

STRUCTURAL, BEHAVIORAL, AND PHYSIOLOGICAL ADAPTATIONS OF BEES (APOIDEA) FOR COLLECTING POLLEN¹

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ABSTRACT

Bees, like their wasp relatives, forage for and transport food to a nest as provisions for their offspring. Unlike female Sphecoidea which transport arthropods one at a time as prey, bees transport pollen requiring specialized scopal (brush) or corbicular (fringed plate) structures to transport the dustlike material externally. Scopae often exhibit further modifications in density and amount of plumosity in relation to the size and ornamentation of the pollen grains they transport. Bees also differ from sphecid wasps by possessing branched body hairs that are relatively densely packed. These hairs, the electrostatic surface potential, and specialized hair groups for extraction of hidden pollen are important in the acquisition of pollen from flowers. Structures for grooming (brushes, combs, and scrapers) and grooming behavior patterns are modified to permit manipulation and packing of pollen in the specialized transport structures. The addition of nectar, so that pollen is packed moist, is a behavior that permits the carrying of pollen of a great variety of sizes and ornamentations in relatively simplified scopae or in corbiculae. The addition of oils to the diet of some bees has resulted in a modified type of scopal structure that has a wooly area basally and stiff guard hairs extending distally and that can transport a mixture of oil and pollen. Special hairs on the fore and mid basitarsi and teeth of hind tibial spurs are modified as oil scraper and manipulation structures. The use of corbiculae in Apidae to transport nesting materials and the hind tibiae in male orchid bees (Euglossini: Apidae) for transporting aromatic compounds involves behavior patterns similar to those for pollen transport in grooming, manipulating, and packing the materials. Other behavioral and physiological adaptations important in the location and acquisition of pollen by bees include individual constancy, oligolecty, seasonal synchrony, preimaginal conditioning, daily synchrony, buzz pollination, and other responses to specific modes of pollen presentation. Most of the behavioral patterns involve learning. They may be modified by extrinsic factors, and they may modify intrinsic structural and physiological characters.

Bees share a common ancestry with sphecoid wasps, but feed on plant materials rather than arthropod prey. Like their wasp relatives, female bees forage from a nest to which they must transport food for their offspring. Sphecoid wasps commonly transport single arthropods held in the mandibles often assisted by the legs, but some advanced sphechids transport their prey in a more rearward position supported primarily by the mid legs or occasionally by special modifications of the sting or pygidial plate (Evans, 1962). Since pollen, the principal brood food of Apoidea, occurs primarily as a fine-grained (5–210 μm), dustlike material, most bees have evolved highly specialized adaptations for pollen transport. Most bees carry some pollen mixed with nectar in the crop or honey stomach. Few bees transport pollen exclusively in the crop as do honey wasps (*Pseudomasaris*: Masaridae) (Torchio, 1970). However, females of all other nonparasitic bees transport pollen externally in specialized structures called scopae (brushes of hairs)

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or corbiculae (flattened or concave plates with long curved hairs on one or more sides). These unique structures are often further modified in relation to specific types of pollen carried. Structures and behavior for grooming are also modified for manipulation and packing pollen. Other behavioral and physiological adaptations are important, the location, synchronization, and host specificity of bees with their pollen plants. Many of these topics have been studied independently, but this paper attempts to present a broad overview for integration of the diverse adaptations of bees for acquiring, manipulating, and transporting pollen, based largely on my own observations and the literature on North American bees.

STRUCTURES FOR POLLEN TRANSPORT

Phylogenetic trends appear in a distal shift in position of the scopal region of the hind legs (Pasteels & Pasteels, 1979) and restriction of the body surface used for pollen transport in bees (Table 1). The primitive scopa in female bees that transport pollen dry includes the trochanter through the tibia of the hind leg (Fig. 1) with accessory scopal areas of different relative importance in various tribes including hairs on the anterior abdominal sternites, hind coxa, hind basitarsus, and laterally on the propodeum and anterior abdominal tergites. The propodeal and femoral areas are sometimes bare centrally and referred to as corbiculae. These are found in the Colletidae, Oxaeidae, Andrenidae, and Halictidae (e.g., Pasteels & Pasteels, 1976, 1979; Roberts & Vallespir, 1978). Simple scopal hairs restricted to the abdominal sternites are characteristic of female pollen collecting Megachilidae (Pasteels & Pasteels, 1974). The Fideliidae carry pollen in the same manner and position as the Megachilidae (Rozen, 1970, 1973, 1977), and the hairs comprising the abdominal scopa appear essentially the same under the scanning electron microscope (Pasteels & Pasteels, 1975). The modified hind legs of Fideliidae females do not transport pollen as suggested by earlier authors, but are used to flip sand from the nest entrances during excavation (Rozen, 1970, 1977). Females of Melittidae and nonparasitic Anthophoridae have scopal hairs restricted primarily to the hind tibia and basitarsus. The most specialized pollen transport structures are the corbiculae of the hind tibia in female pollen-collecting Apidae (Michener et al., 1978).

Exceptions to these trends in position occur when female bees mix pollen and nectar. Female Hylaeinae and Euryglossinae (Colletidae) transport pollen mixed with nectar in the crop or honey stomach (Jander, 1976; Roberts & Vallespir, 1978), and there is no evidence of an external transport apparatus (Pasteels & Pasteels, 1976). Although some authors suggest pollen is transported in the same manner by the Xeromelissinae (=Chilicolinae), Eickwort (1967) describes the scopa of a *Chilicola* as consisting of hairs on metasomal sternites 1–3, the femur of the hind leg, and as accessory scopae, hairs on the hind tibia, trochanter, and coxa, while Toro & Michener (1975) describe another *Chilicola* with scopal hairs on the hind femur and metasomal sternites 2–3. The discrepancies may be due to variability among species since neither Michener (1944) nor Pasteels & Pasteels (1976) found evidence of external scopae on the species they examined. Restriction of the scopal area in female Panurginae (Andrenidae), except *Panurgus*, is related to their behavior of adding nectar to the pollen as it is packed around the hind tibia. The corbiculae of Apidae (Fig. 6) transport pollen mixed with nectar

