Apidologie 30 (1999) 67–74

Original article

The corbiculae of bees

Charles D. Michener

Snow Entomological Division, Natural History Museum, and Department of Entomology, The University of Kansas, Lawrence, KS 66045, USA

(Received 6 July 1998; accepted 23 August 1998)

Abstract – The word corbicula is ordinarily used for the 'pollen basket' on the outer side of the hind tibia of worker honey bees and related forms. Unrelated bees have comparable but nonhomologous structures, often on other parts of the body. Such structures are described on the hind femora and on the propodeum, as well as on the hind tibiae of two diverse groups of bees. © Inra/DIB/AGIB/Elsevier, Paris

bees / Apoidea / corbicula / pollen transport / anatomy

1. INTRODUCTION

Most female bees have areas of long, frequently dense hairs, the scopae, for carrying pollen from its floral sources to nests. A scopa can be on the hind legs, on the underside of the metasoma, or even on the sides of the propodeum. There are various types and densities of scopal hairs, presumably related to the characteristics of the pollen to be carried [10]. A common development is a space surrounded by fringes of long scopal hairs. Such a space has been called a corbicula [10] and serves for transport of a large bulk of pollen; it is probably easier to remove pollen from a corbicula than to remove an equal amount of pollen carried within a brush of hairs. The pollen carried in the tibial corbiculae of the corbiculate Apidae, such as *Apis,* is moistened with nectar to form a firm mass or pellet on each hind tibia. In all other corbiculae the pollen is carried dry.

The case can be made for limiting the word corbicula to structures on the hind tibia that carry moistened pollen, because this is the familiar usage of the word. So limited, it is applicable only to the tribes Apini,

* Correspondence and reprints
E-mail: michener@falcon.cc.ukans.edu

Bombini, Euglossini and Meliponini. However, the term corbicula is used in the present broad sense by some authors [3, 10] and in fact a synonymous generic name for *Canephorula,* which carries dry pollen in a tibial corbicula, is *Corbicula.* Clearly various corbiculae are not homologous, any more than a sternal scopa is homologous to a tibial scopa.

One system for describing parts of legs assumes that the legs are pulled out laterally at right angles to the long axis of the body. I here follow the more traditional system in which legs are considered to be in their normal resting positions, the hind femur directed back beside the body of the bee. Thus the corbicula of *Bombus* is on the outer, not the anterior, surface of the hind tibia and the two tibial spurs would be outer and inner, not anterior and posterior.

