B). The teeth are alternately curved to opposite sides on the outer margin of each seta (Fig. 12 D & F). In *T. latitarsis*, similar setae densely cover the apical third of the basitarsus, the meditarsus, and also the distotarsus. The setae are shorter and less flattened than in *T. chalybaea* but they have the same pattern of short branches on the external margin curving alternately to one side and the other.

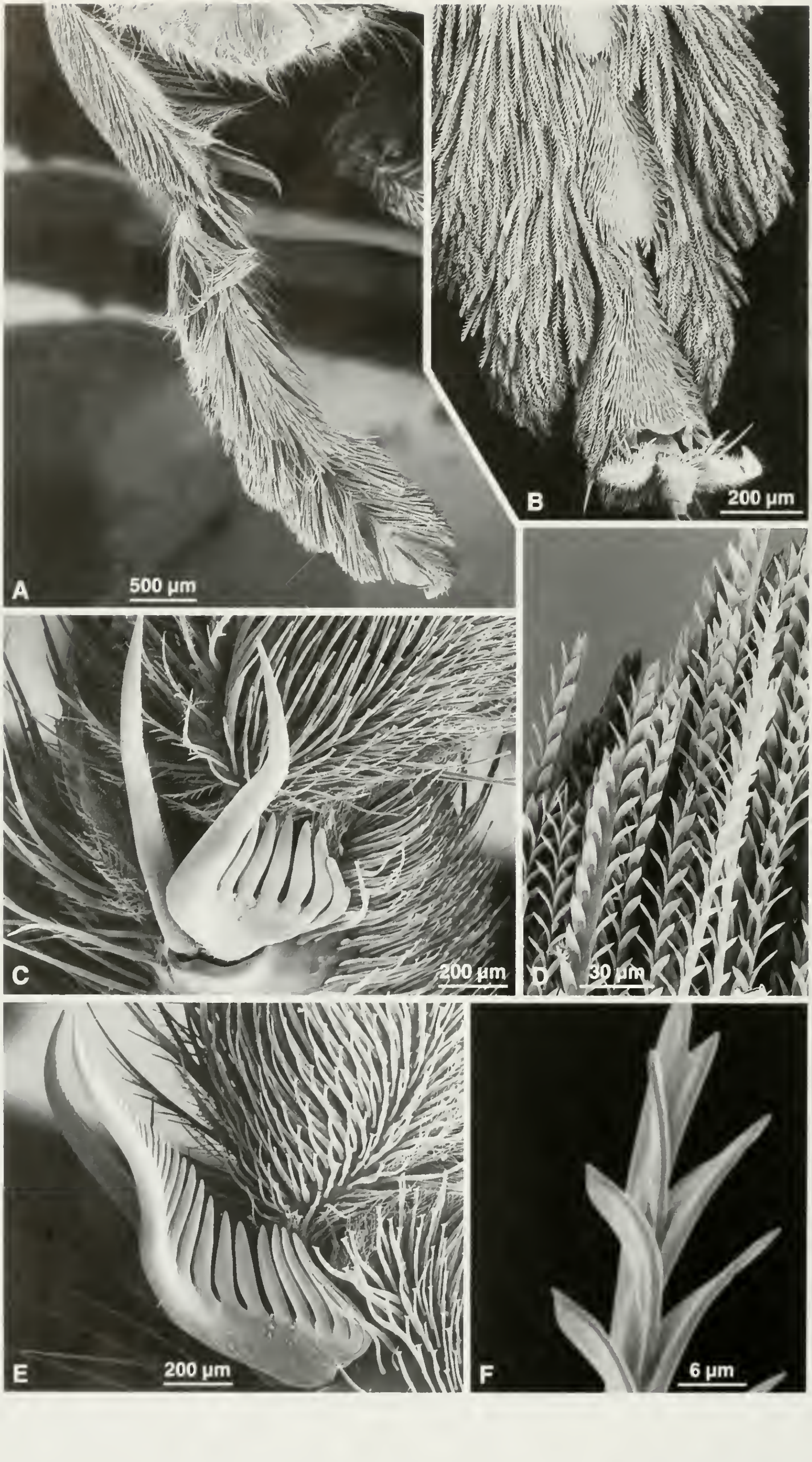
Associated structures of the hind legs. The hind tibial spurs are particularly striking. The anterior (outer) spur (Fig. 12 C) is lined with teeth decreasing in size towards the apex of the spur. The posterior (inner) spur has a strongly sinuate and thick shaft and bears long teeth in its basal section, which are about 1 ½ times longer than the width of the shaft (up to 300 μm long) (Fig. 12 E).