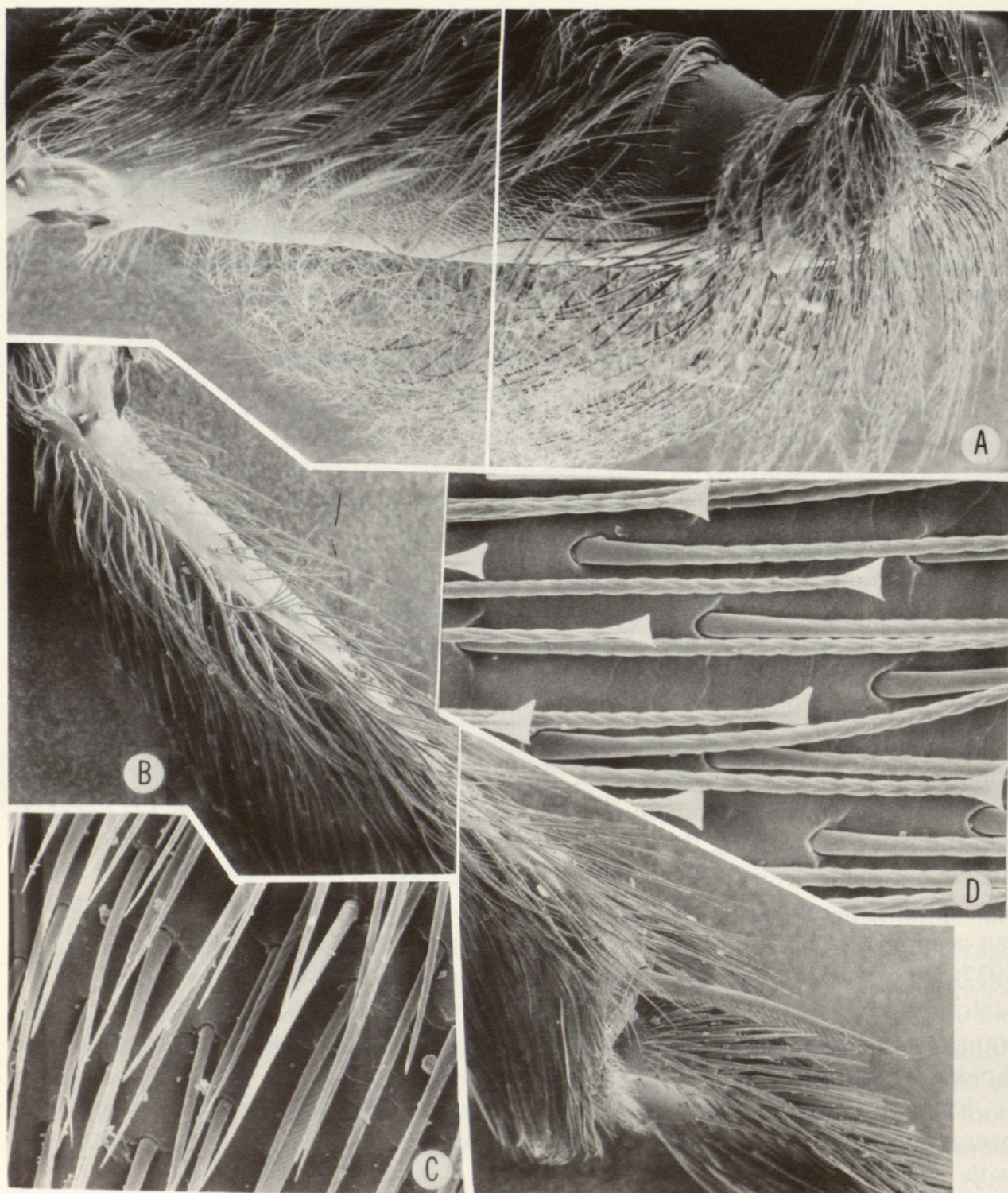


FIGURE 1. Scanning electron micrographs of *Colletes fulgidus* hind leg.—A. Femoral and trochanteral scopa (65 \times).—B. Tibial scopa (62.4 \times).—C. Tibial scopal hairs (250 \times).—D. Wing grooming hairs of inner face of tibia (500 \times).

or honey in the form of doughlike pellets. The eusocial *Lestrimelitta* (Meliponinae: Apidae) obtain pollen by robbing nests of other social Apidae. Since their workers have no corbiculae as do other Apidae, pollen is transported in the crop mixed with honey (Michener, 1974). Female Anthophoridae and Melittidae that transport pollen moistened with oil do not have more restricted scopal areas than their relatives that transport pollen dry (Roberts & Vallespir, 1978). The same is true of Melittidae that moisten their pollen loads with nectar.

TABLE 1. Location of pollen transport structures in Apoidea. The number of + indicates relative importance, the ± indicates deviation from subfamily mode. (Modified after Roberts & Vallespir, 1978.)

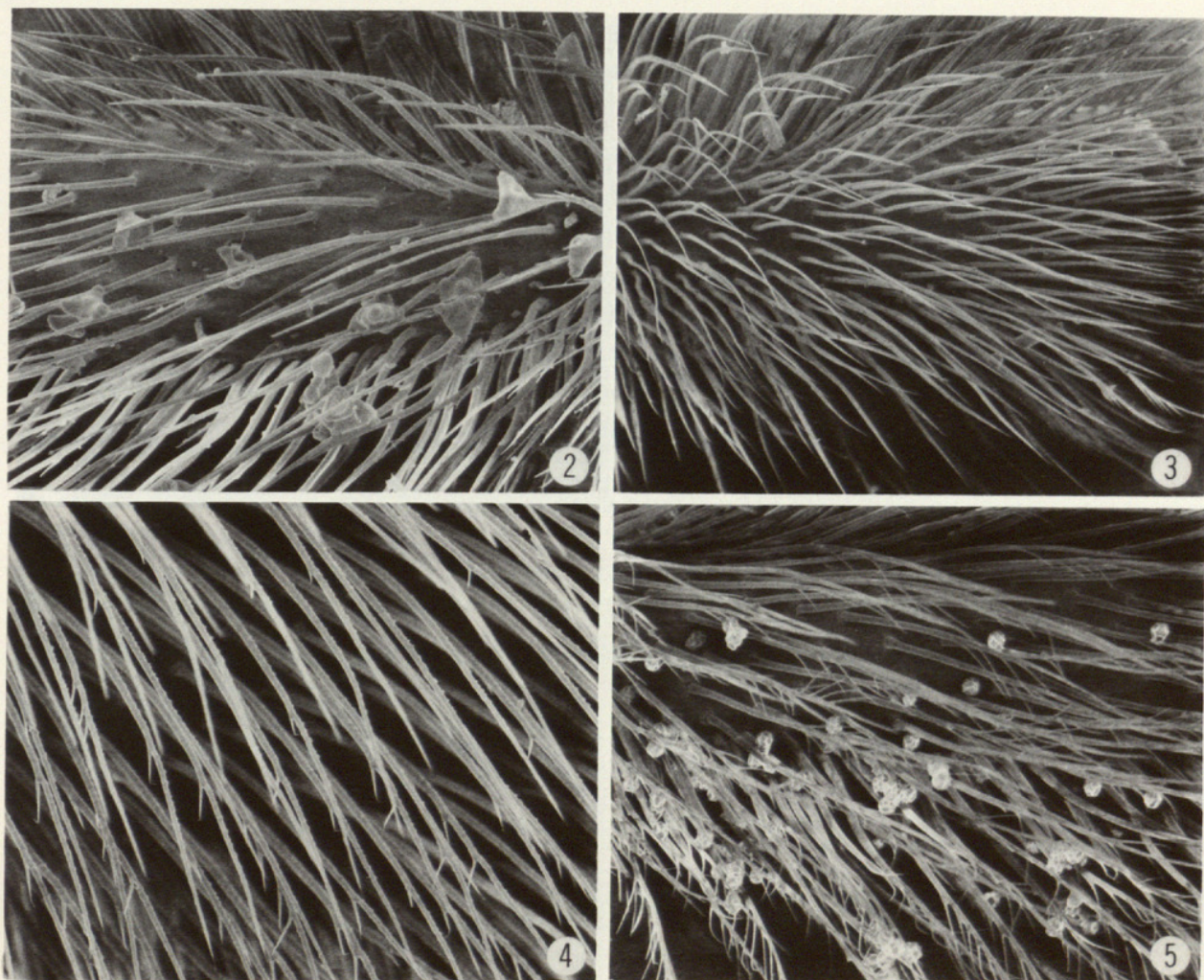
FAMILY Subfamily	Location							Meta- somal ^e Sterna
	Crop	Propo- deum	Hind Leg				Basi- tarsus	
			Coxa	Tro- chanter	Femur	Tibia		
COLLETIDAE								
Colletinae		++		++	+++	+++		
Diphaglossinae ^a		++		++	+++	+++		+(1-5)
Xeromelissinae			+	+	++	+		+++ (1-3)
Hyaelinae	+++							
Euryglossinae	+++							
Stenotritinae				+	+++	+++	+	
OXAEIDAE ^a								
		++		++	+++	+++		+(1-2)
ANDRENIDAE								
Andreninae		++		++	+++	+++		
Panurginae						+++	± ^e	
HALICTIDAE								
Halictinae		+		+	+++	+++	+	+(1-5)
Nomiinae		+		+	+++	+++	+	+(1-5)
Dufoureae		+		+	+++	+++	+	+(1-3)
MELITTIDAE								
Melittinae						+++	+++	
Dasypodinae						+++	+++	+(2-6)
Macropidinae						+++	+++	
Ctenoplectrinae						+++	+++	
								+++ (2-6)
FIDELIIDAE								
MEGACHILIDAE								
Lithurginae								+++ (2-6)
Megachilinae								+++ (2-6)
ANTHOPHORIDAE								
Nomadinae ^b								
Anthophorinae					+ ^d	+++	+++	+ ^d (2-5)
Xylocopinae						+++	+++	
APIDAE								
Meliponinae						+++		
Bombinae						+++		
Apinae	± ^c					+++		

^a Also laterally on metasomal tergite 1.
^b All cuckoo bees, none transport pollen.
^c Only robber bees, *Lestrimelitta*, that lack corbiculae.
^d Some Eucerini (e.g., *Svastra*).
^e Only *Panurgus* females that carry pollen dry on tibia and basitarsus.
^f Metasoma = apparent abdomen (Michener, 1944, 1974). Numbers (in parens) = metasomal segments bearing scopal hairs. The more familiar term, abdomen, is used in the text, except for reference to specific segments.