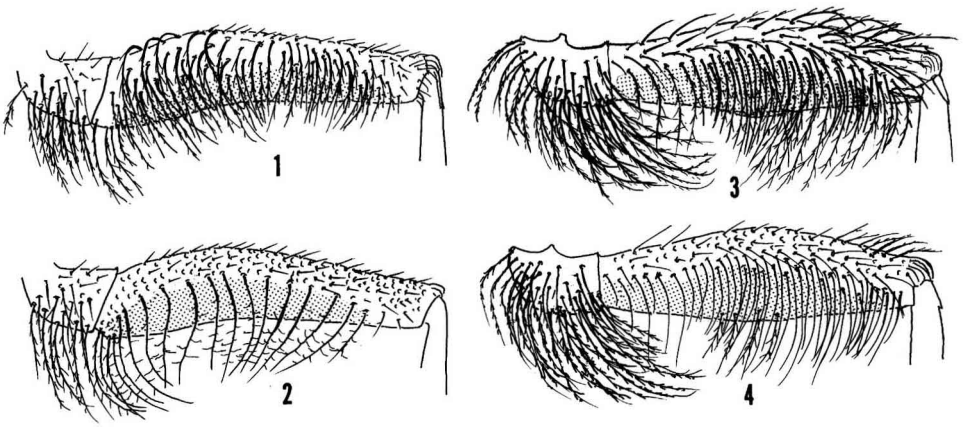
2. FEMORAL CORBICULAE

The most widespread corbicular site is on the underside of the hind femur of many members of the short-tongued bee families Stenotritidae, Colletidae, Andrenidae and Halictidae. While widespread in these families, the femoral corbicula is absent or little developed in the colletid subfamilies Hylaeinae and Euryglossinae, in the andrenid subfamily Panurginae and some small genera of Andreninae, and in the halictid subfamily Rophitinae as well as in parasitic Halictinae. (The higher classification used herein is based on [1] and [8], summarized in [5].) This femoral corbicula is formed by a) a zone of long, frequently plumose hairs that arise on the upper part of the outer surface or even on the upper surface of the femur and curl downward, over the outer femoral surface (*figures 1* and *3*), and b) a band or row of long, sometimes straight hairs that arise on the inner surface, frequently on the lower inner surface, of the femur (*figures 2* and *4*). These are the outer and inner corbicular fringes, respectively. The femoral corbicula is the space between these two zones of long hairs. The femoral surface of the corbicula is typically flattened, hairless, impunctate, often smooth and shining, but sometimes gives rise to a few long hairs or some short hairs. Because the lower surface of the femur is often formed into a strong longitudinal ridge from which the inner corbicular fringe arises, the femoral corbicula is often on the lower outer surface of the femur, rather than on the lower surface in a strict sense. The femoral corbicula is closed basally by basal femoral hairs and principally by the hairs of the trochanter, which are long and curved distad. They are especially well developed in the genus *Andrena* (Andrenidae), in Diphaglossinae (Colletidae), and in Oxaeinae (Andrenidae), where they have been given a special name, the flocculus or floccus (*figures 3* and *4*).

Museum specimens that do not have large pollen loads often have pollen entangled in the corbicular fringes, but not occupying the corbiculae themselves. It is possible that the smooth, hairless or sparsely haired lower femoral surface evolved in some other connection, and not as a pollen-carrying area.

Sometimes the outer and inner corbicular fringes curl until their tips meet and hide or close the corbicula. Such well-developed fringes are found, for example, in the Diphaglossinae and Oxaeinae. On the other hand in some groups, perhaps especially in those *Leioproctus* (Colletinae) with a well-developed sternal scopa, the corbicular fringes are reduced, not being very different from those of long-tongued bees, which are not considered to have a femoral corbicula. Examples are *Leioproctus* subgenera *Hexantheda* and *Cephalocolletes.*

In the halictid genus *Lasioglossum*, subgenus *Sphecodogastra*, the fringes consist of simple hairs and are largely reduced and rather weak. However, the lowermost row of hairs of the outer fringe is isolated by a bare area and consists of long curved bristles. This appears to be an adaptation for the use



Figures 1–4. Femoral corbiculae. **1, 2,** Outer and inner views of posterior trochanter and femur of female *Lasioglossum (Evylaeus) calceatum* (Scopoli). **3, 4,** Same, of *Andrena (Simandrena) pallidifovea* (Viereck). The surfaces of the corbiculae are stippled.

of pollen of Onagraceae which is webbed together by viscin threads.

The short hairs found on hind femora of spheciform wasps (Sphecidae, Crabronidae) are widely distributed and frequently appressed. In some wasps (e.g. *Crabro*), however, the under surface of the hind femur is flattened and shining, with or without short hairs, and the short simple hairs of the outer and inner surfaces are directed downward. The same is true of parasitic bees that do not collect pollen (Nomadinae and Ericrocidini in the Apidae, *Sphecodes* and its relatives in the Halictidae), and of nonparasitic bees that carry pollen in the crop instead of externally (Euryglossinae and Hylaeinae in the Colletidae). In such forms there is no indication of the outer and inner corbicular fringes.

Perhaps only because they are generally more hairy insects, many bees have hind femora that differ from those described in the paragraph above by having longer and often more abundant hairs. The largely bare under surface of the hind femur is therefore better set off from the hairy outer and inner surfaces, the downward-directed hairs of which suggest the corbicular fringes described above. Bees having such femora include the Melittidae (a name here used in the broad sense to include the three related families segregated in [1]) and most nonparasitic long-tongued bees (Megachilidae, Apidae), as well as the short-tongued groups Panurginae (Andrenidae) and Rophitinae (Halictidae). These forms do not carry much pollen on the femora, the tibial scopa being the major pollen-carrying structure. Such femoral structure, however, intergrades with that of most Colletidae, Andrenidae and Halictidae, which (except for the forms mentioned above) have well-developed femoral fringes and corbiculae and appear to carry more pollen on the femora than on the tibiae. The Stenotritidae carry more pollen on the tibiae than the femora, yet have moderately developed although short femoral fringes.