Oil-collection. *Tapinotaspis chalybaea* has been observed collecting oils and pollen only from members of the solanaceous genus *Nierembergia* (Cocucci 1991). The oil-collecting structures and behavior of *T. chalybaea* seem to be particularly well adapted to exploiting oils from at least one species of *Nierembergia* (see table I). *T. chalybaea* lands on the middle of the flattened, spreading, almost circular corolla limb and settles its ventral parts on a central column built by the stamens and the style. The ring-shaped oil-secreting surface on the corolla has the mentioned column at the centre. Trichomes are very sparsely distributed on this surface. The bee lies just above it and sweeps the entire oil surface all around with swinging and alternate movements of the middle legs. Oil is transferred ipsilaterally during the flight after leaving the flower. It has been recorded on film that the oil-soaked middle leg is seized with a scissors-like movement of the spurs of the hind tibia to be squeezed between them.

Tapinotaspis cfr. latitarsis has been observed by one of us (ARA) while collecting oils from *Sisyrinchium platense* (Iridaceae). This bee, half the size of *T. chalybaea*, lands on the flower cup and with the middle legs reaches for the glandular tissue located on the filament column.

Fig. 11: *Caenonomada brunerii*. **A:** posterior view of left forebasitarsus. **B:** detail of A. **C:** proximal ventral surface of the midbasitarsus. **D:** detail of C. **E:** hind tibial spurs. **F:** pollen of Cypella on a hind leg. **G:** metasomal sterna 2, 3 and 4. **H:** detail G. ▷


A
200 µm
B
C
200 µm
D
E
200 µm
F
10 µm
G
300 µm
H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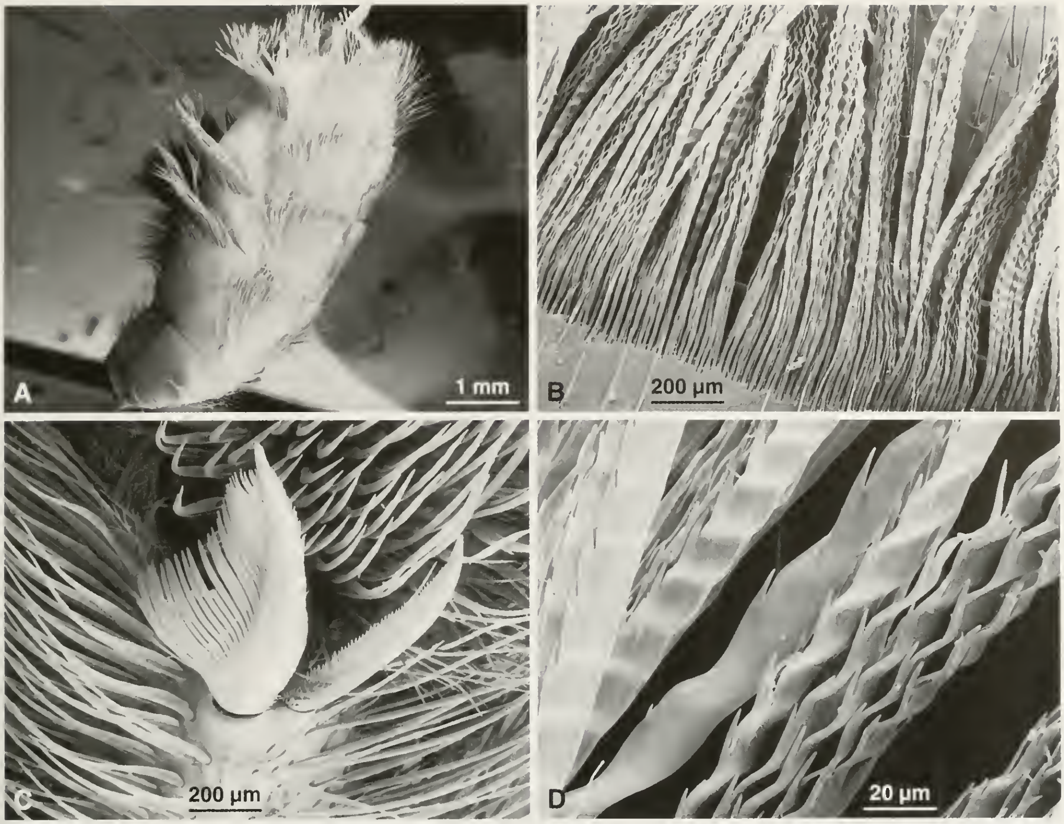

Fig. 13: *Tapinotaspoides tucumana.* **A:** lateral view of metasomal sterna. **B:** detail of one metasomal comb. **C:** spurs of right hind leg. **D:** metasomal setae.