Further modifications of scopae involve deviations from near relatives based on spacing, length, and plumosity of the scopal hairs. Adaptations of these characters occur especially in host specific bees in relation to the size and ornamentation of the pollen grains they collect. Bees that collect small ($<40\ \mu\text{m}$) pollen grains and transport them dry such as Oxaeidae and Caupolicanini (Diphaglosinae: Colletidae) (Linsley & Cazier, 1963) often have very densely packed and multibranched scopal hairs (Pasteels & Pasteels, 1976; Roberts & Vallespir, 1978). Bees that specialize on large ($>100\ \mu\text{m}$) pollen grains such as *Xenoglossa* (Anthophoridae) on *Cucurbita* (Cucurbitaceae) (Hurd & Linsley, 1967) often have scopal hairs which differ from those of their relatives in being stouter and unbranched (Roberts & Vallespir, 1978).

The scopal hairs of most oligolectic (pollen specialist) bees that collect pollen from the Onagraceae tend to be long and simple in contrast to those of their relatives (Linsley, 1958; Thorp, 1969; Pasteels & Pasteels, 1979). This is due to the large size of the pollen grains and to the presence of viscin threads (Skvarla et al., 1978) that tie the grains into webby masses which can be packed only with difficulty in scopae with closely spaced, branched hairs or the corbiculae of *Apis* (Linsley et al., 1963a). All 24 species of *Andrena* (*Onagrandrena*) are oligolectic on Onagraceae and have sparse scopae composed of unbranched setae (Linsley et al., 1963a, 1963b, 1964, 1973; MacSwain et al., 1973). Ten of the 25 species of the related *Andrena* (*Diandrena*) share the same oligolectic behavior and scopal adaptation to Onagraceae (Figs. 2–3), while most other *Diandrena* are oligoleges on Compositae and have dense scopae with branched hairs (Figs. 4–5) (Thorp, 1969). *Lasioglossum* (*Evyllaeus*) *oenotherae* Stevens and *L.* (*Sphecodogastra*) *texanus* Cresson have similarly simplified wide set scopal hairs contrasting sharply with the denser scopae of plumose hairs of other *L.* (*Evyllaeus*) species as shown in the SEM photos by Pasteels & Pasteels (1979). The scopae of *Melissodes* (*Callimelissodes*) *clarkiae* LaBerge and *Diadasia angusticeps* Timberlake, although containing branched hairs, are modified to handle *Clarkia* pollen in contrast to their closest relatives (MacSwain et al., 1973). The *Melissodes* has scopal hairs with fewer long slender branches than do other members of the genus (LaBerge, 1961). The scopal hairs of *D. angusticeps* are more separated and do not completely conceal the hind tibial surface, as they do in other *Diadasia* examined, which appear more closely packed and conceal the tibia. Several other oligoleges of Onagraceae do not show special modifications since their closest relatives possess simple scopal hairs (e.g., *Megachile*, *Synhalonia*, and *Anthophora*); have reduced scopae (e.g., *Ceratina*); or pack their pollen moist in loose scopae (e.g., *Perdita* and *Hesperapis*) and are thus preadapted to handle onagraceous pollen.

The hind tibial corbicula of *Apis* (Fig. 6) and its accessory structures (Figs. 7–8) have been well described and figured by Casteel (1912) and Hodges (1952). The important elements are the slightly concave outer face of the apically widened tibia which is surrounded by long curved simple hairs (Fig. 6). Near the apico-posterior corner is a single long hair and between it and the apical margin is a row of minute apically flattened hairs (Fig. 7). At the base of the hind basitarsus, opposite these hairs is a plate that is angled toward the outer face of the tibia and is covered with small tubercles, the auricle (Fig. 7). On the inner face of the hind

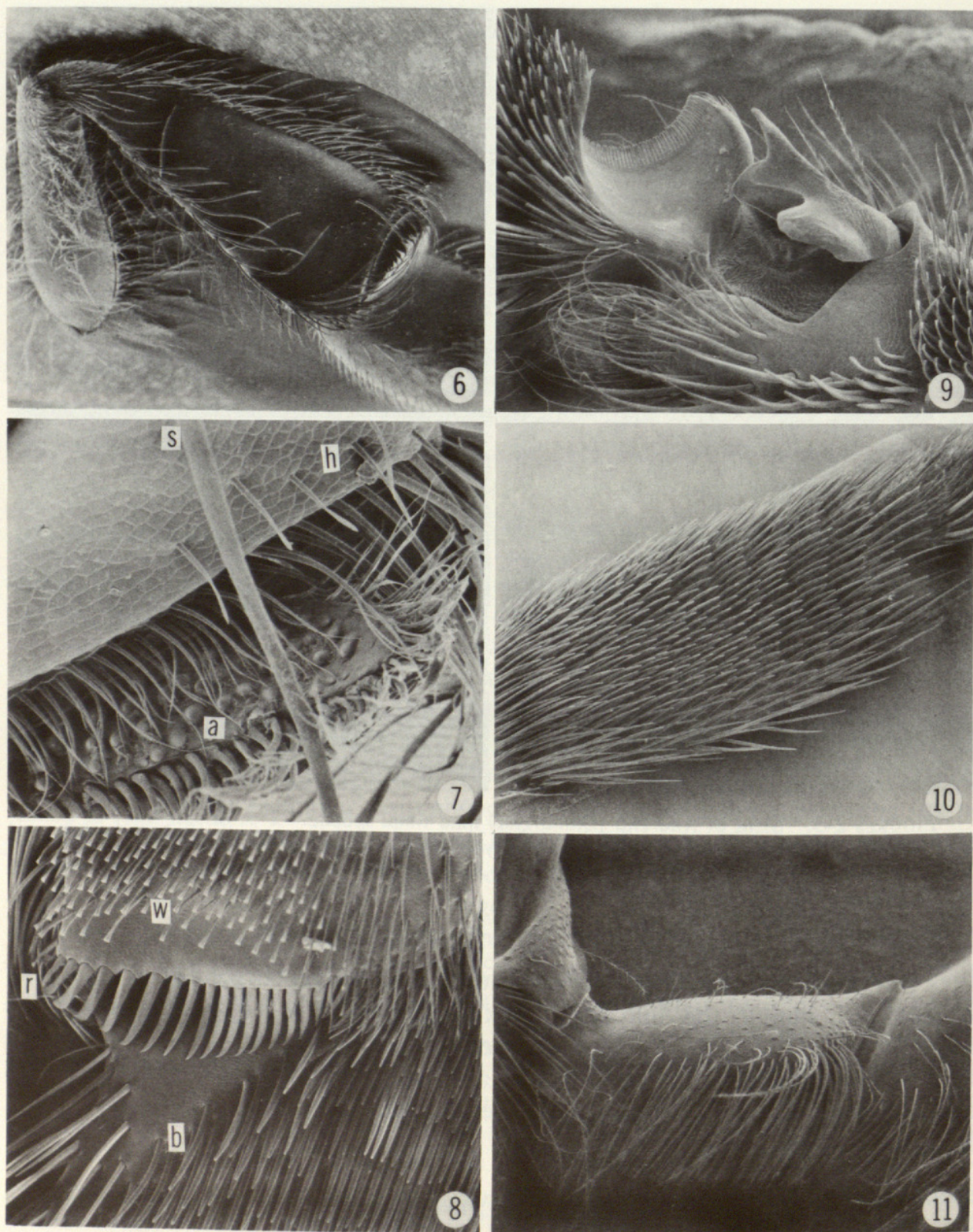


FIGURES 2–5. SEM of *Andrena* (*Diandrena*) hind tibial scopae.—2–3. Simple hairs of *Camissonia* (*Onagraceae*) *oligoleges*.—2. *A. (D. sperryi)* (100 \times).—3. *A. (D.) macswaini* (50 \times).—4–5. Branched hairs of *oligoleges* on *Compositae*.—4. *A. (D.) submoesta* on *Lasthenia* (200 \times).—5. *A. (D.) chalybioides* on *Agoseris* (80 \times).

tibia is a comb of stout setae, the rastellum (Fig. 8). The corbicular structures of *Bombus* are similar, the hind tibial apex of Euglossini is very expanded and the auricular area and rastellum are relatively small, and the Meliponinae lack the auricle and often have a stiff elongate hair comb projecting posteriorly from the anteroapical corner of the hind tibia, the pencillum (Winston & Michener, 1977; Michener et al., 1978).