The long-tongued bees, however, are not as uniform as the above comments suggest. For example, in the Megachilidae, *Lithurgus* has long, curved hairs on the outer femoral surface, some of them arising on the upper surface, and many hairs on the inner surface as well. Thus there is an approach to fringes although they do not carry much pollen. The same statements apply to *Cer-*

atina and *Allodape* in the apid subfamily Xylocopinae, but *Xylocopa* in the same subfamily has only short femoral hairs. In these forms, the more or less smooth and largely hairless lower surface of the femur is as in bees with a femoral corbicula. The apid tribes Bombini and Euglossini, however, completely lack femoral fringes and the lower femoral surface or much of it is punctate with short hairs, much like the other surfaces. The tribes Apini and Meliponini have scattered short hairs and no suggestions of fringes or of a femoral corbicula. Thus the corbiculate Apidae differ distinctly from other Apinae.

The absence of a femoral corbicula in Melittidae and long-tongued bees supports the previous conclusion [1] that the short-tongued family Melittidae is ancestral to or the sister group of the long-tongued bees. The well-developed femoral corbicula of most Colletidae, Andrenidae and Halictidae may be a synapomorphy of these groups, lost in parasites and those that transport pollen only in the crop, and reduced in the Panurginae (Andrenidae) and Rophitinae(Halictidae). Thus these three families may constitute a clade derived from or sister to the melittid-long-tongued bee clade. For a fuller discussion of relationships among these groups, see [5].

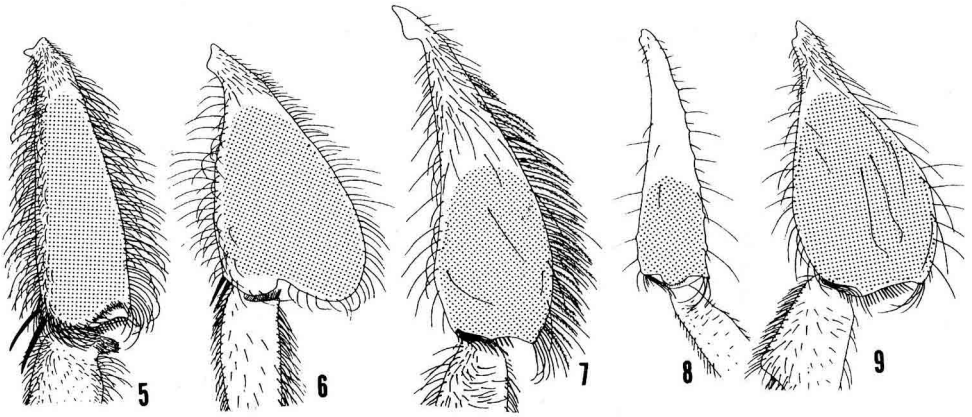
3. PROPODEAL CORBICULAE

A common propodeal hair pattern among females of short-tongued bees includes long, dense, erect hairs projecting laterally from the upper margin of the lateral surface of the propodeum. Below these long hairs the propodeal surface usually bears shorter hairs. All these hairs often carry some pollen. In some Colletinae and Diphaglossinae (Colletidae) and most *Andrena* [3] (Andrenidae), the dorsal zone of long hairs extends posteriorly and downward along the lateral angle, demarking the posterior propodeal surface. Thus there are dorsal and posterior fringes around an area that is usually bare or only sparsely haired and serves as a corbicula. In many species of *Andrena* there is in addition a vertical fringe along the anterior margin of the side of the propodeum. Thus a propodeal corbicula is formed, demarked by dorsal, posterior and anterior fringes (*figure 13*).