Tapinotaspoides

Location and structure of the oil-collectors. In *Tapinotaspoides tucumana* no obvious oil-collecting structures are present on the legs. Instead, narrow lines of long and specialized setae form broom-like combs on the posterior margins of the metasomal sterna 3, 4 and 5 (Fig. 13 A). The flattened, wavy and serrate sternal setae are up to 1 mm long (Fig. 13 A & B). The teeth of any one seta are situated on the ventral margin and curved to one side (Fig. 13 D). Those setae on the left side of the comb have most setal teeth curved to the left, and those on the right have most setal teeth curved to the right.

In *Tapinotaspis* long setae are present on the metasomal sterna, but they are fine, straight and branched. The same kind of setae is evident in *Tapinotaspoides* at the margin on the sixth metasomal sternum.

Associated structures of the mid- and hind legs. On the midleg branched setae cover the tibia and basitarsus. A particular slender and pectinate tibial spur is present. On the hind leg the anterior (outer) spur is doubly pectinate (Fig. 13 C). The posterior (inner) spur is strongly pectinate with teeth 2-4 times longer than the diameter of the shaft (up to 180 μm long). The shaft is not strongly sinuate as in *Tapinotaspis*. The pattern of specialized hairs of the metasomal sterna is similar in the four species of the genus (Roig-Alsina 1997).

Oil-collection. Oil-collection has not yet been observed for any species of *Tapinotaspoides*. Neff & Simpson (1981) report the presence of masses of a lipoidal substance on the metasoma. Metasomal mopping, as

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Fig. 12: *Tapinotaspis chalybaea.* **A:** dorsal view of left midleg. **B:** ventral view of oil-collector on the meditarsus. **D, F:** setae of the oil-collector. **C, E:** anterior (C) and posterior (E) spurs of left hind leg.

known for *Ctenoplectra* (VOGEL 1990b), may also be the behavior of oil-collection in *Tapinotaspoides*. The bilateral pattern of the tooth arrangement on the serrate setae also suggests that these bees collect oils with wavy movements of the metasoma over the oil secreting surface. An examination of the pollen of one female revealed several pollen types none of which belong to any plant family known to have oil flowers. The pollen found on the body is dominated by a lamiaceous species which most probably belongs to a nectar flower. Other pollen types found were unaperturated *Croton*-like grains, asteraceous, and some undetermined tricolpate and striate pollen grain types.

Table 1: Oil sources of Tapinotaspidini[1].

Oil-collecting bee	Oil sources		Source
Arhysoceble huberi	Scrophulariaceae:	*Angelonia* sp. (illeg.)	VOGEL & MACHADO, 1991
A. melampoda	Iridaceae:	*Herbertia tigridioides*	SCHLINDWEIN, 1995
		Cypella sp.	VOGEL, 1974
		Ennealophus ssp.(=*Sphenostigma*)	
	Solanaceae:	*Nierembergia calycina*	SCHLINDWEIN, 1995
A. sp.	Scrophulariaceae:	*Basistemon spinosus*	VOGEL & COCUCCI, 1995
Caenonomada brunerii	Iridaceae:	*Cypella gracilis*	this work
Ch. caeruleus	Scrophulariaceae:	*Calceolaria crenatifolia*	JANVIER, 1926
		C. filicaulis	SÉRSIC, 1994
		C. integrifolia	VOGEL, 1974
		C. prichardii	
	Iridaceae:	*Sisyrinchium arenarium*	COCUCCI & VOGEL, unpublished
Ch. calceolariae	Iridaceae:	*Ennealophus* sp.	RASMUSSEN, 1999
	Scrophulariaceae:	*Calceolaria* cfr. *pavonii*	
		C. sp.	
Ch. cocuccii	Solanaceae:	*Nierembergia browallioides*	COCUCCI, 1991
		N. linariaefolia	
		N. rigida	
Ch. crassifaciatus	Iridaceae:	* *Sisyrinchium arenarium*	ROIG-ALSINA, 1999
Ch. goeldianus	Iridaceae:	*Sisyrinchium laxum*	COCUCCI & VOGEL, unpublished
	Solanaceae:	*Nierembergia ericoides*	
Ch. herbsti	Iridaceae:	* *Sisyrinchium arenarium*	ROIG-ALSINA, 1999
Ch. luciane	Solanaceae:	*Nierembergia rigida*	COCUCCI, 1991
Ch. muelleri	Iridaceae:	*Cypella herberti*	ROITMAN, com. pers.
		Sisyrinchium spp.	SCHLINDWEIN, 1995
Ch. neffi	Solanaceae:	* *Nierembergia* sp.	ROIG-ALSINA, 1999
Ch. nigripes	Solanaceae:	*Nierembergia linariaefolia*	COCUCCI, 1991
Ch. parvus	Solanaceae:	*Nierembergia aristata*	COCUCCI, 1991
		N. rigida	
Ch. perimelaena	Scrophulariaceae:	*Calceolaria luxurians*	SÉRSIC, 1994
Ch. rasmusseni	Scrophulariaceae:	*Calceolaria tripartita*	MOLAU, 1988 RASMUSSEN, 1999
Ch. roitmani	Iridaceae:	*Cypella herberti*	ROITMAN, pers. com.
		Cypella gracilis	