POLLEN MOISTENING BEHAVIOR

The behavior of moistening pollen by adding nectar or oil to it as it is packed in an external transport apparatus allows a wide variety of pollen grains with different sizes and surface ornamentations to be transported by the same apparatus. Thus, the scopae of female Panurginae (*Andrenidae*) and *Melittidae* that add nectar to their pollen loads consist of sparse, short, only moderately branched hairs. Females of these groups may be oligolectic on flowers with extremely small pollen (e.g., *Boraginaceae*), large pollen (e.g., *Cactaceae*, *Malvaceae*), or large pollen with viscin threads forming webby masses (e.g., *Onagraceae*). Pollen is also packed moist with nectar or honey in the types of corbiculae of the *Apidae*.



FIGURES 6–11. SEM of *Apis mellifera* corbicula, accessory pollen packing and grooming structures.—6. Corbicula of hind leg (20 \times).—7. Tuberculate surface of auricle of base of hind basitarsus (a) with single hair (s) and row of minute flattened tip hairs (h) of tibial corbicula above (270 \times).—8. Inner face of hind tibiobasitarsal junction with rastellum (r), wing grooming hairs (w), and basitarsal brush (b) (65 \times).—9. Antennal cleaner of fore leg with apically expanded brush hairs of the inner face of the basitarsus and adjacent tibial field (80 \times).—10. Brush of trochanteral venter and adjacent field at base of femur of mid leg (55.2 \times).—11. Brush of inner face of mid basitarsus (42 \times).

This permits considerable flexibility with host specialization at the individual level, but generalization at the population or species level. This flexibility is important in a group of predominantly social species whose colonies survive beyond the bloom period of their floral hosts.

The scopae of bees that add oil to their pollen loads may consist of two types of hairs: long, stiff, unbranched guard hairs and short, flexible, multibranched hairs forming a woolly underlayer (Linsley & Cazier, 1963) (Fig. 12); or of one type that has a long, stiff shaft with dense, short, slender branches basally but not apically. Functionally, the two types are similar with the oil being trapped in the dense undercoat, while the stiff guard hairs provide protection and support (Roberts & Vallespir, 1978).

STRUCTURES FOR ACQUIRING POLLEN

The relatively dense vestiture of bees often with long hairs that branch (cf. Pasteels & Pasteels, 1972) in contrast to the sparse, short simple hairs of sphecoid wasps, provides a large surface for pollen acquisition. The electrostatic charges on the surface of bees are influenced by environmental conditions and may cause effects in bee behavior (Erickson, 1975; Warnke, 1976). Bees returning to a hive have positive surface potentials that tend to be higher than those leaving, indicating flight activity increases charge (Erickson, 1975). Since a high percentage of pollen carries a negative electrostatic charge (Stanley & Linskens, 1974), the differences in electric potential may enhance accumulation of pollen on the surfaces of bees.

Accessory structures for extracting pollen from certain flowers have evolved on some female bees. These involve specialized long hairs, usually hooked or wavy at the tips, near the mouthparts, or on the proboscis, (Figs. 14–15) or fore legs (Michener, 1944; Timberlake, 1954; Stage, 1966; Zavortink, 1972) (Table 2). Similarly, most female anthophorid bees that collect and add oils to their pollen loads have special combs on the fore and mid basitarsi (Fig. 13) for manipulating the oil (Vogel, 1974; Simpson et al., 1977; Roberts & Vallespir, 1978). Hind tibial spurs of bees that transport oils are often conspicuously pectinate (Roberts & Vallespir, 1978).

STRUCTURES FOR GROOMING AND POLLEN MANIPULATION

In addition to morphological adaptations for extracting and transporting pollen, structures involved in normal grooming behavior have been elaborated and new structures evolved for manipulation and transfer of pollen from the body surface of bees into their transport structures (Table 3). The concept of morphogenetic fields of hair types on bees was proposed by Pasteels & Pasteels (1973). It is supported by their subsequent studies with the scanning electron microscope on the structure, function, location, and evolution of hair types in bee scopae (Pasteels & Pasteels, 1974, 1975, 1976, 1979). These authors find that where fields of different hair types are contiguous the boundary contains hairs tending to be morphologically intermediate or an irregular mosaic of several hair types. These authors also have identified "regional fields" in which a hair type occurs on adjacent segments and may grade into other hair types peripherally. Abdominal

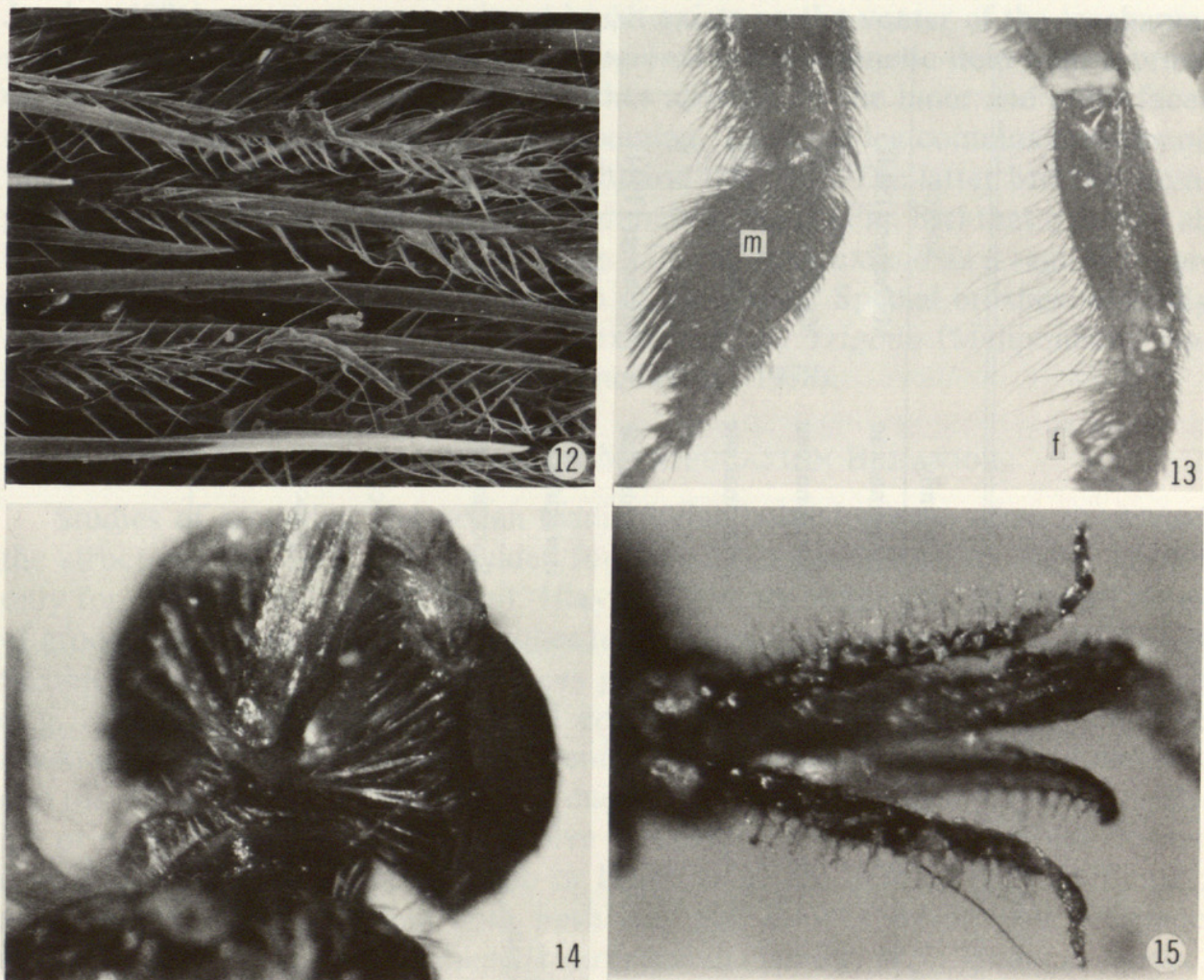
TABLE 2. Structures used in grooming and pollen manipulation in Apoidea. Symbols: + = present; ± = weakly developed; - = absent; footnotes identify limited occurrences of structures.

