

Grooming and pollen manipulation in bees (Apoidea): the nature and evolution of movements involving the foreleg

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Abstract

Three modes of self cleaning occur in insects: nibbling by the maxillae, scraping one structure by another in one direction only, and rubbing back and forth while the respective parts are in continuous contact. This paper describes a comprehensive and comparative account of this behaviour in bees, with special reference to the cleaning of or by the forelegs.

Bees, like all Hymenoptera, clean various parts of the head, including the mouthparts and the antennae, with the forelegs. Lower Hymenoptera scrape each antenna with either foreleg; in the species of Aculeata that possess the antenna cleaner (strigil) on the foreleg, only the ipsilateral leg is used. The thoracic dorsum of most bees, as in many sphecoid wasps, is scraped in a forward direction by the middle leg; *Tripeolus* spp., however, use the hind leg, and the Anthophorinae the foreleg.

Some beetles and lacewings clean their forelegs in the mouthparts by nibbling and scraping. Most higher Hymenoptera as a rule scrape the foreleg between the ipsilateral maxilla and the labium; bees, however, clamp the foreleg between the flexed ipsilateral middle leg and then scrape it. An evolution of this behaviour is postulated via several intermediate forms derived from original stepping movements.

Halictidae and Andrenidae clamp the foreleg for scraping underneath the middle tibia, whereas all other bees nearly always clamp it underneath the middle basitarsus. Very similar movements are used in various species for transferring pollen, oil, or nest materials from the foreleg to the middle leg.

It is argued that the original way of pollen carrying

in bees must have been by filling the crop through direct eating or by scraping pollen off the foreleg between the ipsilateral maxilla and the labium. The latter movement is widespread among bees and is homologous to the normal foreleg cleaning in the mouthparts of most other Hymenoptera. The efficiency of this behaviour is enhanced in many lower bees by a comb on the galea, which is the homologue of a similar structure widespread among aculeate wasps. In higher bees, Apidae and Anthophoridae, the galeal comb is replaced by an equifunctional stipes comb. Many bees have neither of these types of maxillary combs.

Introduction

Comparative ethology is an essential and powerful tool for elucidating the evolutionary events that gave rise to the behaviour of higher bees, behaviour which may be considered as the most advanced and most complex among the insects. Within the bees (superfamily Apoidea) extensive comparative ethological studies are available only for social interactions, nest-building and brood-care (recent reviews: v. Frisch, 1965, 1967; Wilson, 1971; Michener, 1974). In addition, some comparative data on gravity orientation are available (Jander & Jander, 1970). To these four categories of behaviour the present paper adds a comparative study of self-grooming from three points of view. First, elementary cleaning movements are traced through the line of descent from the primitive tracheates to the bees, and then in greater detail among adult bees. This is done by establishing homologies and analogies according to the methodological principles of Remane (1956), Hennig (1950, 1966), Wickler (1961, 1965), Voss *et al.* (1973) and others. Second, the results on the bees are utilized to supplement our knowledge of the

cladistic relationships among the major taxa of the bees, following the principles established by Hennig (1966) and Ashlock (1974). Previously, the theory of bee cladistics and evolution was based mainly on morphological characters (Michener, 1944, 1974). Third, the knowledge about self-grooming in bees is compared with information about pollen collecting and handling movements. There is already evidence that these are derived from grooming behaviour (Beecken, 1934; Schremmer, 1972), and certain manipulations of nest materials also appear to be of this origin.

This paper is a continuation and amplification of previous comparative studies on self-grooming in insects (Jander, 1966; Valentine, 1973) and in Hymenoptera (Wagner, 1959; Farish, 1972). For bees there are in general few descriptions to be found in the literature, but these will be mentioned in the text where relevant. For the present, description will be restricted to the role of the forelegs in self-grooming because of the complexities of the problems involved; a subsequent paper will deal with the functions of the other legs. Grooming of sixty species of bees was studied. In addition, many other species of insects, especially Hymenoptera, were investigated in order to gain broad background knowledge. Observations and conclusions mentioned without references are those of the author.

Methods, Definitions and Species list

Bees were collected in the field, mostly on flowers, and then usually observed in the laboratory without visual aid, through a hand lens, or through a stereo-microscope. For observation of grooming, the bees were either confined in rectangular optically perfect cuvettes, or were free to move on a hand-held stick or on the laboratory window. Advantage was taken of the fact that bees are more apt to self-groom after feeding, 'waking', a sudden increase in light intensity, or after being sprayed with water (Minnich, 1919; Pflumm, 1970). As much information as possible, especially newly discovered aspects, was spoken into a tape recorder for later transcription and analysis. Whenever enough specimens were available, recording was continued until the observer was capable of making reliable qualitative predictions about the species-specific movement patterns. Observations of pollen manipulation were made on flowers in the field or in bee rooms. Statistical methods were rarely employed because they were

considered inappropriate at this early descriptive stage of the analysis. Some representative movements were photographically recorded. Illustrations were made from such photographs when possible; in the other cases the figures are reconstructions from memory, from taped information, or from dead specimens.

Observations were directed especially toward the following questions. First, which are the structures engaged in cleaning movements? (Many of the descriptions in the literature stop at this point, reducing their relevance for the present analysis.) Second, what is the mode of cleaning or pollen manipulation? In insects there are three, usually distinct, modes, here termed 'rubbing', 'scraping' and 'nibbling'.

In *rubbing*, two body parts mutually stroke each other or the one strokes the other, back and forth without losing close contact throughout the action. Even though during rubbing the effective movements are bidirectional, dirt is gradually pushed out distally due to the nearly uniform unidirectional orientation of hairs, bristles and spines. Rubbing is a terminal cleaning movement insofar as it eliminates dirt from some body area rather than transferring it from one area to another. In *scraping*, on the other hand, the effective action is unilateral with a clear distinction of the cleaning and cleaned areas. The cleaning segment touches one restricted area to be cleaned and strokes along it. Then a return stroke without physical contact may follow, if the scraping is repeated. Scraping transfers dirt or pollen from the cleaned to the cleaning segment. The movements during scraping may be by either or both segments concerned. *Nibbling* is a cleaning movement in which an antenna or leg is taken between the opened mouthparts and then pulled through them while the maxillae perform gentle biting movements. Virtually all the cleaning and pollen manipulating activities described below are scraping movements, but rubbing and nibbling are precursors that must also be studied if the evolution of the behaviour is to be understood.

Guided by the above considerations, all the self-grooming movements from sixty species of bees (Table 1) collected in Germany, Costa Rica and the U.S.A. (mostly Kansas) were described as completely as possible. In all the species, females (workers of social species) were studied, and in twelve, males were too (asterisks in Table 1). No sexual dimorphism in self-grooming was detected, so the sexes are not distinguished below.

Table 1. Species list of bees from Germany (G), Costa Rica (C), Kansas, U.S.A. (K) and Colorado, U.S.A. (CO) (*species in which both males and females were observed)