4. TIBIAL CORBICULAE: THE CORBICULATE APIDAE

By far the best known corbicula, and the one widely known as the corbicula, is on the outer side of the hind tibia of the Apini, Bombini, Euglossini and Meliponini (Apidae). These are the bees in what was called the apine clade in recent phylogenetic studies [8]; this is not the apine line of Silveira [9]. The suggestion has been made, by Dr Rudolf Jander and simultaneously by others, that instead of being called representatives of the apine clade, the tribes listed above should be called the corbiculate Apidae. I believe that this is a useful term even though, as described below, at least one species of Eucerini (also in the Apidae) also has tibial corbiculae. The family name Apidae has been applied to the group of four corbiculate tribes alone [4], but this usage is inappropriate as shown by the phylogenetic studies cited above.

Michener [4] illustrated the tibial corbiculae of the four tribes of corbiculate Apidae. Modified versions of some of those illustrations are shown in *figures 5–9*. These tibial corbiculae serve not only to transport masses of moistened pollen, but also of resin, wax, mud, feces, etc. The fringes (anterior and posterior or if the tibia is extended horizontally, then upper and lower) and the distinctive flat or concave and usually smooth corbicular surface are lost in parasitic genera or subgenera and in robber genera (*Lestrimelitta, Cleptotrigona*) and are weakened in the necrophagous species of *Trigona* that do not visit flowers or collect pollen.



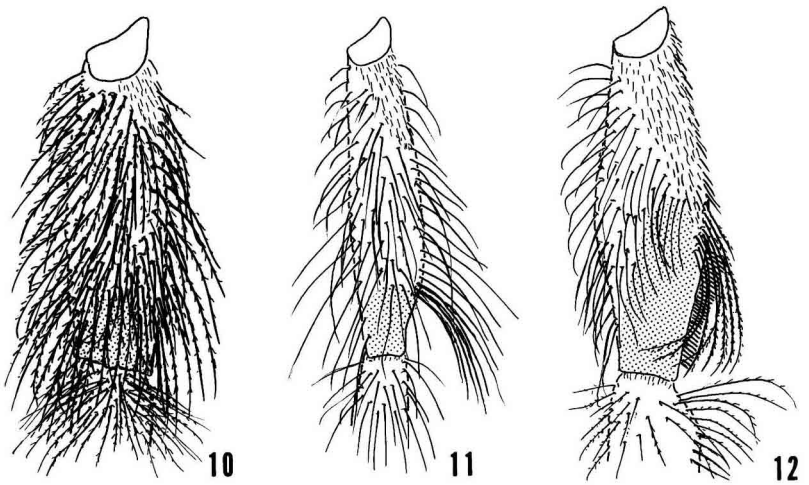
Figures 5–9. Tibial corbiculae of corbiculate Apidae; outer views of posterior tibiae of female (**6**) or workers. **5,** *Bombus pennsylvanicus* (Degeer). **6,** *Euglossa imperialis* Cockerell. **7,** *Trigona (Trigona) amalthea* (Olivier). **8,** *Trigonisca longitarsis* (Ducke). **9,** *Partamona bilineata* (Say). Surfaces of the corbiculae are stippled. The basal limits of these corbiculae are often indefinite and are shown arbitrarily. (Modified from [4].)

The tibial corbicular fringes of Apini and Bombini are made up of hairs that project more or less laterally and thus delimit the corbicula. In Euglossini and many Meliponini, however, the hairs of the posterior fringe project posteriorly, thus expanding but not enclosing the corbicular area. As shown in *figures 6* and *7*, the hairs of the fringes can be remarkably sparse. In *Partamona* (*figure 9*) the tibia is greatly broadened so that the corbicula is large in spite of the sparse fringes. In *Trigonisca* (*figure 8*), however, the tibia is slender and the hairs so sparse that no corbicula would be recognized except for the presence of a firm pollen mass on each hind tibia.