Location of Grooming Structures	Apoidea Families								
	Colletidae	Oxaeidae	Andrenidae	Halicidae	Melittidae	Fidelidae	Megachilidae	Anthophoridae	Apidae
Mouth parts									
Galea comb	+	-	+	+ ^e	+ ^f	-	-	± ^l	-
Stipes comb	-	-	-	-	-	-	-	+	+
Fore leg									
Antennal cleaner	+	+	+	+	+	+	+	+	+
Basitarsal brush and field (inner)	+	+	+	+	+	+	+	+	+
Mid leg									
Basitarsal brush (inner)	+	+	+	+	+	+	+	+	+
Tibial brush (outer apex)	+	+	+	+	+	+	+	+	+
Tibial comb (inner)	+	-	+	+	+ ^g	-	-	-	-
Femoral comb (ventral base)	+ ^a	-	+ ^c	±	+ ^h	-	-	-	-
Femoral brush (ventral base)	+ ^b	+	+ ^d	-	-	+	+ ^j	+	-
Trochanteral brush (ventral)	± ^b	±	+ ^d	-	+ ⁱ	±	± ^k	+	+
Hind leg									
Basitarsal brush (inner)	+	+	+	+	+	+	+	+	+
Tibial brush and field (inner)	+	+	+	+	+	+	+	+	+

^a *Colletes*.
^b *Lonchopria* and *Caupolicana*.
^c Panurginae.
^d Andreninae.
^e *Nomia* and *Corynura* (Jander, 1976).
^f *Dasypoda* (Jander, 1976).
^g Some *Hesperapis* and *Macropis* (Jander, 1976).
^h *Hesperapis*.
ⁱ Melittini.
^j Strong in Lithurginae, weak in Megachilinae.
^k Weak in Megachilinae, absent in Lithurginae.
^l *Ceratina* (Jander, 1976).

and hind leg scopae exemplify these regional morphogenetic fields (Pasteels & Pasteels, 1974, 1975, 1976, 1979) as do some grooming structures (Table 3). Hairs which form these fields appear to be derived from common body hairs.

The phylogeny of many grooming structures has been discussed by Grinfel'd (1969) and Jander (1976). The mouthpart combs that clean the fore legs of bees



FIGURES 12–15. Specialized hairs for transport and manipulation of oils, and extraction of hidden pollen.—12. Hind tibial scopa of *Exomalopsis* sp. with two types of hairs characteristic of oil collecting species (SEM) (200 \times).—13. Oil combs of fore (f) and mid (m) basitarsi of *Centris* sp.—14. Pollen extracting hairs on gena near proboscoidal fossa of *Perdita bellula*—15. Labial palpal hairs of *Proteridactylus jacinctana*. Photos 13–15 by D. L. Briggs.

and aid in ingestion of pollen are figured and discussed by Jander (1976). The antennal cleaner of the fore leg consists of the modified tibial spur and the notch of the basitarsus it opposes (Fig. 9). This structure occurs in both sexes throughout the higher Hymenoptera (Grinfel'd, 1969). The brush on the inner face of the fore basitarsus usually consists of unbranched setae with enlarged tips. This type of seta also often occurs apically on the inner face of the tibia (Fig. 9) forming a regional morphogenetic field (cf. Pasteels & Pasteels, 1973). Grinfel'd (1969) argued that the mid legs are more conservative than others due to the need for support on at least two adjacent pairs of legs when at rest and mentioned only the brush of the inner face of the mid basitarsus (Fig. 10) as a grooming tool. The mid basitarsal brush is universal among bees (Jander, 1976) and the best developed brushes have an oblique groove to receive and clean the fore leg with more efficiency than a flat brush. Jander (1976) also figures and describes opposing combs on the inner face of the mid tibia and the ventrobasally on the mid femur. The tibial comb is most extensive in Andrenidae and Halictidae, the two families that lack the oblique furrow of the mid basitarsus. In addition to the structures

TABLE 3. Specialized areas with hooked hairs for extracting pollen hidden within flower structures

Bee Taxa	Family	Areas with Hooked Hairs	Pollen Host
<i>Proteriades</i> , most species	Megachilidae	Labial palpi 1-2	<i>Cryptantha</i>
<i>Osmia</i> , very few species	Megachilidae	Labial palpi 1-2	<i>Cryptantha</i>
<i>Andrena</i> (<i>Scoliandrena</i>) <i>osmioides</i> Cockerell and undescribed species	Andrenidae	Galea and prementum	<i>Cryptantha</i>
<i>Calliopsis</i> (<i>Verbenapis</i>), 4 species	Andrenidae	Fore tarsi	<i>Verbena</i>
<i>Hesperapis elegantula</i> group, 3 species	Melittidae	Mandibles, stipes, and gena near fossa	<i>Coldenia</i>
<i>Perdita</i> (<i>Heteroperdita</i>) <i>arenaria</i> Timberlake and 6 relatives	Andrenidae	Gena near fossa	<i>Coldenia</i> and <i>Heliotropum</i>
<i>Hesperapis</i> <i>laticeps</i> Crawford	Melittidae	Mandibles, stipes and gena near fossa	<i>Mentzelia</i> and <i>Eucnide</i>
<i>Megandrena</i> (<i>Erythrarendra</i>) <i>mentzeliae</i> Zavortink	Andrenidae	Fore tarsi	<i>Mentzelia</i>

Jander (1976) mentions, a prominent brush exists on the venter of the trochanter in many bees and may form part of a regional morphogenetic field with a brush on the base of the femur (Fig. 11). Brushes apically on the inner and outer faces of the mid tibia may also function in grooming. The hind leg contains brushes on the inner faces of the basitarsus (Fig. 8b) and the tibia. The latter brush is composed of spatulate or chisel-tipped nonbranching setae (Fig. 8w) that occur in all bees (Pasteels & Pasteels, 1972) (cf. Fig. 1D) and may extend as a regional morphogenetic field to the apical inner face of the femur. Special brushes ventrally on the mesepisternum, mid and hind coxae in many *Trigona* (Meliponinae: Apidae) function in pollen transfer (Michener et al., 1978).

GROOMING AND POLLEN MANIPULATION BEHAVIOR

Studies of grooming and pollen manipulation behavior have often elucidated the structures involved and provided functional interpretations for those known only for their morphological detail. Hlavac (1975) identified two functional types of grooming structures: pressure-squeeze in which pressure applied to the tips of flexible setae squeezed together forces particles trapped between them outward (e.g., antennal cleaner of bees); and combs (single rows) or brushes (multiple rows) of slanted setae opposed by interdigitating bristles (e.g., basitibial brushes and the surfaces they clean). The two major types of interactions between grooming or pollen transfer structures involve scraping: contact only while the cleaner is moving in the direction its comb or brush setae are pointed (unidirectional); and rubbing: contact during both push and pull strokes resulting in alternate mutual cleaning of the parts rubbed (bidirectional) (Jander, 1976; Jander & Jander, 1978). Scraping movements are involved in pollen manipulation and packing. Rubbing movements terminate grooming by ridding the structures of debris. Thus, although Hlavac (1975) stated pollen collection is "grooming in reverse," this oversimplification applies only to the final movement of loading the pollen transport apparatus. Grooming behavior in most insects involves scraping of an area or structure with an appendage and then rubbing that appendage with its counterpart to get rid of debris. Pollen manipulation in bees requires integration of scraping cleaning behavior of a series of successive grooming structures to move pollen rearward to the transport apparatus. Loading the pollen transport apparatus involves the substitution of a scraping movement for the final rubbing motion that would shed any debris.

An exception to the rearward movement of pollen occurs in bees that have combs on the maxillary galea or stipes. In these bees the fore leg cleans the head and is in turn cleaned by a mouthpart comb (Jander, 1976). This aids in ingestion of pollen. This forward movement of pollen appears to be unique to bees possessing these combs and does not involve pollen cleaned from the rest of the body by the mid and hind legs (Michener et al., 1978).