Fam. Colletidae	
1.	<i>Colletes fodiens</i> (Fourcroy) (G)
2.	<i>Colletes inaequalis</i> Say (K)
3.	<i>Colletes mandibularis</i> Smith (K)
4.	<i>Colletes robertsoni</i> Dalla Torre (K)*
5.	<i>Hylaeus illinoisensis</i> (Robertson) (K)
6.	<i>Hylaeus pratensis</i> (Geoffroy) (G)
7.	<i>Hylaeus bisinuatus</i> Förster (K)
Fam. Halictidae	
8.	<i>Agapostemon texanus</i> Cresson (K)
9.	<i>Augochlora pura</i> (Say) (K)
10.	<i>Augochlorella striata</i> (Prochancher) (K)*
11.	<i>Augochloropsis metallica</i> (Fabricius) (K)
12.	<i>Dufourea marginata</i> (Cresson) (K)
13.	<i>Halictus confusus</i> Smith (K)
14.	<i>Halictus rubicundus</i> (Christ) (G)*
15.	<i>Lasioglossum zephyrum</i> (Smith) (K)*
16.	<i>Lasioglossum imitatum</i> (Smith) (K)*
17.	<i>Nomia heteropoda</i> (Cresson) (K)*
18.	<i>Nomia triangulifera</i> Vachal (K)
19.	<i>Sphecodes fuscipennis</i> (Germer) (G)
Fam. Andrenidae	
20.	<i>Andrena accepta</i> Viereck (K)*
21.	<i>Andrena forbesii</i> Robertson (K)
22.	<i>Andrena imitatrix</i> Cresson (K)*
23.	<i>Andrena miserabilis</i> Cresson (K)
24.	<i>Calliopsis andreniformis</i> Smith (K)
25.	<i>Perdiia octomaculata</i> (Say) (K)
Fam. Melittidae	
26.	<i>Hesperapis carinata</i> Stevens (K)
Fam. Megachilidae	
27.	<i>Anthidium manicatum</i> (Linnaeus) (G)
28.	<i>Chalicodoma campanulae</i> (Robertson) (K)
29.	<i>Coelioxys bisoncornua</i> Hill (K)
30.	<i>Coelioxys modesta</i> Smith (K)
31.	<i>Coelioxys rufitarsus</i> Smith (K)
32.	<i>Heriades variolosus</i> (Cresson) (K)
33.	<i>Hoplitis hypocrita</i> (Cockerell) (CO)
34.	<i>Megachile mendica</i> Cresson (K)
35.	<i>Megachile petulans</i> Cresson (K)
36.	<i>Prochelostoma philadelphia</i> (Robertson) (K)
Fam. Anthophoridae	
37.	<i>Ceratina spec.</i> (<i>dupla</i> Say or <i>calcarata</i> Robertson) (K)
38.	<i>Xylocopa virginica</i> (Linnaeus) (K)*
39.	<i>Anthophora abrupta</i> Say (K)
40.	<i>Melissodes bimaculata</i> (Lepeletier) (K)*
41.	<i>Melissodes desponsa</i> Smith (K)
42.	<i>Melissodes agilis</i> Cresson (K)
43.	<i>Nomada vineta</i> Say (K)
44.	<i>Nomada spec.</i> (K)
45.	<i>Peponapis pruinosa</i> (Say) (K)
46.	<i>Ptilothrix bombiformis</i> (Cresson) (K)
47.	<i>Svastra obliqua</i> (Say) (K)
48.	<i>Tripeolus concavus</i> (Cresson) (K)
49.	<i>Xenoglossa strenua</i> (Cresson) (K)
Fam. Apidae	
50.	<i>Apis mellifera</i> Linnaeus (K)*
51.	<i>Bombus agrorum</i> (Fabricius) (G)
52.	<i>Bombus americanorum</i> (Fabricius) (K)*
53.	<i>Bombus griseocollis</i> (De Geer) (K)
54.	<i>Bombus lapidarius</i> (Linnaeus) (G)
55.	<i>Bombus ruderatus</i> (Fabricius) (G)
56.	<i>Bombus terrestris</i> (Linnaeus) (G)
57.	<i>Euplusia surinamensis</i> (Linnaeus) (C)
58.	<i>Melipona fasciata</i> Latreille (C)
59.	<i>Psithyrus variabilis</i> (Cresson) (U)
60.	<i>Trigona jaty</i> Smith (C)

Observations

Cleaning of the antennae

Primitive tracheates clean one antenna at a time by lowering it, then depressing and pulling it with the ipsilateral foreleg and passing it from base to tip through the mouthparts (Jander, 1966). This plesiomorphous cleaning pattern has disappeared in various evolutionary side branches of the insects but is retained by the beetles, the only holometabolous insects in which plesiomorphous antenna cleaning is known (Jander, 1966). Despite various differences in detail, apomorphous or derived antennal cleaning is found in all the Hymenoptera, as in all other insect taxa, where it occurs as a form of scraping by the forelegs down the antennae (Jander, 1966).

Since derived antennal cleaning pre-dates the emergence of present day Hymenoptera, it is necessary to scrutinize other taxa for transition states that help understand its origin. Among holometabolous insects, the only order showing both plesiomorphous and apomorphous antennal cleaning is the Coleoptera (Jander, 1966; Valentine, 1973; Green, 1975), and a transition state is found in the common soldier beetle *Chauliognathus marginatus* (Cantharidae). These beetles may clean their antennae in the plesiomorphous (prototypic) bending fashion, one at a time, with the help of ipsilateral forelegs and the mouthparts, nibbling with the maxillae. This mode of cleaning sometimes involves no foreleg, as one antenna can be actively bent down into the mouth. More important is the observation that frequently one foreleg scrapes with the basitarsus along one ipsilateral antenna, without pulling it into the mouth. Thus this is undoubtedly a primordial type of the apomorphous (derived) antennal cleaning, first originating as an adjunct to plesiomorphous antennal cleaning.

Panorpa (Mecoptera) and many lower Hymenoptera lack specialized cleaning structures on their forelegs and tend to scrape one antenna at a time between both fore tarsi (Gennerich, 1922; Wagner, 1959; Jander, 1966; Farish, 1972). *Panorpa communis* (Germany) moves both forelegs virtually in synchrony, whereas the lower Hymenoptera tend to move them more or less out of phase. In addition, all Hymenoptera with this cleaning pattern may also scrape an antenna with only one foreleg at a time. Species of Hymenoptera that scrape each antenna with both forelegs belong to the families Tenthredinidae, Siricidae, Braconidae, Ichneumonidae,

Cynipidae, Chalcididae, Proctotrupidae and Evaniidae (Wagner, 1959; Farish, 1972). I have observed this behaviour in *Athalia colibri*, *Tenthredo mesomelas* (Tenthredinidae) (Germany), *Diprion frutetorum*, *D. laricis* (Diprionidae) (Germany), *Cephus pilosulus* (Cepidae) (Germany) and *Leucospis gigas* (Chalcidoidea) (Yugoslavia)

Virtually all Hymenoptera pass their antennae during cleaning through the cleft formed by the apical tibial spur and the basitarsus of the foreleg. And at precisely this location the cleaning apparatus evolved, being well developed in almost all Aculeates (Gennerich, 1922). The analogous strigil of the ground beetles is found in a subapical position on the foretibia. It is certainly more than mere coincidence that according to observations by Wagner (1961), Farish (1972) and myself on numerous species of Aculeates, each antenna is cleaned only by the ipsilateral foreleg that grasps it in its cleaning structure. The only known exception to this rule is the masarid wasp *Pseudomasaris vespoidea* (Colorado) which has a rudimentary cleaning apparatus that is incapable of enclosing the club-shaped antennae; this wasp tends to clean each antenna with both forelegs.

There is a striking parallelism in the antennal cleaning of the Hymenoptera and the Mecopteroidea which has not been noted before, despite long knowledge of the relevant facts. *Panorpa*, as already mentioned, and some Diptera with long antennae clean one antenna with both forelegs (Heinz, 1949; Jander, 1966) just as the lower Hymenoptera tend to do. Most Lepidoptera, including the primitive genus *Micropteryx*, have a cleaning spur on their forelegs and always clean one antenna at a time with the ipsilateral foreleg as most aculeates do (Jander, 1966).

Antennal cleaning among bees was found to be remarkably uniform: only quantitative species specific differences were discovered. The bees studied, typically scrape one antenna at a time by stroking it distad with the ipsilateral foreleg cleaner. In preparation for this movement the vertex of the head is turned toward the cleaning foreleg and the antenna is lowered. Whenever antennal cleaning is part of a longer cleaning bout, raising of the forebody is also apparent. The subsequent scraping motion of the foreleg is assisted by counter-rotation of the head which helps to pull the antenna through the cleaner.

Distinct acts of antennal cleaning are inserted into longer sequences of behaviour, such as walking,

feeding and other cleaning movements. Bouts of various head cleaning movements by the forelegs almost invariably include antennal cleaning; sometimes antennal cleaning simultaneously occurs with other cleaning movements such as hindleg cleaning.