5. TIBIAL CORBICULAE: THE EUCERINI

The only other bees with tibial corbiculae, in this case for carrying dry pollen, are in the tribe Eucerini (family Apidae). In this tribe, the outer surface of the hind tibia of the female normally ends in a small impunctate hairless area (*figure 10*). So far as I know, it has no corbicular function, although when the bee is carrying a large pollen load this area is probably filled. An Argentine species, *Canephorula apiformis* (Friese), has distinct tibial corbiculae, however. It was placed in its own tribe, the Canephorulini, in 1955 [6], but in a recent phylogenetic study [8], it came out among the Eucerini, or more particularly, in the subtribe Eucerina. It has certain characters, such as the simple rather than doubly arched gradulus of S2 of the female, that are probably plesiomorphic relative to other Eucerina. A more detailed study of the Eucerina may show *Canephorula* to be the sister group of the other Eucerina, possibly to be called a subtribe of its own, the Canephorulina. Its most remarkable feature, the hind tibia with a corbicula margined posteriorly by a single row of coarse bristles and a tuft of long plumose hairs, is shown in *figure 12* (see also illustration by Friese [2]). The anterior fringe consists of long hairs that curve over and partly hide the corbicula.

A second Argentine eucerine with a suggestion of a corbicula is the recently described *Hamatothrix silvae* Urban. It lacks



Figures 10–12. Corbicula-like structures of eucerine bees; outer views of posterior tibiae and bases of basitarsi of females. **10,** *Gaesischia (Dasyhalonia) mimetica* (Brèthes), showing the small smooth hairless area (stippled) found in most Eucerini. **11,** *Hamatothrix silvai* Urban. **12,** *Canephorula apiformis* (Friese). Surfaces of corbiculae or corbicula-like structures are stippled.

the unusual, possibly plesiomorphic characters of *Canephorula*, and is thus a more ordinary eucerine, close to the genus *Gaesischia*. The possible corbicula (*figure 11*) is small, scarcely larger than th7 bare space found in most Eucerini (*figure 10*). The clump of strong bristles on its posterior margin basally suggests the plumose hairs of *Canephorula*. If the comblike row of bristles and long hairs of *Canephorula* comb pollen into the corbicula, the similarly positioned long hairs or bristles of *Hamatothrix* probably have the same function.

6. CONCLUSIONS

Large spaces surrounded by scopal hairs of bees have arisen at least once in the short-tongued families (femoral corbiculae, *figures 1–4*), once in the Andrenidae (propodeal corbiculae, *figure 13*), once in the corbiculate Apidae (tibial corbiculae, *figures 5–9*), and once in the Eucerini (tibial corbiculae of *Canephorula*, *figure 12*). Studies of how the corbiculae are loaded and emptied would be of much interest; such studies have been made for the Apini and at least started for

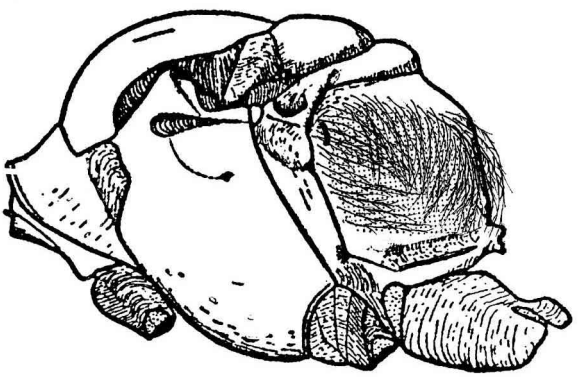


Figure 13. Lateral view of thorax of *Andrena*, pubescence omitted except for the side of the propodeum where the hairs forming the propodeal corbicula are shown, based on *A. pallidifovea* Viereck, female. The surface of the corbicula is stippled.

other corbiculate Apidae [7]. For other types of corbiculae, no such information exists and indeed their importance in pollen transport is not verified.

Résumé – Les corbicules des abeilles. Les corbicules, qui servent à transporter le pollen et d'autres matériaux au nid, désignent l'espace qu'entourent les franges des longs poils de la brosse à pollen. Elles sont bien connues sur les tarses des pattes postérieures chez les Euglossini et les Bombini (bourdons), ainsi que chez les ouvrières des Apini (abeilles mellifères) et des Meliponini (abeilles sans dard), c'est-à-dire chez les Apidae à corbicules. Par contre il n'est généralement pas reconnu qu'elles existent aussi sur la partie inférieure des fémurs des pattes postérieures des femelles de la plupart des abeilles à langue courte, sur les côtés du propodeum (premier segment abdominal en avant du pétiole) de nombreuses espèces d'andrènes (*Andrena* sp.) et sur les tibias des pattes postérieures d'au moins une espèce de la tribu des Eucerini. Sur les figures les parties en pointillés représentent la surface de l'intérieur des corbicules. La corbicule fémorale représente le type le plus courant et peut être une synapomorphie des Andrenidae, des Colletidae et des Halictidae, qui unit ces familles en un clade provenant d'une abeille ancestrale; de même la corbicule du tibia est une synapomorphie unissant en un clade les quatre tribus des Apidae à corbicules. © Inra/DIB/AGIB/ Elsevier, Paris