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[1] Nomenclature adjusted to ROIG-ALSINA (1999) for the Tapinotaspidini, to COCUCCI & HUNZIKER (1993, 1995) for *Nierembergia*, to GOLDBLATT (1990) for the Iridaceae, and to MOLAU (1988) and DESCOLE & BORSINI (1954) for *Calceolaria*. Oil sources for specimens cited by SCHLINDWEIN (1995) as *Lanthanomelissa goeldiana* are not included here since they could be either species of *Chalepogenus* or *Lanthanomelissa*. The asterisk (*) indicates indirect evidence, obtained from collection labels.

Arhysoceble

The oil-collector has been described (under *Paratetrapedia*) by Vogel (1974), Neff & Simpson (1981) and Vogel & Cocucci (1995). The strongly flattened forebasitarsus has a dorsal projection. The dorsal margin bears a comb formed by several lines of short, simple and stiff setae clumped to small, tooth-like groups. The posterior surface of the tarsus is covered with fine, branched setae. The hind tibial spurs are similar to those of *Chalepogenus*: the anterior spur is doubly serrate while the posterior one is pectinate.

Oil sources of *Arhysoceble* have been reviewed by Vogel & Cocucci (1995). *Arhysoceble* collects oil from trichome elaiophores and may exploit illegitimately (without performing pollination) epithelial elaiophores of Malpighiaceae.

Table 1: (continued).

Oil-collecting bee	Oil sources		Source
Ch. rozeni	Scrophulariaceae:	* *Calceolaria thyrsiflora*	Roig-Alsina, 1999
		* *Calceolaria* sp.	
Ch. rufipes	Scrophulariaceae:	*Calceolaria ruiz-pavoni*	Sérsic, 1994
		C. schickendantziana	Vogel, 1974
		C. teucrioides (illeg.)	
		C. umbellata	
Ch. vogeli	Scrophulariaceae:	*Calceolaria argentea*	Molau, 1988
		C. polyclada	Sersic, 1994
		C. ruiz-pavoni	Vogel, 1974
		C. salicifolia	
		C. schickendantziana	
		C. teucrioides (illeg.)	
Ch. sp.	Iridaceae:	*Herbertia pulchella*	Schlindwein, 1995
Ch. sp.	Scrophulariaceae:	*Calceolaria argentea*	Molau, 1988
		C. cajabambae	
		C. pavonii	
		C. rosmarinifolia	
		C. salicifolia	
		C. tripartita	
Lanthanomelissa discrepans	Iridaceae:	*Sisyrinchium chilense*	Cocucci & Vogel, unpublished
		S. laxum	
		S. micranthum	Schlindwein, 1995
		S. pachyrrhizum	Roig-Alsina ,1997
		S. platense	
		S. setaceum	
L. betinae	Iridaceae:	*Sisyrinchium* sp.	Bustos Singer pers. com.
		S. spp.	Cocucci & Vogel, unpublished
L. mageliae	Iridaceae:	*Sisyrinchium setaceum*	Cocucci & Vogel, unpublished
Paratetrapedia bunchosiae	Malpighiaceae:	*Bunchosia gaudichaudiana* (illeg.)	F. Müller (see Vogel, 1974)
P. calcarata	Orchidaceae:	*Ornithocephalus* sp.	Dodson (see Vogel, 1974)
	Melastomataceae:	*Mouriri myrtilloides*[2]	Buchmann & Buchmann, 1981
P. testacea	Orchidaceae:	*Ornithocephalus* sp.	Dressler & Dodson (see Vogel, 1974)
P. sp.	Malpighiaceae:	*Byrsonima* sp.(illeg.)	Vogel, 1974
Tapinotaspis chalybaea	Solanaceae:	*N. linariaefolia*	Cocucci, 1991
T. cfr. *latitarsis*	Iridaceae:	*Sisyrinchium platense*	Roig-Alsina unpublished

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[2] This plant has not been shown to be pollinated by oil-collecting bees (Renner, 1989)

Trichome elaiophores are swept with an effective movement towards the body of the bee. Oil is transferred ipsilaterally before leaving the flower.