Table 2. Frequency distribution of stroke repetition in antennal cleaning. Numbers at head of columns indicate strokes per act; numbers in these columns indicate numbers of observations. m=number of individuals; F=female; M=male; W=worker.

Species name	Sex	n				
		1	2	3	4	m
Colletidae						
<i>Hylaenus stevensi</i>	F	10	42	1	0	3
<i>Colletes robertsoni</i>	F	15	50	2	1	3
	M	9	74	3	1	2
Halictidae						
<i>Agapostemon texanus</i>	F	9	38	3	0	1
<i>Augochlora pura</i>	F	3	40	7	0	2
<i>Augochlorella striata</i>	M	8	36	6	4	4
	F	3	44	3	0	5
<i>Lasioglossum zephyrum</i>	M	9	33	9	0	5
Andrenidae						
<i>Andrena accepta</i>	F	30	34	0	0	2
	M	4	5	0	0	1
<i>Andrena imitatrix</i>	M	15	63	19	1	9
<i>Calliopsis andreniformis</i>	F	46	6	0	0	2
Megachilidae						
<i>Chalicodoma campanulac</i>	F	50	0	0	0	4
<i>Coelioxys rufitarsus</i>	F	18	0	0	0	4
<i>Heriades variolosus</i>	F	50	0	1	0	0
Anthrophoridae						
<i>Ceratina spec.</i>	F	4	29	16	1	5
<i>Melissodes desponsa</i>	M	50	0	0	0	2
<i>Nomada spec.</i>	F	6	35	1	0	2
<i>Peponapis pruinosa</i>	F	50	0	0	0	1
<i>Svastra obliqua</i>	F	36	0	0	0	1
<i>Nylocopa virginica</i>	F	41	2	0	0	1
Apidae						
<i>Apis mellifera</i>	W	88	3	0	0	10
	m	44	4	0	0	10
<i>Bombus griseocollis</i>	W	49	0	0	0	3

Acts of antennal cleaning are composed of one to many unilateral or simultaneous bilateral consecutive scraping movements. Bilateral cleaning of both antennae by the respective forelegs was rare in most species looked at here, or not seen at all. For instance, in addition to the 1241 unilateral antennal cleaning movements in twenty different species entered into Table 2, only twenty-one bilateral antennal cleaning movements were observed in six taxonomically widely dispersed species.

The common unilateral antennal cleaning acts lend themselves to a more detailed quantitative analysis. For this purpose, groups of not more than

three conspecific individuals at a time were continuously observed and all cleaning acts scored as to the number of consecutive scraping movements. The following conclusions can be drawn from the overall outcome presented in Table 2. All species in most instances scrape their antenna not more than twice in succession and then turn to other behaviour. Larger numbers of consecutive scraping movements always occurred in antennal cleaning during long intensive cleaning bouts. In contrast to this, most of the antennal cleaning scored in Table 2 is 'casual'. With the exception of the intermediate *Andrena accepta*, all twenty species of bees scored in Table 2 fall into one of two categories with respect to casual antennal cleaning, the 'uniscrapers' and the 'biscrapers'. The distribution of these two types among the six families studied is not very consistent. However, the lower bees (Colletidae, Halictidae and Andrenidae) are mostly 'uniscrapers' and the higher bees (Megachilidae, Anthophoridae and Apidae) tend to be 'biscrapers'. No explanation for this rule and its exceptions is evident. Finally, in all the species in which both sexes were studied, the sexes were always of the same antennal scraping type.

Head and thoracic cleaning

Head cleaning in bees is almost exclusively done by the forelegs. One exception was seen in bumblebees (*Bombus americanorum*) which, when cleaning the back of the thorax with forward scraping movements of the middle leg, might continue this movement and thus also scrape the vertex of the head. Honeybees occasionally clean their eyes with ipsilateral mesotarsi (Beecken, 1954).

All head cleaning movements in bees are scraping movements of various types that vary and intergrade, thus rendering precise description and classification difficult. Therefore, only a rough overview is given. The direction of the head scraping in all bees is forward to downward. Contact takes place mainly with the foretarsi. All sides of the head are cleaned, most often the eyes, less often the upper side and still less the underside. Cleaning of the underside of the head is done with the upper side of the foretarsus and of the foretibia. Cleaning of the mouthparts is preceded by opening the mandibles and extending the proboscis. The outer surface of the mandible is scraped downward by the ipsilateral tarsus, the inner side similarly by the contralateral tarsus. The unfolded proboscis of the higher bees (Melittidae to

Apidae) may be scraped on the upper or underside by one foretarsus or both foretarsi scrape simultaneously, frequently taking it between them. Except for the more elaborate proboscis cleaning of the higher bees, no characteristic difference in head cleaning between the various taxa was apparent.

Any part of the thorax may be cleaned in Hymenoptera with various legs and leg combinations (Farish, 1972). Only for the cleaning of the dorsal side are enough observations available to allow thorough comparison of bees and other Hymenoptera. Apparently all bees, like many other Hymenoptera, clean the underside of the thorax by scraping backward with the foretarsi. Pleural grooming was seen as forward scraping with the tibia and femur of the folded middle leg. In addition, whenever the dorsal side of the thorax is cleaned, the lateral sides may also be scraped simultaneously by the proximal part of the acting leg.

Taking all the reports in the literature and my own observations together, it appears that most Hymenoptera clean their thoracic dorsum by forward scraping with the foretarsi. Among the aculeates this holds exclusively for Formicidae and Vespidae (Wilson, 1971; Wagner, 1959; Farish, 1972) and is here confirmed for the vespoids *Pseudomasaris vespoides* (Colorado), *Odynerus parietum* (Germany), *Monobia quadridens* (Kansas), *Polistes fuscatus* (Kansas), *Dolichovespula saxonica* (Germany), *Vespa mandarinia* (Japan) and several other species. For the Pompilidae, thorax cleaning has not been reported in the literature. I saw cleaning of the dorsum with the foretarsi similar to that of vespoids in the three European species *Pseudagenia carbonaria*, *Anoplius infuscatus* and *Psammochares abnormis*.

The Sphecidae, according to Farish's studies on a dozen species, clean the thoracic dorsum with either the forelegs or the middle legs. I noted forward scraping with the middle legs in *Ammophila sabulosa* (Germany), *Sceliphron javanum* (Malaysia), *Crabro spec.* (Germany) and *Trypoxylon texense* (Kansas). Similarly, all the bees belonging to the Colletidae, Halictidae, Megachilidae and Apidae (Table 1) scrape the thoracic dorsum with forward movements of the middle legs (Fig. 1a). Despite extensive observations, none of the Andrenidae was seen cleaning the dorsal side of the thorax in any way.

The genera *Certina*, *Xylocopa*, and *Nomada* of the family Anthophoridae perform the dorsal thorax cleaning in the typical way with the middle legs. Other Anthophoridae, however, do not follow this rule. *Triepeolus concavus* was seen using the hindlegs