The rearward sequence of pollen movement begins with the antennae being cleaned by the antennal cleaner of the fore leg. The basitarsal brush and field of the fore leg cleans most of the head and mouthparts. In most Anthophoridae it also cleans the thoracic dorsum (Jander, 1976). The fore leg is drawn between the folded mid leg. This is the most specialized leg cleaning motion in the Hymenoptera (Farish, 1972). The comb of the mid tibia and the comb of the base

of the mid femur scrape and remove pollen from the fore leg in the primitive bees (Jander, 1976). The outer apical brush of the mid tibia may groom the inner rear of the fore leg during the "elusive rudimentary" movement mentioned by Jander (1976). In many bees, especially Anthophoridae and Apidae, a brush on the venter of the trochanter scrapes pollen from the inner basitarsal brush of the fore leg, while the outer face of the fore leg is cleaned by the brush of the mid basitarsus. Pollen is scraped from the mid trochanteral brush and dorsum of the thorax by the brush of the mid basitarsus. Pollen concentrated in this latter brush is then applied directly to the hind leg scopa of most bees or the corbicula of most Meliponinae, or to the brush on the inside of the hind basitarsus in bees with abdominal scopae and Apidae with a well-developed auricle between the hind tibia and basitarsus (Michener et al., 1978). Wings are groomed between the side of the abdomen and the inner faces of the hind tibia and basitarsi with the hind leg as the primary cleaner of all wing surfaces and the abdomen laterally (Jander & Jander, 1978). However, my observations on grooming in honey bees suggest that only the brush of spatulate hairs of the inner face of the hind tibia and apex of the femur cleans the wings and lateral abdomen. Pollen is cleaned from these brushes by the opposite (contralateral) hind basitarsal brush. Pollen accumulated in the hind basitarsal brushes is scraped and packed into abdominal scopae or removed by the contralateral rastellum (Fig. 8) and moved to the outer face of the hind tibial corbicula in Apidae with a well-developed auricle (Fig. 7). Pollen on the hind basitarsal brush in other bees cannot be packed in the pollen transport apparatus, but may not be rubbed off until the female unloads pollen in her brood cell.

Pollen packing in the corbicula of *Apis* has been well described by Casteel (1912) and Hodges (1952), and of *Bombus* by Sladen (1912). Basically, pollen is scraped from the opposite hind basitarsal brush by the rastellum and accumulates behind the rastellum. It is forced up and out onto the corbicula by the auricle as the tibiobasitarsal joint is closed. The single hair on the corbicula in *Apis* is assumed to play a role in securing the pollen load (Casteel, 1912; Hodges, 1952) and a similar role is suggested for the two or three hairs at the "entrance to the corbicula" in *Bombus* (Sladen, 1912). Legge & Bole (1975) noted variations in position of the single hair in honey bees and suggested that it was not essential for the formation of pollen loads since it was absent or too close to the posterior border in some bees to be functional. Hodges (1967) removed the single hair from one corbicula of two bees and found that the pollen load on the corbicula without the hair was smaller (about one-third the weight) than that on the corbicula of the leg with the hair. Witherell (1972) found that a small proportion of hairless mutant workers were able to gather small oddly positioned pollen loads despite the lack of the single corbicular hair and with only 5–10% of normal body hair. Thus, although the absence of the single corbicular hair does not completely prohibit formation of pollen loads, it is evident from the last two studies that the hair is important in the formation of a normal full pollen load.

Michener et al. (1978) have critically compared pollen manipulation in the family Apidae and described the types of pollen packing behavior. The placement of pollen directly onto the corbicula by the mid legs (Type I) that occurs rarely in some *Trigona* (Meliponinae) collecting large sticky *Cucurbita* pollen is similar to the manner most bees load the scopa of the hind leg. The application of pollen

on the outside of the tibiotarsal joint and the subsequent pushing it basad on the corbicula by scraping the hind leg along the mid leg and by flexing the basitarsus (Type II, ipsilateral) is characteristic of many Meliponinae and probably Euglossini. Pollen may be scraped from the brush on the inner face of the hind basitarsal brush by the rastellum of the opposite leg and pushed through the auricle onto the outer face of the corbicula (Type II, contralateral) in *Apis*, *Bombus*, and rarely in Melioninae. The corbicular structure and pollen packing behavior along with other derived characters was used by Winston & Michener (1977) to show the phylogenetic distinctness between Meliponinae and Apinae.

The loading of nesting materials (e.g., mud, resins, cerumen, etc.) in the corbicula of Meliponinae, Apinae, and Euglossini and the collection of aromatic compounds by male Euglossini are similar to Type I pollen packing (Michener et al., 1978).

When a pollen-laden female returns to her nest, the pollen is deposited in a brood cell presumably by a final grooming motion. Removal of pollen loads in the brood nest has not been well studied since relatively few bees have been studied in observation nests. *Apis* and *Bombus* workers extend the hind legs into a pollen storage cell and simultaneously remove both pollen pellets from the corbiculae with their mid basitarsi. Even *Apis* that have lost their pollen loads in a trap at the hive entrance will complete deposition behavior before returning to forage (McDonald, 1968). Bees transporting dry pollen in scopae presumably scrape pollen from the scopa with the structure used in loading the scopa (i.e., mid or hind basitarsal brushes) and remove it by rubbing opposing brushes of each leg pair. The mid basitarsal brushes may also be scraped by the hind basitarsal brushes which are then rubbed together to deposit pollen in the brood cell.

FORAGING BEHAVIOR

Bees exhibit many other behavioral adaptations in foraging behavior that facilitate the collection of pollen in addition to those already discussed for packing pollen for transport (modification of grooming behavior) and for overcoming structural limits to size of pollen grains that can be packed (e.g., moistening pollen). Many of these behaviors involve some degree of learning or modification of behavior to fit specific situations.

FLORAL CONSTANCY

Most bees exhibit a high degree of constancy to floral species at the individual level when foraging for pollen (Grant, 1950; Linsley, 1958; Free, 1963, 1970). This increases foraging efficiency and exploitation of a rewarding resource by reducing time and effort involved in learning to locate new sources and to manipulate diverse floral mechanisms. Efficiency in exploiting floral resources by eusocial Apidae is further enhanced by elaborate dance communication in *Apis* (von Frisch, 1967; Lindauer, 1967); by trail marking in Meliponini (Lindauer, 1967; Esch, 1967); and by constantly monitoring the changing floral community through a process of majoring and minoring (Heinrich, 1976; Oster & Heinrich, 1976) in bumble bees since they lack the ability to communicate food source location to their hive mates.

Constancy to pollen sources at the population and species level is called oligolecty (Robertson, 1925). Linsley & MacSwain (1958) define oligolectic species as those "in which the individual members of the population, throughout its range and in the presence of other pollen sources, consistently and regularly collect pollen from but a single plant species or a group of a similar or related plant species, turning to other sources, if at all, only when there is a local shortage or absence of that pollen." The origin of this type of host specificity was hotly debated by Robertson (1912, 1914, 1925) and Lovell (1912, 1913, 1914, 1918). Robertson suggested oligolecty arose from interspecific competition while pollen was limiting. Lovell argued that there were always sufficient supplies of pollen, but that individuals specializing on a pollen source were more efficient and therefore produced more progeny. However, the two hypotheses are not necessarily mutually exclusive. During times of pollen stress the species with individuals that compete best for the limited pollen available from a plant species will leave the most progeny. During periods of pollen abundance those individuals most efficient at obtaining pollen from the plant host will leave the most progeny. Thus, the two mechanisms may reinforce each other, enhancing the rate of evolution toward host specificity. Some bees may survive interspecific competition by specializing on plants unattractive to others due to unusual floral characteristics such as pollen larger than average size, hidden from most visitors, presented only during unusual and restricted periods, or held together in webby masses by viscin threads.