Comparison of relative leg segments lengths in *Chalepogenus*, *Tapinotaspis* and *Tapinotaspoides*

Lengths of the legs and leg segments relative to the intertegular distance are given in Fig. 14. The following patterns can be observed:

Both species lacking oil-collectors on the front legs (*Tapinotaspis chalybaea* and *Tapinotaspoides tucumana*) have unique leg length relationships. *T. chalybaea* is the only species studied with midlegs almost as long as the hind legs. In addition, this species has the greatest difference in length between the fore- and midlegs, the latter being 38 % longer than the former. It is also the only species studied with the longest femora being those of the midlegs (21 % longer than the forefemora, and 14 % longer than the hind femora). It is further the only one in which the midbasitarsi are much longer than the basitarsi of the other legs (64 % longer than the forebasitarsi, and 10 % longer than the hind basitarsi). The midmeditarsi are the longest among the species studied, whereas the forebasitarsi – lacking oil-collectors – are the shortest among the species studied. Thus, an increased overall length of the midleg is achieved through relatively elongate femora, basitarsi and meditarsi. Consequently, the oil-collectors of *T. chalybaea*, placed on the midtarsal segments are capable of sweeping an extended elaiophore surface such as that of *Nierembergia*. The increased length of the midfemora facilitates control of the oil-collector`s movements at a distance from the body.

As in the previous species, in *T. tucumana* the midlegs are relatively long, but here the hind legs are even longer, so that there is a great difference between them (18 %). The increased length of the midlegs, especially due to long femora and basitarsi, is presumably needed for the gleaning of harvested oil from the metasomal collector.

Ch. vogeli has the relatively shortest legs (Fig. 14) and is the only species studied where the forebasitarsi are longer than the basitarsi of the other legs (17 % longer than the midbasitarsi, and 5 % longer than the hind basitarsi).

Ch. parvus is exceptional in having the forelegs almost as long as the midlegs, the latter being only 1 % longer.

Ch. nigripes is exceptional in having the femora of the forelegs longer (4 %) than those of the midlegs.

It is also noticeable that *Ch. caeruleus*, *Ch. rufipes* and *Ch. vogeli* are the only species studied in which the midmeditarsi are longer than those of the other legs (38 to 43 % longer than the foremeditarsi, and 8 to 30 % longer than the hind meditarsi). These three species are regular visitors of *Calceolaria* where the bees have to grasp the broad corolla lip by extending the midlegs to reach its margin (Sérsic 1994).

Discussion

According to a recent phylogenetic study (Roig-Alsina & Michener 1993) oil-collecting structures have independently evolved three or four times among the long-tongued bees in the Apidae, Subfamily Apinae: Tetrapediini, Centridini, Tapinotaspidini and Ctenoplectrini; the last two tribes are given as sister groups in some cladograms. Among the short-tongued bees, oil-collecting structures have independently evolved once or twice in the Melittidae, depending on the unstudied relationships of the genus *Rediviva*.

Following this outline it must be assumed that within the Apidae four-legged collectors evolved convergently in the Neotropics: in *Monoeca* (Tapinotaspidini) and in the Centridini. In Melittidae, four-legged collectors are present in the Holarctic genus *Macropis* (Vogel 1986) and probably also in some species of *Rediviva*.