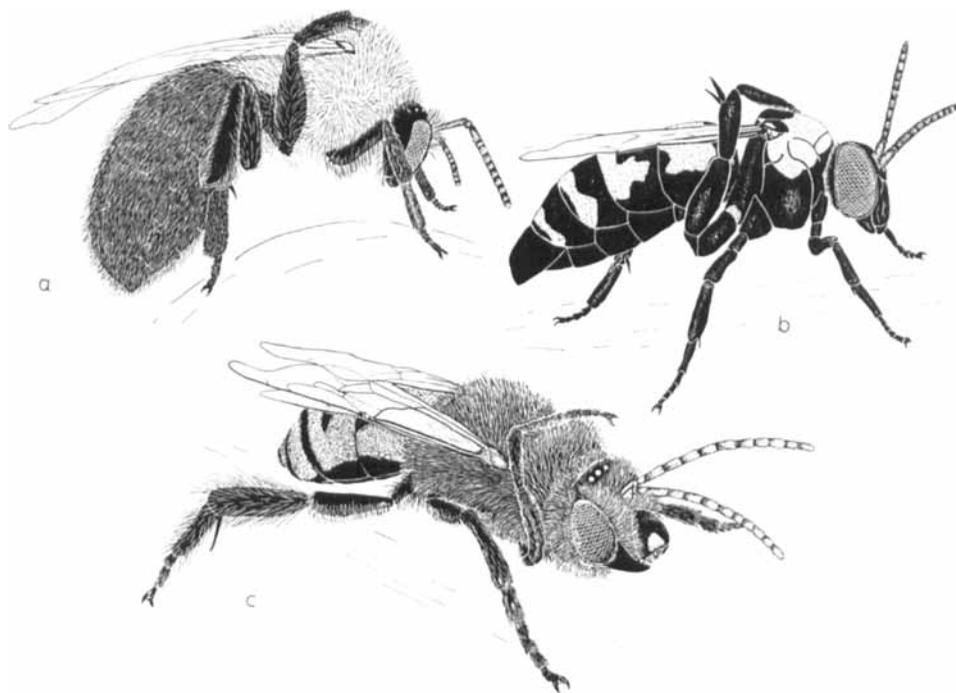


Fig. 1. Cleaning of the thoracic dorsum by bees: (a) with the middle leg in *Bombus griscocollis*; (b) with the hindleg in *Tripeolus concavus*; (c) with the foreleg in *Peponapis pruinosa*.

(Fig. 1b) as has been described for flies (Heintz, 1949). The Anthophorinae of the genera *Anthophora*, *Melissodes*, *Xenoglossa*, *Peponapis* and *Svastra* all scrape their thorax in the forward direction with the forelegs (Fig. 1c). Whether and how *Ptilothrix* cleans its thoracic dorsum is still not known. From this distribution of thorax cleaning it is obvious that the aberrant types of movement mentioned above arose within the Anthophoridae and are therefore convergent with the similar movements of the Pompilidae and flies.

Cleaning of the forelegs

Hymenoptera typically and primitively clean their forelegs one at a time with the mouthparts. This cleaning movement is the only one in the Hymenoptera that can be traced back to the common origin of the insects and myriapods (Jander, 1966). It was, however, never seen in any bees, even in rudimentary form. After cleaning the antennae, Hymenoptera usually clean the forelegs; bees do this always with the middle leg (as described below) rather than with the mouthparts as in most other Hymenoptera.

This contrasts with Farish's (1972) conclusion that bees clean their forelegs with the mouthparts, an error which might well be due to his failure to discriminate between cleaning of the mouthparts by the forelegs and the converse operation. In the former movement, which occurs in all bees, the foretarsi scrape distad along the mouthparts whereby the same tarsal point contacts the whole length of the part to be cleaned. During the return stroke of the foreleg there is usually no contact with the mouthpart being cleaned. In foreleg cleaning, on the other hand, most Hymenoptera other than bees pull the tarsus and various lengths of the tibia through one place in the inner mouthparts. During the return stroke, which is in the opposite direction from the return stroke during mouthpart cleaning, there is again no contact between the opposing parts.

Closer inspection of the cleaning of the forelegs by the mouthparts in various insects reveals two subtypes. The cockroach *Periplaneta americana* and the beetle *Chauliognathus marginatus* nibble with the maxillae along the leg (as along the antenna) to be cleaned. Twelve hymenopterous species in the families Chalcididae, Ichneumonidae, Tiphiidae,

Formicidae, Vespidae and Sphecidae, however, all scrape their forelegs through the cleft between the ipsilateral maxilla and the labium without any nibbling movement. Thus, this scraping use of the mouthparts for foreleg cleaning appears to be typical at least for the suborder Apocrita and perhaps for all Hymenoptera except bees.

According to the continuity principle of evolution, a transition state ('missing link') between nibbling and scraping of the foreleg must have existed and may still exist. After searching for it among holometabolous insects, it was found in two unidentified species of *Chrysopa* (Planipennia). These lacewings either nibble their foretarsi between their maxillae or pull them through the inner mouthparts as described for the Hymenoptera. Similar dimorphic cleaning of the forelegs in the mouthparts has been described for some beetles (Valentine, 1973). Thus the likely sister groups, Coleoptera and the Neuropteroidea (Hennig, 1969; Mickoleit, 1973), share a common cleaning pattern, one mode of which they share with Orthoptera and the other with Hymenoptera. Taking the Hymenoptera-Mecopteroidea taxon as the sister group to the Coleoptera-Neuropteroidea taxon (Hennig, 1969; Mickoleit, 1973), the dimorphic method of foreleg cleaning probably represents the original behaviour of the holometabolous insects. The higher Hymenoptera (perhaps all Hymenoptera) subsequently lost one of those two original modes, and the Mecopteroidea, according to the data of Heinz (1949) and Jander (1966), lost both of them.

Two modes of cleaning the forelegs have been described for bees, scraping of the foreleg by the ipsilateral middle leg, and rubbing the two forelegs against each other (Beecken, 1934; Farish, 1972). The latter mode appears to be rare and will not be discussed further. The commonly seen scraping of the foreleg by the middle leg is (as pointed out by Farish, 1972) the most specialized leg cleaning motion known in the Hymenoptera. But in the form described by Farish, as a scraping of the foreleg through the half closed joint between middle tibia and middle femur, is not typical of any of the species studied in the present work. Rather, the foreleg was scraped between the distal part of the tibia or the basitarsus and the proximal section of the middle leg, which was completely folded and drawn fairly close to the body (see below). This scraping with the folded middle leg was sometimes preceded by a quick, apparently rudimentary movement in which the inner to rear side of the foreleg was scraped down by

the front of the middle tibia. This elusive movement has not been described previously, but was found in most species and all families in Table 1.

In order to understand the phylogenetic origin of this highly specialized, bee-characteristic cleaning motion, various other species of Hymenoptera were searched for similar behaviour. The main objective was to find a set of cleaning movements that could be arranged in a linear sequence, with the most likely ancestral movement at one end and the most specialized at the other. Thus the following hypothesis was developed.

The only known well-coordinated leg movements that could have given rise to mutual leg cleaning are stepping movements. It takes only a slight modification of stepping in order for the acting leg to touch its neighbour and scrape down it. Such primitive undifferentiated leg movements, in which only one leg is active and the one to be cleaned is resting on the ground, can be seen in various species of Hymenoptera. For instance, *Diprion frutetorum* (Diprionidae) (Germany), *Smicromyrme rufipes* (Mutillidae) (Germany), *Odynerus parietum* (Eumenidea) (Germany) and *Hylaeus pratensis* (Colletidae) (Germany) were all observed stepping occasionally with the foreleg on the outside of the resting middle leg. The converse action, stepping with the middle leg on the resting foreleg, appears less common but was recorded, for instance, from the typhiid wasp *Myrmosula parvula* (Kansas).

The complexity of the movement virtually doubles with the next phase of the inferred phylogenetic sequence, since in various Hymenoptera adjacent legs are both actively involved. First they are both lifted from the ground and moved into proper position, then one leg scrapes down along its partner with its tibia or tarsus while the partner aids this action by a movement in the opposite direction. This movement appears to be rare in bees, but was seen occasionally in *Hylaeus pratensis* (Colletidae) (Germany), with the front leg scraping down the middle leg, and in *Ammophila sabulosa*, a European sphecid, with the foreleg and middle leg alternately scraping each other in this way.

As compared to nibbling or scraping with the mouthparts, this kind of cleaning movement is less efficient, affecting only one side of the treated leg. Various means have been evolved for both the foreleg and the middle leg to remedy this deficiency. The plesiomorphous cleaning of the middle leg by the mouthparts had been lost prior to the emergence of the Hymenoptera, but an efficient substitute move-

ment is present in virtually all Hymenoptera including the bees. In this substitute, the middle leg is taken between the hindlegs and scraped toward its apex (Wagner, 1959; Farish, 1972). In addition, the middle leg may also be cleaned efficiently by pulling it through the antenna cleaner (strigil) of the contralateral foreleg, as is typical for ants (Wilson, 1962; Farish, 1972), or by scraping of the two surfaces with both forelegs, as frequently seen in *Leucospis gigas* (Chalcididae) (Jugoslavia) or various vespids such as *Polistes fadwigae* (Japan) and *Vespa crabro* (Germany). The Stenogastrinae (Vespoidea) have even returned to scraping the middle leg by the mouthparts, probably a unique behaviour among the Hymenoptera.