Oligolecty occurs at levels of organization above the species, including the subgenera *Onagrاندrena*, *Diاندrena* (*Andrena*: Andrenidae) (Linsley et al., 1963a, 1963b, 1964, 1973; Thorp, 1969; MacSwain et al., 1973) and *Sphecodogastra* (*Lasioglossum*: Halictidae) (Linsley et al., 1963b; Kerfoot, 1967b); the genera *Hesperapis* (Melittidae) (Stage, 1966), *Proteriades* (Megachilidae) (Timberlake & Michener, 1950), *Diadasia* (Anthophoridae) (Linsley & MacSwain, 1957, 1958) and *Xenoglossa* (Anthophoridae) (Hurd & Linsley, 1967). Although all members of some of these taxa are oligolectic on single plant genera or families (e.g., *Xenoglossa* on *Cucurbita*, *Andrena* (*Onagrاندrena*) on Onagraceae) some contain species oligolectic on distinctly different plant hosts from their relatives. Thus, most *Diاندrena* are oligolectic on Onagraceae (10) or ligulate Compositae (10) while others are oligolectic on nonligulate Compositae (3), *Ranunculus* (1), and *Arenaria* (1) (Thorp, 1969); similarly most North American *Diadasia* are oligolectic on Malvaceae (14) while others are oligolectes of *Opuntia* (3), *Convolvulus* (1), *Clarkia* (1), and *Helianthus* (1) (Linsley & MacSwain, 1957). Verbal models to account for speciation and host shifts within higher taxa of oligolectic bees have been proposed by Linsley & MacSwain (1957, 1958), Thorp (1969), and Cruden (1972).

Bees not only express fidelity to crop species, but also to areas within a crop (Singh, 1950; Thorp, unpubl.). They tend to forage through the crop in the most economical pattern, e.g., tending to visit nearest-neighbor flowers (Levin & Kester, 1969) and to fly in the direction of their previous flight (Levin et al., 1971). Smaller more host specific bees tend to fit near-neighbor foraging models more closely than larger polylectic bees (Estes, Thorp & Briggs, unpubl.).

SEASONAL SYNCHRONY

Oligolecty usually involves close seasonal synchrony between the flight period of the adult bee and the bloom period of its pollen hosts (Robertson, 1929) based on observations at the flower. However, there may be considerable variation from season to season when first emergence of bees from their nests is related to first bloom (Linsley, 1958). Still, seasonal synchronization remains reasonably close. The extrinsic stimuli and intrinsic responses that govern this synchrony are not well understood, especially since the environments of the plant and bees are quite different (Linsley, 1958). The seasonal appearance of a vernal oligolectic bee (*Hesperapis*: Melittidae) and the flowers of its pollen host (*Geraea*: Compositae) in October following unseasonal rains of more than 25 cm in the Colorado Desert of California (Hurd, 1957) is strong supportive evidence that the plant and the bee respond ultimately to the same extrinsic stimuli. There is evidence that both plants and bees can holdover unfavorable seasons and delay their appearance up to two years, e.g., an *Andrena* (Andrenidae) oligolectic on *Limnanthes* (Limnanthaceae) and a polylectic *Trachusa* (Megachilidae) during the 1975–1976 drought years in California (Thorp, unpubl.). The foregoing suggests moisture is the critical extrinsic stimulus; however, it is well known that temperature is the critical factor determining emergence of the alfalfa leafcutting bee, *Megachile rotundata* (Fabricius). Most bees of seasonal environments (temperate, and semi-arid tropical) holdover the unfavorable parts of the year in diapause (physiological arrestment) in their natal cells as adults (many vernal active species) or more often as postdefecating larvae. This physiological adaptation is an important part of the mechanism for synchronizing bloom and bee activity seasonally.

LOCATING POLLEN SOURCES

Once a female bee has emerged, mated, and constructed her nest to the proper stage, she must locate a pollen source. Flowers produce a wealth of recognition cues, e.g., chemical, visual, and even tactile that correspond to the sensory capabilities of bees and other pollinators. Bees even perceive some cues man does not (e.g., ultraviolet patterns) (Lutz, 1924; Daumer, 1956, 1958; von Frisch, 1967). Many of these cues are used by bees to recognize and discriminate rewarding from nonrewarding flowers, but which, if any, of these stimuli elicit innate responses attracting naive bees has not been well demonstrated. Chemical stimuli may be most important, since the only experience a newly emerged solitary bee has had with an appropriate pollen source is the pollen in its natal cell (Linsley, 1958). In this regard specific chemicals of pollen may serve as attractants (Stanley & Linsens, 1974) or at least recognition cues for bees. A pollen lipid has been identified as attractive to honey bees (Lepage & Boch, 1968; Hopkins et al., 1969, 1975). This preimaginal conditioning to pollen odors assumes an important role in reinforcing intrinsic adaptations associated with the host specificity and in the model proposed by Thorp (1969) to account for host switches among species of oligolectic taxa.

Evidence that suggests a brief period of searching and learning is involved in finding the proper pollen source comes from *Andrena* (*Onagrandrena*) *linsleyi*

TABLE 4. Examples of daily synchrony between oligolectic bees and their pollen hosts.

Daily Period ^a	Bee Taxa	Family	Pollen Host	
Matinal	<i>Andrena (Onagrاندrena)</i> <i>mojavensis</i> Linsley & MacSwain and 5 relatives	Andrenidae	<i>Camissonia</i>	Or
	<i>Andrena (Diandrena)</i> <i>chalybaea</i> (Cresson) and 8 relatives	Andrenidae	<i>Camissonia</i>	Or
	<i>Andrena (Diandrena)</i> <i>chalybioides</i> (Viereck) and 7 relatives	Andrenidae	<i>Agoseris</i>	Co
	<i>Hemihalictus lustrans</i> (Cockerell)	Halictidae	<i>Pyrrhopappus</i>	Co
	<i>Xenoglossa</i> , all 7 species, and <i>Peponapis</i> , all 13 species	Anthophoridae	<i>Cucurbita</i>	Cu
Late Afternoon	<i>Andrena (Onagrاندrena)</i> <i>rozeni</i> Linsley & MacSwain	Andrenidae	<i>Camissonia</i>	Or
	<i>Andrena (Onagrاندrena)</i> <i>vespertina</i> Linsley & MacSwain	Andrenidae	<i>Camissonia</i>	Or
Matinal & Late Afternoon	<i>Andrena (Onagrاندrena)</i> <i>raveni</i> Linsley & MacSwain	Andrenidae	<i>Camissonia</i>	Or
	<i>Lasioglossum (Evylaeus)</i> <i>galpinsiae</i> Cockerell	Halictidae	<i>Oenothera</i>	Or
Crepuscular & Nocturnal	<i>Perdita (Xerophasma)</i> <i>pallida</i> Timberlake	Andrenidae	<i>Oenothera</i>	Or
	<i>bequaertiana</i> Cockerell			
	<i>Lasioglossum (Sphecodogastra)</i> <i>texanum</i> (Cresson)	Halictidae	<i>Oenothera</i>	Or
	<i>noctivagum</i> Linsley & MacSwain			
	<i>Megalopta centralis</i>	Halictidae	<i>Solanum</i>	So
Diurnal	<i>Andrena (Diandrena)</i> <i>submoesta</i> Viereck	Andrenidae	<i>Lasthenia</i>	Co
	<i>puthua</i> (Cockerell)			

TABLE 4. Continued.

Daily Period ^a	Bee Taxa	Family	Pollen Host	
	<i>Andrena (Diandrena)</i> <i>lewisorum</i> Thorp	Andrenidae	<i>Clarkia</i>	Or
	<i>Hesperapis regularis</i> (Cresson)	Melittidae	<i>Clarkia</i>	Or
	<i>Megachile (Derotropis)</i> <i>gravita</i> Mitchell	Megachilidae	<i>Clarkia</i>	Or
	<i>pascoensis</i> Mitchell			
	<i>Diadasia angusticeps</i> Timberlake	Anthophoridae	<i>Clarkia</i>	Or
	<i>Diadasia enavata</i> (Cresson)	Anthophoridae	<i>Helianthus</i>	Co
	<i>Svastra obliqua</i> <i>expurgata</i> (Cockerell)	Anthophoridae	<i>Helianthus</i>	Co

^a Daily periods as defined by Linsley & Cazier (1970).