Within the Tapinotaspidini the positions and structures of the oil-collectors are very diverse, including genera with collectors on the forelegs *(Chalepogenus, Lanathanomelissa, Caenonomada, Arhysoceble, Trigonopedia,* and *Paratetrapedia),* on the midlegs *(Tapinotaspis),* on the fore- and midlegs *(Monoeca),* and on the metasoma *(Tapinotaspoides).* The phylogeny within the Tapinotaspidini is only partly resolved (Roig-Alsina 1997). Depending on the outgroup chosen, two sets of genera may be considered alternatively as more basal: *Arhysoceble* and *Chalepogenus* on the one hand, and *Tapinotaspis*, *Caenonomada* and *Tapinotaspoides* on the other. The first alternative unambiguously supports the origin of the oil-collecting habit via oil-collectors on the front basitarsus. The second alternative is ambiguous as to whether the front tarsus or the middle tarsus type of oil-collector is ancestral for the tribe. According to Roig-Alsina (1997), among

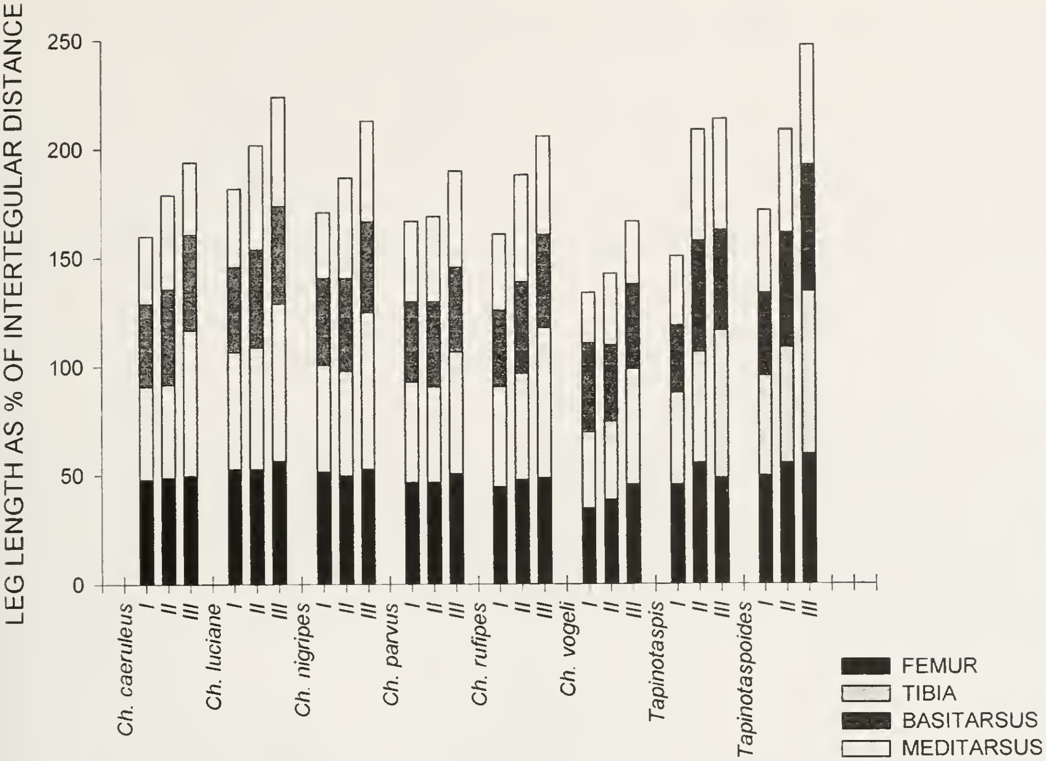

Fig. 14: Comparison of leg segment lengths in species of *Chalepogenus*, *Tapinotaspis* and *Tapinotaspoides*, measured as % of the intertegular distance. I: front leg, II: midleg, III: hind leg.

the several outgroups that he took into consideration, the Emphorini share with the Tapinotaspidini some unique features not present in other bees, making it the most probable sister group. When this outgroup is considered, the genera *Arhysoceble* and *Chalepogenus* are basal in the cladograms, rendering the above mentioned first alternative the most likely scenario for the evolution of the Tapinotaspidini. The presumably most basal Tapinotaspidini *(Arhysoceble* and basal *Chalepogenus)* have Iridaceae as the main oil-sources. *Arhysoceble melampoda* is a generalist as it has the ability to collect oils from various genera of Iridaceae and from the solanaceous genus *Nierembergia* (see table I). Other species of *Arhysoceble* also visit Scrophulariaceae, including *Angelonia*, a plant genus not adapted to these particular bees. Their main oil-sources appear to be Iridaceae of the tribe Tigridieae (sensu GOLDBLATT 1990), including several genera (RAVENNA 1981, 1983, 1986, 1989) which share with *Arhysoceble* a common centre of diversity (MICHENER & MOURE 1957).