Cleaning of both surfaces of the foreleg by the middle leg is achieved by further differentiation of the scraping movement. In this third postulated evolutionary step, the original scraping down the outside of the foreleg is performed twice in one cleaning act but modified so that the inside of the foreleg is scraped down by the outside of the middle tibia and basitarsus. Such scraping of both surfaces of the foreleg is especially frequent and stereotyped in forms that have reduced or lost the plesiomorphic cleaning of the foreleg by the mouthpart, as in the Scoliidae and Mutillidae, though Typhiidae such as *Myzium quinquecinctum* (Kansas) typically clean the foreleg with the mouthparts. *Scolia bicincta* and *Dasyntilla occidentalis* (Kansas), after cleaning an antenna with the foreleg, regularly scrape this leg with the middle leg first on its outside and then the inside, as described above. A similar foreleg cleaning pattern was seen in the eumenid wasp *Zethus spinipes* (Kansas) in twenty-four out of thirty instances after antenna cleaning; in six instances the mouthparts were used. Thus, foreleg cleaning in *Zethus* has advanced to the third evolutionary step, but not to the complete loss of the plesiomorphic pattern. Little is yet known for the Sphecidae, but *Ammophila sabulosa* (Germany) also displayed both plesiomorphic and apomorphic (step 3) foreleg cleaning.

The fourth step in this sequence is characteristic for all the bees. *Scolia*, *Ammophila*, etc., require two movements to clean both sides of the foreleg with the middle leg, whereas the bees fold the middle leg around the foreleg and then scrape down it on both sides as described above. The homology of this step 4 movement with that of step 3 is suggested by the vestigial scraping down of the inner side of the foreleg by the middle leg prior to the cleaning with

the folded middle leg. Thus, in its rare complete form, bee foreleg cleaning entails a double stroke as in the step 3 pattern. Because of the similarity of the movements involved, the rudimentary first phase seen in bees appears homologous with the cleaning of the *inner* surface of the foreleg of step 3, and the cleaning with the folded middle leg homologous with the cleaning of the *outer* surface in step 3. Comparison with the pattern in *Ammophila sabulosa*, indicates two evolutionary changes between steps 3 and 4. First, the sequential order of the two phases was reversed and, second, one phase regressed while the other phase was further transformed to achieve cleaning of both surfaces with one stroke.

Within the bees only one taxon-specific differentiation in the cleaning pattern of the foreleg was discovered. In the colletid genera *Colletes* and *Hylaeus* it is either the distal middle tibia or the corresponding basitarsus of the folded middle leg that scrapes over the foreleg. Not enough observations are yet available to establish the relative frequencies of these two possibilities. In all Halictidae and Andrenidae it is invariably the distal middle tibia that scrapes, and in all Megachilidae, Anthophoridae and Apidae it is the basitarsus. No observations are available for the Melittidae. These behavioural differences between families are correlated with the morphological characters of the middle leg.

Cleaning structures on the middle legs

On the middle legs of bees there are two types of cleaning structures, combs and brushes. These are related to the cleaning of the foreleg and to pollen transfer movements derived from that behaviour. A comb is a narrow line of close, stiff, bristle-like setae with relatively blunt ends. Adjacent setae within a comb are of about the same length. Frequently, combs project conspicuously above the neighbouring, unspecialized setae, which tend to be short, sparse, and inclined close to the cuticle. Brushes are dense pads of relatively short, similarly lengthed hairs either sticking out perpendicular to the surface, or all slanting in the same direction. Some cleaning devices are intermediate in appearance between combs and brushes. Both sexes usually have morphologically similar combs and brushes, but those of the males are generally smaller. Both combs and brushes were always observed to be moved in such a way that the tips of their hairs pointed in the direction of the scraping motion. Thus, comb or brush orientations allow inferences about the

directions of the scraping in species whose movements have not yet been observed.

The distribution of combs and brushes on the middle legs within major taxonomic groups was determined from museum specimens of 102 species of eighty-three genera in addition to the species listed in Table 1. The results will be discussed family by family. Descriptions all refer to females unless otherwise specified.

All bees have some brush on the underside of the basitarsus of the middle leg. In the Colletidae such brushes range from narrow and almost rudimentary in *Hylaeus* to wide and conspicuous in species with scopa (see below) and well-developed hair cover, as for instance in the genera *Colletes* and *Cadeguala*. The hairs in these well-developed brushes are pointed obliquely downward and backward with respect to the long axis of the leg segment. Sometimes, especially in the best-developed brushes, there is an oblique furrow within the brush which runs in the same direction that the hairs of the brush point (e.g. *Cadeguala nigroventris* and *Caupolicana yarrowi*). The orientation of brush hairs and furrow match the direction in which the foreleg is scraped by the basitarsus of the middle leg as observed in *Colletes* and *Hylaeus*. The furrow presumably contains the foreleg as the scraping stroke occurs, and must increase the surface cleaned as compared to a flat brush.

On the mesotibia of Colletidae no conspicuous brush or comb is found. Frequently, however, there is a strip of hairs sticking out along the inner side of the tibia at the same location where halictids and andrenids carry genuine combs as described below. On the base of the femur, precisely opposing the basitarsus of the flexed middle leg, a well-developed comb was discovered in *Colletes*.

All these structural differentiations of the middle legs of the Colletidae are taken as circumstantial evidence that within this family the forelegs are mainly cleaned while clamped between the basitarsus and the basal part of the femur of the middle leg. It is highly suggestive that this is also the main, if not the exclusive, movement for transferring pollen from the foreleg to the middle leg which then passes this material on into the scopa of the hindleg.

The Halictidae and the Andrenidae can be discussed together due to the similarity of cleaning structures on their middle legs. The basitarsal segment is narrow or of moderate width, and thus the brush on it is not highly developed and lacks a furrow. Instead, all species studied, including parasitic species like *Sphecodes*, have a well-developed

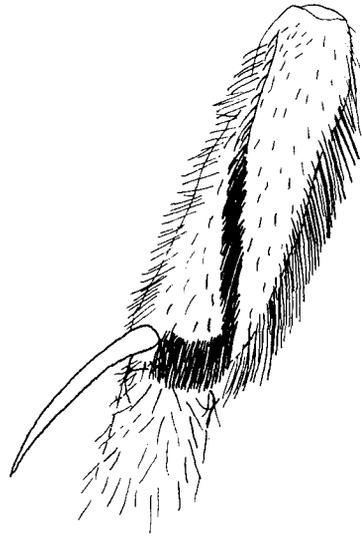


Fig. 2. Middle tibia from the inside of *Agapostemon texanus* showing tibial comb.

comb along the distal portion (one-half to three-quarters) of the middle tibia. The orientation of the comb is slightly oblique with respect to the long axis of the tibia. Near the end of the tibia the comb bends strongly towards the tibial spur. The structure of the comb is best discerned by viewing the middle tibia from the underside as illustrated in Fig. 2. Male tibial combs, as a rule, are distinct but smaller, or, rarely, totally absent as on the peculiar middle legs of *Nomia heteropoda*.

It is uncommon for both the Halictidae and the Andrenidae to have another comb or elongate, more brush-like cleaning structure on the inner side of the basal part of the femur precisely opposing the tibial comb in the flexed leg posture. In female *Nomia heteropoda*, this basifemoral comb is recessed due to a slight but distinct concavity in the femur. It is obvious from the foregoing descriptions that the tibio-femoral cleaning structures of the two families under discussion are located at those sections of the middle leg which clamp the foreleg during scraping as indicated in Fig. 3.