Timberlake (Linsley et al., 1963a). This bee is an oligolege on the nocturnal blooming *Oenothera* on which it forages for residual pollen in the early morning. Early in their activity season females forage for pollen in the morning and afternoon on *Oenothera* and late afternoon opening species of the related *Camissonia*, but as the bloom of the former increases, the females of *A. linsleyi* shift their foraging to the preferred *Oenothera* in the early morning.

DIURNAL SYNCHRONY

Flowers often present pollen at specific and limited times of day and many bees adapt their foraging period for daily synchrony with their host. Many oligolectic bees and their host plants are matinal, a few are late afternoon, or crepuscular or nocturnal, and some are active all day (Table 4). Even within limited daily foraging periods a complex of oligolectic bee species may further partition a pollen resource with distinctly separated diurnal peak foraging times although their total foraging periods overlap, e.g., matinal *Andrena* (*Onagrandrena*) and *A. (Diandrena)* on *Camissonia* (Linsley et al., 1964, 1973; Thorp, 1969). Thorp (1969) found two sites with 8–12 species of *A. (Diandrena)* with six species each coexisting on the same species of *Camissonia*. The division is often related to adaptations of size and color with the largest and darkest forms visiting earliest in the day (Thorp, 1969; Linsley, 1978). Similar patterns occur with groups of polylectic species adapted to matinal plants such as *Solanum* (Linsley & Cazier, 1963; Bowers, 1975), *Cassia* (Thorp & Estes, 1975).

Some bees regularly forage both morning and late afternoon, e.g., oligolectic *Andrena (Onagrandrena) raveni* Linsley & MacSwain (Linsley et al., 1963b) and polylectic Caupolicaniini (Linsley & Cazier, 1970). Other bees apparently learn proper timing, e.g., *Andrena linsleyi* (Linsley et al., 1963a). Knerer & MacKay (1969) found that oligolectic *Lasioglossum (Evylaeus) oenotherae* (Stevens) females shifted their foraging period on *Oenothera* from morning and evening to morning only after a brief learning period.

The time sense of honey bees has been demonstrated frequently (Ribbands, 1953; von Frisch, 1967). This sense permits honey bees to return to a food source in synchrony with its presentation. Usually some bees will arrive early each day. As food is successfully collected and returned to the hive, bees that have had experience with the crop are stimulated to forage by the odor of the incoming food. This type of conditioned response (Wenner & Johnson, 1966) can be used in training experiments, since introducing a training odor into the hive will stimulate trained bees to return to the training arena (Gary & Witherell, 1971). New recruits are directed to the crop by dance communication and odor.

Most polylectic and many oligolectic bees are associated with diurnal plants that have pollen available all day long, e.g., *Clarkia* (MacSwain et al., 1973); *Larrea* (Hurd & Linsley, 1975) and *Helianthus* (Hurd et al., 1980). These bees usually divide the diurnal foraging period into overlapping periods based on consistent differences in behavior (Linsley, 1978). Thus, Hurd & Linsley (1975) identified four diurnal foraging patterns of bees on *Larrea*: early morning and early afternoon; early to mid morning; mid morning to late afternoon; and throughout much of the day.

Diurnal synchrony of foraging by bees with pollen presentation of their hosts

appears to be primarily learned behavior. It may be delayed by extrinsic factors such as cloud cover, fog, or rain, but is often resumed in the same synchronous sequence when the weather ameliorates (Thorp, 1969; Estes & Thorp, 1975; Linsley, 1978). Bees may possess special structural adaptations, e.g., enlarged ocelli of crepuscular or nocturnal bees (Kerfoot, 1967a) or behavioral mechanisms, e.g., thermoregulation (Heinrich, 1974) that permit flight at lower light intensities or lower temperatures than their relatives are capable of.

RESPONSES TO UNUSUAL POLLEN PRESENTATION

Bees often exhibit special behavioral adaptations to unusual modes of pollen presentation or to material with pollenlike characteristics. Anthers of about 544 genera and an estimated 15,000–20,000 species of flowering plants dehisce through apical pores. Representatives of 444 of these genera may require vibratory behavior by bees to release pollen (Buchmann, 1978). Bees grasp apically pored anthers and vibrate them making an audible buzz by shivering the indirect flight muscles of the thorax. This shivering is adapted from normal flight, but with the wings remaining reflexed over the abdomen and is used in thermoregulation as preflight warm-up. This application of shivering behavior not only releases pollen from anthers with apical pores onto the bee where it can be groomed and packed, but also elevates the temperature of the bee, a useful by-product for early morning foragers (Bowers, 1975; Thorp & Estes, 1975). Some flowers with nonporicidal anthers are vibrated by their visitors, e.g., a *Melampyrum* (Scrophulariaceae) (Meidell, 1944) and a *Pedicularis* (Scrophulariaceae) (Macior, 1968).

The pollen grains of most buzz-pollinated flowers are usually small, unsculptured, and without pollenkitt (Buchmann & Hurley, 1978). Thus it is not surprising that in the complex of bees on *Solanum* studied by Linsley & Cazier (1963) most had dense scopae or added oil or nectar to the pollen loads.

In addition to buzzing apically dehiscent anthers, bees may also milk them by grasping an anther near its base with the mandibles and pulling apically (Thorp & Estes, 1975). Biting anthers with the mandibles is not an uncommon method among bees to release more pollen. However, biting their way into an unopened flower to collect pollen from anthers that dehisce just prior to anthesis (floral opening) is rare, but has been reported for a *Perdita* on *Proboscidea* (Hurd & Linsley, 1963). Although most zygomorphic flowers present their pollen so that it will be distributed either nototribically or sternotribically (Macior, 1974), some bees that are not the proper size to pick up pollen the proper way may modify their behavior, e.g., due to the size disparity between small bees like *Panurginus* and the large flowers of *Downingia bacigalupii*, the anther column does not contact the bee nototribically as in most other *Downingia* species so the bee collects pollen sternotribically while hanging upside down at the end of the column (Thorp, 1976). Some bees also may learn to operate special trip or trigger mechanisms to make pollen more readily available for collection, such as the trigger hairs of *Downingia* (Thorp, 1976). Bees, especially of the family Apidae, will sometimes collect pollen from anemophilous plants (Bogdan, 1962; Soderstrom & Calderón, 1971; Pojar, 1973). Honey bees frequently collect corn pollen and occasionally other pollenlike materials, such as rust spores (Chapman, 1964), feed mill dust, and sawdust. Some bees glean pollen that has fallen from the

anthers onto other floral parts (Wille, 1963). Females of *Trigona* (*Scaura*) exhibit morphological and behavioral adaptations for gleaning pollen from flower parts and leaves (Michener et al., 1978). A few bees will even collect pollen from the body surface (Laroca & Winston, 1978) or the scopae of other bees (Thorp & Briggs, 1979).

CONCLUSIONS

Bees exhibit many adaptations for the acquisition, manipulation, and packing of pollen for transport to their brood nests. These include structures that may not be modified from those normally used in grooming to the unique scopae and corbiculae evolved for the transport of the dustlike material, pollen, that serves as brood food for bees. These unique structures also may be used to transport other food materials such as oils, or to transport nesting materials such as mud, resin, or cerumen. Scopal hairs may show further modification in their spacing and amount of branching in relation to the size and structure of the pollen grains they normally carry. Other special hair groups have evolved in some bees for the extraction of cryptic pollen and the manipulation of plant oils. Enlarged ocelli are present in many bees which forage at periods of low light intensity.

Physiological adaptations include diapause during unfavorable parts of the year and for holding over unfavorable years so that bees can be seasonally synchronized with their pollen sources. Time sense makes possible daily synchrony with specific pollen presentation periods. The shivering mechanism for thermoregulation in some permits flight at low temperatures, and is sometimes applied in releasing pollen from buzz-pollinated plants. The general visual, chemical, and tactile senses are attuned to the recognition cues presented by plants, including the ability to see ultraviolet patterns invisible to man.

Behavior patterns, including grooming, adding nectar to pollen loads, host specificity, preimaginal conditioning, interfloral flight patterns, adaptability in responding to diverse structures and modes of pollen presentation, can be applied to new situations and be used to modify innate structural and physiological adaptations. Most of the behavioral patterns involve learning which promotes considerable flexibility in response to new situations. Fidelity to area, near-neighbor, and directional foraging have important effects on the genetic structure of plant populations.

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