Apoidea / abeille / corbicule / transport de pollen / anatomie

Zusammenfassung – Die Körbchen bei Bienen. Die Körbchen der Bienen zum Transport von Pollen und anderem Material zum Nest sind Bereiche am letzten Beinpaar, die von langen, mit Fransen versehenen Haaren umrandet sind. Allgemein bekannt sind die Körbchen an den Tibien der Hinterbeine. Diese kommen bei den Euglossini (Prachtbienen) und Bombini (Hummeln), sowie bei den Arbeiterinnen der Apini (Honigbienen) und Meliponini (stachellosen Bienen) vor, also bei den corbiculaten Apidae. Weniger bekannt ist dagegen, daß sich Körbchen bei Weibchen der meisten kurzrüsseligen Bienen auch an der Unterseite des hinteren Femur, bei vielen Andrenaarten (Sandbienen) an den Seiten des Propodeum am Thorax und bei mindestens einer Art der Gattung Eucerini (Langhornbienen) an der hinteren Tibia befinden. Die punktierten Bereiche auf den Bildern zeigen jeweils die Oberfläche innerhalb der Körbchen. Das Körbchen am Femur ist der häufigste Typ und ist möglicherweise eine Synapomorphie von Andrenidae (Sandbienen), Colletidae (Seidenbienen) und Halictidae (Schmalbienen), die diese Familien zu einem Zweig mit gemeinsamer Abstammung von einer Urbiene zusammenfaßt. Entsprechend ist das Körbchen an den Tibien eine Synapomorphie, die die vier Stämme der corbiculaten Apidae zu einem anderen Zweig vereint. © Inra/DIB/AGIB/ Elsevier, Paris

Bienen / Apoidea / Körbchen / Pollentransport / Anatomie

REFERENCES

[1] Alexander B.A., Michener,C.D., Phylogenetic studies of the families of short–tongued bees, Univ. Kansas Sci. Bull. 55 (1995) 377–424.

[2] Friese H., *Canephorula apiformis* Friese (Hym.), eine Bienen-Art mit dem Beginne der Körbchen-Bildung aus Argentinien, Zool. Jahrb., Abt. Syst., Geogr. Biol. Tiere 43 (1920) 461–470.

[3] Lanham U.N., A subgeneric classification of the New World bees of the genus *Andrena*, Univ. California Publ. Entomol. 8 (1949) i–iv + 183–237.

[4] Michener C.D., Classification of the Apidae, Univ. Kansas Sci. Bull. 54 (1990) 75–153.

[5] Michener C.D., The Bees of the World: A Comprehensive Guide, Johns Hopkins University Press, Baltimore, 1999.

[6] Michener C.D., LaBerge W.E., Moure J.S., Canephorulini, a tribe of South American bees, Dusenia 6 (1955) 207–212.

[7] Michener C.D., Winston M.L., Jander R., Pollen manipulation and related activities and structures in bees of the family Apidae, Univ. Kansas Sci. Bull. 51 (1978) 575–601.

[8] Roig-Alsina A., Michener C.D., Studies of the phylogeny and classification of long-tongued bees, Univ. Kansas Sci. Bull. 55 (1993) 124–162.

[9] Silveira F.A., Phylogenetic relationships of the Exomalopsini and Ancylini, Univ. Kansas Sci. Bull. 55 (1993) 163–173.

[10] Thorp R.W., Structural, behavioral, and physiological adaptations of bees (Apoidea) for collecting pollen, Ann. Missouri Bot. Garden 66 (1979) 788–812.