The small neotropical family Oxaeidae, formerly closely associated with the Andrenidae by virtue of a subantennal area defined by two sutures and also some other common characters (Michener, 1944), is, however, characterized by well-developed meso-basitarsal brushes which may contain an oblique furrow as described for colletids, as for instance in the genus *Protoxaea*. This and the absence of

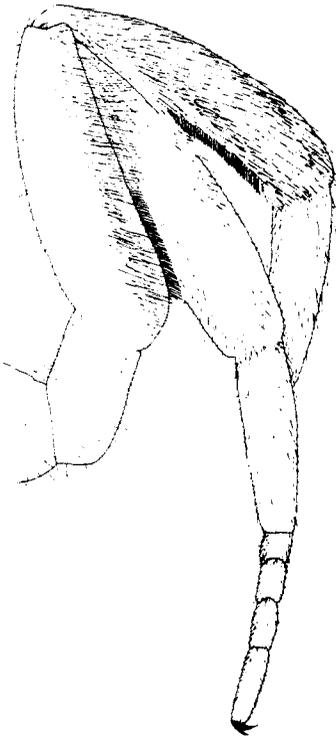


Fig. 3. Foreleg scraping with tibial and femoral combs of the flexed middle leg in *Agapostemon texanus*. During actual use the middle leg is closed much more, so that the combs disappear in the hairs of the foreleg.

mesotibial combs set this group well apart from the Andrenidae, a conclusion which is further substantiated by distinct features of the larvae which led Rozen (1964) to give the group family status.

In the Melittidae, for which no behavioural data are at hand, the cleaning structures on the middle leg do not allow unambiguous interpretation. Even though the basitarsal brushes are well-developed and generally large, a comb-like strip of hairs on the inner side of the tibia can frequently be recognized, as in *Hesperapis carinata* and *Macropis labiata*. After comparing the cleaning structures of the Melittidae with the corresponding structures of other bees, I suspect that melittids clean the foreleg between the basitarsus and femoral base of the middle leg.

The remaining families of bees, the Fideliidae, Megachilidae, Anthophoridae and Apidae, are all characterized by the absence of mesotibial combs. This is consistent with their habit of cleaning the foreleg clamped under the mesobasitarsus, and with

the well-developed brush on that segment, often with an oblique furrow.

Foreleg cleaning and the evolution of pollen collecting behaviour

There is general agreement that the basic components of collecting behaviour, especially that for pollen, are to be derived phylogenetically from self-cleaning (e.g. Braue, 1913; Beecken, 1934; Schremmer, 1972). The end result of such gathering movements is the storage of the pollen in a secure place on the body for the purpose of transport. There are two basic types of storage in bees, storage within the crop which is the posterior expansion of the foregut, or storage in scopae, external organs mainly built out of modified hairs mostly on the hindlegs or the abdomen. Exclusive crop carriers are the Hylaeinae and Euryglossinae (Michener, 1944, 1965); all other non-parasitic bees carry at least part of the pollen in scopae. The question now is, how does the pollen get into the carrying sites?

Until recently, the crop was thought to be filled directly by eating movements on the substrate. Schremmer (1972) was the first to infer, on morphological grounds, that *Xylocopa* and other anthophorids get pollen into the mouth by scraping the dusted foreleg through a comb on the ipsilateral maxillary stipes. A more general account of the role of the foreleg in crop filling can now be given.

Hylaeus (probably *bisinuatus*) was observed (under $\times 3$ magnification) collecting pollen in the flowers of *Hypericum kalmianum*. Mouthparts and forelegs were extensively applied in nibbling and scraping the anthers. Between such movements which served to loosen the pollen and perhaps involved direct eating of it, one foreleg at a time was put forward and pulled back from the distal tibia to the end of the tarsus through the ipsilateral side of the protruded inner mouthparts. Even though the exact details could not be seen due to the small size of the parts involved, it can safely be inferred from the morphology that the forelegs can pass through the cleft only between the ipsilateral maxilla and the labium. Taking all aspects together, this is a movement pattern so similar in form and context to foreleg cleaning by the mouthparts in Hymenoptera other than bees that there can be little doubt about the homology of the two behaviours. This movement in *Hylaeus*, as in other bees, does not occur in the ancestral context of self-cleaning but only in the context of pollen gathering, a conclusion supported

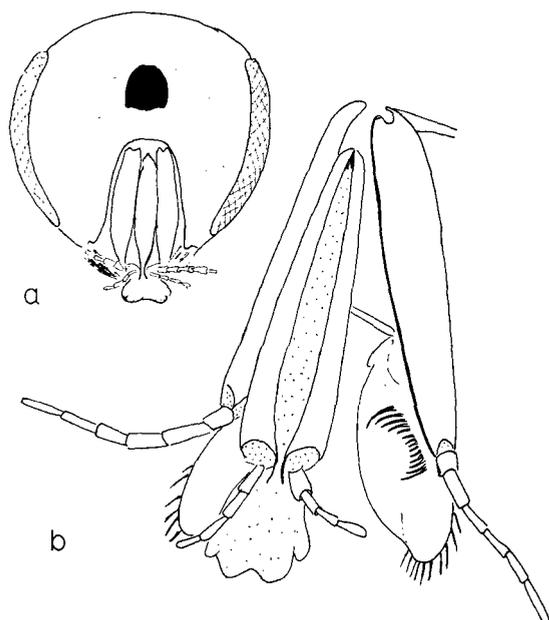


Fig. 4. Location of the galeal comb in *Hylaeus*. (a) Position of the mouthparts as seen from below the head. (b) Enlarged inner mouthparts as seen from the same direction but one maxilla spread to the side to show the location of the galeal comb.

by the presence of a comb on the inner side of the galea that is similar in structure to pollen-gathering combs on the legs (Fig. 4a, b). Furthermore, since there is frequently pollen in this galeal comb, it must serve for pollen gathering (Demoll, 1908).

Pulling the foreleg through the inner mouthparts (proboscis) was also directly observed in pollen collecting *Andrena*, *Ceratina* and *Bombus*, and can thus be traced all the way through the main line of the bee evolution. Some finer details of this movement could be recognized in queen *Bombus americanorum* because of its large size. As the bee backed out of the flower tube of a foxglove, *Digitalis ambigua*, it kept its proboscis extended, then spread one maxilla to the side and pulled its foreleg through the cleft between the maxilla and the labium as illustrated in Fig. 5. At precisely the point where the foreleg is pulled through, there is a comb recessed in a shallow concavity on the lower edge of the stipes.

Knowledge about the distribution of the galeal combs and stipes combs among the bees is important because of the correlation between these structures and the scraping of pollen off of the forelegs. From

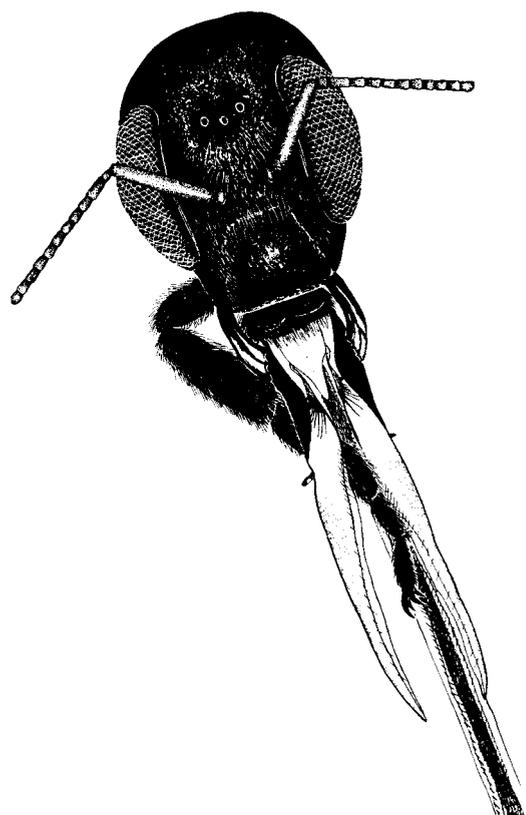


Fig. 5. Scraping the foreleg past the stipes comb of the extended proboscis in pollen eating by *Bombus americanorum*.

the accounts of Demoll (1908), Cockerell (1924), Michener (1944), and my own observations, galeal combs are found well developed not only in *Hylaeus*, *Colletes* and *Andrena*, but are characteristic of the whole respective families, Colletidae and Andrenidae. In the Halictidae, galeal combs are usually absent but still occur in *Nomia* (Michener, 1944) and the primitive halictine genus *Corynura* (Eickwort, 1969). Within the remaining families, a galeal comb is known only from *Dasygaster plumipes* (Melittidae). In *Ceratina* (Anthophoridae) rudiments of a galeal comb can be recognized. Distinct stipes combs are common, but not universal among the Anthophoridae (Demoll, 1908; Cockerell, 1924; Michener, 1944; Schremmer, 1972); a typical example is illustrated in Fig. 6 a, b). Among the Apidae, only bumble bees are known to carry a stipes comb. Whether the absence of both a galeal and a stipes comb as in *Apis* is also associated with a loss of the foreleg scraping movement is still an open question.