The alliance *Monoeca-Trigonopedia-Paratetrapedia* is consistent in any alternative phylogeny. It contains tropical bees reportedly or putatively associated with Malpighiaceae. No actual observations exist on the biology of *Trigonopedia* and *Monoeca*, but Malpighiaceae are the suspected oil-sources of *Monoeca* because of the presence of combs on four legs in concordance with the four oil-gland sets present in the flowers of this plant family (NEFF & SIMPSON 1981). *Paratetrapedia* can exploit the epithelial elaiophores of Malpighiaceae, but in an "illegitimate" way. Instead orchids seem to be their co-adapted partners (VOGEL 1974). The association with Malpighiaceae and Orchidaceae, as well as the particular leg structures of the bees that evolved to collect their oils, represent secondarily derived conditions within the Tapinotaspidini.

While ours are the only observations available on oil sources of *Caenonomada*, they also show a relationship between these oil-collecting bees and the Iridaceae.

Species of the genera *Tapinotaspis, Lanthanomelissa*, and most species of *Chalepogenus* are apparently more specialized with regard to their oil sources than *Arhysoceble*. They seem to be dependent on one or few species of a single plant genus *(Nierembergia, Calceolaria* or *Sisyrinchium)* and rarely forage oils from plants of other families. Exceptions to this pattern are *Ch. caeruleus* and *Ch. calceolariae*. *Lanthanomelissa* has

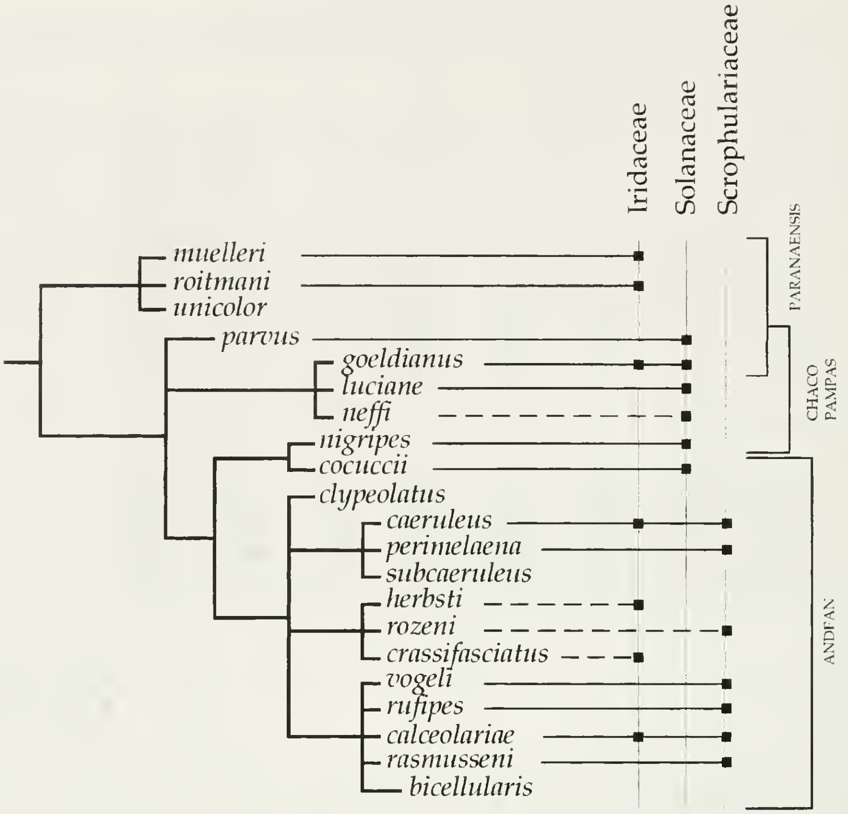

Fig. 15: Phylogenteic relationships among species of *Chalepogenus*, plant families with which they are known to be associated, and geographic distribution. Solid lines indicate direct observations, broken lines indicate indirect evidence obtained from collection labels.

specialized to take oils only from *Sisyrinchium*. According to available data (Cocucci 1991) there is a close co-adaptation between *Tapinotaspis chalybaea* and *Nierembergia* which suggests a dependence of the bee on only one or probably few species of this plant genus.