Foreleg cleaning movements are also of import-

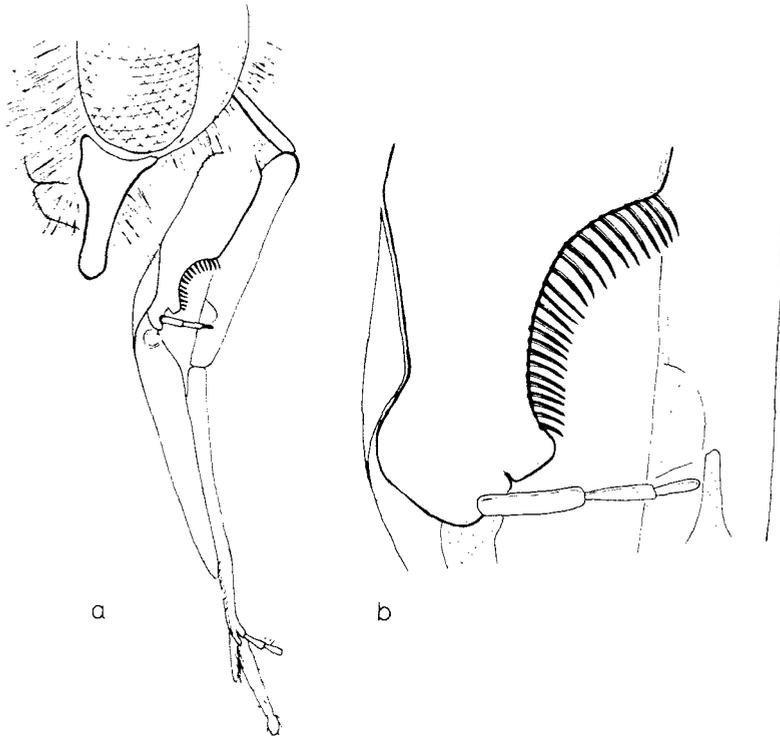


Fig. 6. Stipes comb of *Melissodes bimaculatus*. (a) Location of the comb on the extended proboscis. (b) structural details of the enlarged comb.

ance in transferring pollen into the scopae. Typically, pollen is transferred from the foreleg to the middle leg and from there either directly into a scopa on the hindleg or the hindlegs take over the pollen and then transfer it into a scopa. These latter actions differ from pure cleaning and also differ between taxonomic groups and will be discussed in a subsequent paper. Transfer of pollen from the foreleg to the middle leg is indistinguishable from the corresponding cleaning movement as studied in *Colletes*, *Andrena*, *LasioGLOSSUM*, *Megachile*, *Ceratina*, *Xylocopa*, *Melissodes*, *Bombus* and *Apis*.

Various Apidae also carry nest material in the pollen basket on the hind tibia. Such material is transferred from the foreleg to the middle leg with movements that, at least superficially, resemble foreleg cleaning in the sense that the foreleg moves backward against the forward swinging middle leg, which then flexes at the tibio-femoral joint while grasping with the tarsus. After this, the middle leg swings back, scraping the material from the foreleg, and then presses it from the outside into the corbula. This pattern holds for cerumen collecting in the

stingless bee *Trigona postica* (Sakagami & Camargo, 1964), propolis collecting in the honey bee *Apis mellifera* (Meyer, 1956), and mud collecting in *Melipona fasciata*.

Foreleg cleaning and bee evolution

In this discussion, the major steps in the evolution of bees will be related to foreleg cleaning and the pollen collecting movements derived from it. The frame of reference will be the partially tentative dendrogram of Fig. 7, relating the major bee taxa. This dendrogram is a reflection of Michener's (1974) most recent theory about bee evolution with some modifications that will be discussed and justified in turn.

Ever since Müller (1872) first recognized the close relationship between the bees (Apoidea) and the digger wasps (Sphecoidea), that relationship has never been in serious doubt (Michener, 1944; Malyshev, 1968; Brothers, 1974; etc.). This relationship is now further supported by the common occurrence of dorsal thorax cleaning with the

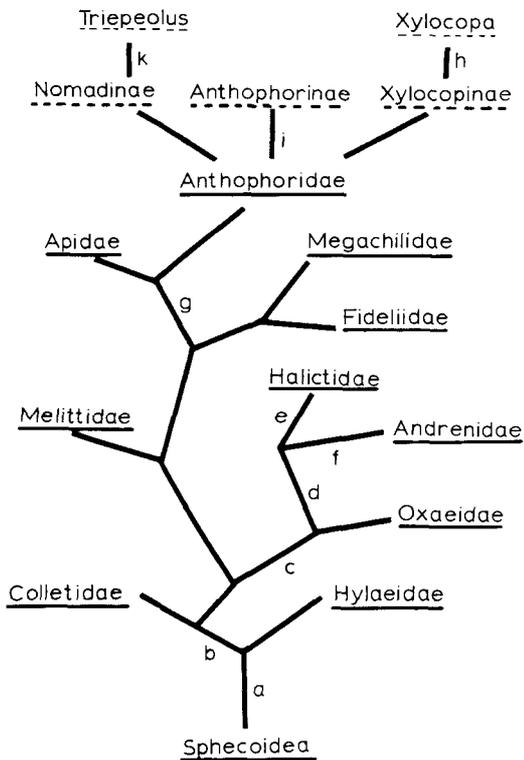


Fig. 7. Dendrogram of various bee taxa. The letters refer to evolutionary transformations as discussed in the text.

middle legs, a behaviour that is not common in other aculeates. No additional synapomorphous cleaning movements (i.e. these derived from a common source) for these two groups are yet known. Despite the great morphological similarities between the apoidea and sphecoidea, there are considerable behavioural differences that also include foreleg cleaning. Homologizing should help bridge this gap.

With the genesis of the bees out of the sphecoidea wasps (Fig. 7a), two major changes took place with respect to foreleg cleaning: a functional change and a behavioural substitution. The ancestral cleaning of the forelegs with the mouthparts lost its original function and now serves exclusively as a means of pollen transport into the mouth. As an efficient functional substitute for cleaning the forelegs, the characteristic single stroke scraping with the flexed middle leg evolved out of the less efficient double stroke foreleg scraping with the middle leg as found in sphecoidea and other wasps. Since the cleaning behaviour of the sphecoidea is still incompletely known, it cannot be ruled out that some of these changes took place within the Sphecoidea.

With the new more detailed knowledge about the origin of pollen gathering movements from cleaning movements, a crucial question about the early evolution of bees can now be answered: which mode of pollen carrying came into being first, internal (i.e. crop-carrying), or external (i.e. scopa-carrying)? Five arguments clearly favour the first proposition.

First, crop-carrying in primitive bees like *Hylaeus* involves only morphological and behavioural components (eating, regurgitating, foreleg scraping through the inner mouthparts past a galeal comb) that were in existence already among the sphecoidea wasps. The galeal comb, in particular, is not an innovation in the bees, as its homologue is apparently widespread among aculeate Hymenoptera in general and the sphecoidea in particular (Michener, 1944). Such a structure has been described for ants (Gotwald, 1973); it is present in the vespid *Polistes fuscatus* and the sphecoidea *Sphecius speciosus* (Fig. 8).