The association between species of *Chalepogenus* and Scrophulariaceae is a late event in the evolution of the genus (Fig. 15). The species depending only on *Calceolaria (Ch. rasmusseni, Ch. rufipes* and *Ch. vogeli)* have a particular and derived type of oil-collecting structure on the forelegs. Their lack of a compound comb is probably related to the way they obtain oil from the elaiophores. Here, the oil is sucked by capillarity, whereas the other species of *Chalepogenus* scrape it by sweeping the surface of the gland and retaining the collected substances against the compound comb. Those more specialized species also have a subtropical and temperate distribution. Interestingly, *Calceolaria* and *Sisyrinchium* are very probably lineages of subantarctic origin (Goldblatt 1990; Molau 1988; Raven & Axelrod 1974). *Nierembergia* has its centre of distribution in the Paranaensic region (a floristic area shared by Southern Brazil, northeastern Argentina and Uruguay), but its range is linked to the subantarctic flora by a disjunct species *(N. repens)* growing in southern Chile (Cocucci, unpublished). A pattern similar to that of *Nierembergia* is also apparent among the oil-bearing Iridaceae of the tribes Tigridieae and Mariceae. Several oil-bearing species and genera of this group are native to southern Brazil, Uruguay and northeastern Argentina *(Cypella, Cipura, Catila, Onira, Herbertia, Alophia,* and *Trimezia)*, while one species of *Alophia* is shared with Chile.

Biogeographical connections between the Paranaensic region and the southern Andes are evident in the distinctly disjunct distribution of several mostly primitive plant taxa (Rambo 1951, 1954). In the Paranaensic region these taxa represent a pauperized subantarctic flora (Rambo 1951) which suggests an eastward migration. In addition to the above, more modern taxa such as *Nierembergia* and the *Tigridieae* have their centre of distribution in the Paranaensic region and show a migration pattern westward to the Andes. The latter two taxa also have an amphitropical distribution pattern, with some (oil-bearing?) relatives in Mesoamerica and southern North America.

Assuming that among the Tapinotaspidini the oil-based relationships with flowers originated in the Paranaensic region, the bees must have followed the same westward migration pattern as their host plants. Subsequently, more derived Tapinotaspidini could have interacted with flowers of the subantarctic flora, promoting speciation in genera such as *Calceolaria* and *Sisyrinchium*. This scenario is clearly supported by the phylogenetic hypothesis proposed by Roig-Alsina (1999) for the species of *Chalepogenus*. The association of *Chalepogenus* with *Calceolaria* would have allowed the extension of the oil-based bee-flower relationships to southern *(Ch. caeruleus)* and northern *(Ch. rufipes, Ch. rasmusseni* and *Ch. vogeli)* regions of the Andes.

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Zusammenfassung

Die Morphologie der Öl-Kollektoren der Weibchen von 17 Arten, die zu 6 der 9 bekannten Gattungen ölsammelnder Bienen der Tribus Tapinotaspidini gehören, wurde mit dem REM analysiert. Die Öl-Quellen dieser Bienen wurden anhand der Literatur und eigener Beobachtungen revidiert. Die Öl-Kollektoren können an den Vorderbeinen *(Chalepogenus, Caenonomada, Arhysoceble, Paratetrapedia)*, an den Mittelbeinen *(Tapinotaspis)* oder am Metasoma *(Tapinotaspoides)* lokalisiert sein. Die primitivsten und tropischen oder subtropischen Tapinotaspidini *(Arhysoceble)* haben Iridaceen, Scrophulariaceen und Solanaceen als Ölwirte. Eine Art kann Öl auf verschiedenen Planzengattungen sammeln. Die wärmeliebenden subtropischen Bienen der Gattungen *Chalepogenus, Lanthanomelissa* und *Tapinotaspis* haben sich auf bestimmte Ölwirte spezialisiert. In der Regel sammeln sie nur an einer oder wenigen Arten einer einzigen Pflanzengattung *(Calceolaria, Nierembergia* oder *Sisyrinchium). Chalepogenus*-Arten, die nur auf *Calceolaria* Öl sammeln *(Ch. rasmusseni, Ch. rufipes* und *C. vogeli)*, tragen einen besonderen, wahrscheinlich abgeleiteten Öl-Kollektor. Diese Arten besitzen verhältnismäßig längere und kollektorenlose Mittelbeine, die möglicherweise zum Greifen der breiten *Calceolaria*-Unterlippe angepasst sind. Die Öl-Kollektoren tragenden Mittelbeine von *Tapinotaspis*, die wegen einer Verlängerung der Femora, Basitarsi und Meditarsi auch relativ lang sind, stellen möglicherweise eine Adaptation an die ausgedehnten Elaiophoren von *Nierembergia* dar. Die Gattungen *Monoeca, Trigonopedia* und *Paratetrapedia* bilden eine rein tropische Gruppe, die wohl mit Malpighiaceen assoziiert ist. Die Struktur ihrer Öl-Kollektoren ist denjenigen von *Centris* und *Epicharis* aus der Tribus Centridini erstaunlich ähnlich.

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