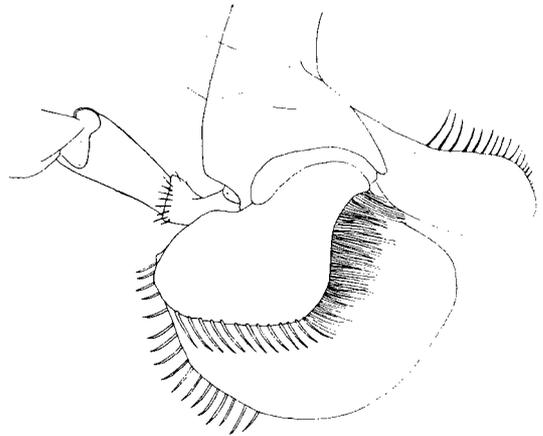


Fig. 8. Comb composed half of spines and half of hairs on the inner face of the galea in *Sphecius speciosus* (Sphecoidea).

Accordingly, all that is necessary for a typical sphecoidea wasp to provide pollen to its brood is to arrange the available behavioural components in the proper sequence. External pollen carrying, on the other hand, requires morphological and behavioural innovations like hair cover and a scopa for pollen storage, modified grooming behaviour for filling the scopa rather than cleaning it, and a turn around movement in the nest followed by pollen transfer from the scopa into the brood cell.

Second, pollen gathering into the crop with the help of scraping of the foreleg and cleaning of it by a behavioural substitute is found in homologous

form not only in the morphologically primitive family Colletidae but also in most, if not all, major branches of bee evolution. Hence, the root of these two behaviours must lie in the early phase of bee evolution if not in sphecoid evolution.

Third, exclusive internal pollen carrying is known only from the morphologically primitive Hylaeinae and Euryglossinae (Michener, 1944, 1965), exclusive external pollen carrying only from advanced bees like *Apis mellifera*.

Fourth, the honey-wasps or Masaridae can be taken as a model for the early extinct phase of bee evolution, because their nectar and pollen gathering methods are less advanced than those of any living bee. The only cleaning movements the Masaridae use for pollen gathering is scraping the head (*Celonites abbreviatus*; Schremmer, 1959) or scraping the dorsum of the thorax (*Pseudomasaris vespoides*) with the foreleg and then scraping the foreleg in the mouthparts as bees do (Torchio, 1974; and personal observation). Despite these striking similarities in pollen gathering behaviour, even the most primitive bees are more advanced than *Pseudomasaris vespoides* in employing different movements for foreleg pollen-gathering and cleaning.

Fifth, pollen-gathering in *Hylaeus* is inefficient insofar as only pollen on the forelegs and head can be collected, since there are no cleaning movements available that could move pollen or other material forward from the thorax and abdomen. Masarids, on the other hand, have the advantage over early bees of normally cleaning both the head and the thoracic dorsum with the forelegs. When there is a scopa present in bees, it is always located posteriorly, on the hindlegs or the abdomen. In normal bee cleaning, dirt from any body part is transferred backward, so pollen can be moved backward and packed into the scopa by modified cleaning movements. Thus, external pollen carrying affords greater versatility and efficiency. Given these facts it can be argued that the evolutionary transition from a less efficient (as in *Hylaeus*) to a more efficient and versatile (as in *Colletes*) mode of pollen carrying is more likely and reasonable than the converse sequence.

The inferred evolutionary precedence of internal over external pollen gathering is consistent with the early hypothesis (Müller, 1872) that regurgitation into the brood cell constitutes the first behavioural innovation in the earliest evolution of bees.

A possible counter-argument against the primitive behavioural state of *Hylaeus* is the specialized

nesting in excavated pithy stems or holes in wood, rarely in soil. Such a nest site is incompatible with the notion of ground nesting in primitive bees, based on the fact that the majority of species in both bees and sphecoid wasps excavate nests in the ground and have basitibial and pygidial plates presumably used for working in soil (Michener, 1944). However, this argument can be convincingly turned around by suggesting that *Hylaeus* is a surviving group of an early adaptive radiation of primitive bees. It is further suggested that, except in Australia, these primitive bees were out-competed at their normal nesting sites by more advanced bees with more efficient pollen-gathering techniques. But in Australia the Euryglossinae, close relatives of the Hylaeinae, persisted in both, carrying pollen exclusively in the crop and predominantly nesting in the soil. For nesting in narrow burrows in stems, the primitive state of hairlessness and less efficient internal pollen-carrying is less disadvantageous, as attested by the anthophorid genus *Ceratina* that converged towards *Hylaeus* by nesting in stems and thereby secondarily became almost hairless, and probably reduced its scopa. The superficial convergent morphological similarities between *Hylaeus* and *Ceratina* are so striking that they once were considered as genuinely related (Friese, 1891). It appears likely that *Ceratina*, with its small scopa, must carry a substantial part of the pollen in the crop, as does the related genus *Xylocopa* (Schremmer, 1972). *Xylocopa valga* and perhaps other congeners are unique among bees in improving internal pollen gathering by passing pollen from the middle leg that scrapes the thoracic dorsum to the foreleg and thence into the mouth (Schremmer, 1972).

After the transformation of sphecoids into bees ('a' in Fig. 7), less pronounced phylogenetic changes in foreleg activities occurred. With the introduction of external pollen-carrying, foreleg cleaning by the middle leg became an element of the pollen transfer movements to the scopa ('b' in Fig. 7). Since this proved to be a crucial event in the overall evolution of bees, separation of *Hylaeus* into a family (Hylaeidae) independent from the Colletidae seems appropriate (Fig. 7). However, formalization of this change in rank still requires an investigation of the taxonomic positions of the Euryglossinae and Xeromelissinae (= Chilicolinae).

Next, a new but still tentative arrangement of the families Oxaeidae, Andrenidae and Halictidae is suggested. The Halictidae and the Andrenidae are considered as sister groups, linked by the common

origin of their unique character of cleaning the foreleg with the middle tibia which carries a well-developed comb ('d' in Fig. 7). From the evidence available, it appears that the Andrenidae lost the faculty of cleaning the thoracic dorsum ('f' in Fig. 7). The Andrenidae and Oxaeidae are linked by the unique characters of subantennal areas defined by two sutures ('c' in Fig. 7). With respect to the Andrenidae, the Oxaeidae are considered more ancestral due to the absence of a tibial comb. Given that this relationship holds, the early Halictidae must have lost one of the two subantennal sutures ('e' in Fig. 7).

All the remaining families of bees, including the Oxaeidae (formerly included in the Andrenidae), are characterized by cleaning the foreleg clamped under the basitarsus of the middle leg. No behavioural difference is known between the insufficiently studied Oxaeidae and Melittidae and the Megachilidae.

Another important transformation took place near the root of the sister families Apidae and Anthophoridae ('g' in Fig. 7). The galeal comb becomes nonfunctional and at best is only found in vestigial form, as for instance in *Ceratina*. It is replaced by the new stipes comb found well-developed in the Bombini, Anthophorinae and Xylocopinae. No well-developed galeal combs or stipes combs are known from the Megachilidae and the Nomadinae, a subfamily of the Anthophoridae; but neither group has been thoroughly surveyed in this respect.

Within each of the three subfamilies of the Anthophoridae some further evolutionary change took place. Transferring pollen from the middle leg to the foreleg in *Xylocopa* ('h' in Fig. 7) has already been mentioned. All Anthophorinae studied scrape the back of the thorax with the foreleg instead of the middle leg ('i' in Fig. 7, Fig. 1c). This new movement might allow rapid and efficient transfer of pollen from the thoracic dorsum to the stipes comb for pollen eating. If this interpretation is correct, then this new behaviour of the Anthophorinae is equifunctional with the middle leg to foreleg pollen transfer in *Xylocopa*. Finally, with respect to dorsal thorax cleaning, precisely the opposite change characterizes *Triepeolus* which uses the hindlegs instead of the middle leg ('k' in Fig. 7, Fig. 1b).

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