The Biology and External Morphology of Bees

With a Synopsis of the Genera of Northwestern America

Agricultural Experiment Station √ Oregon State University √ Corvallis

Northwestern America as interpreted for taxonomic synopses.

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W. P. STEPHEN, G. E. BOHART, and P. F. TORCHIO

Introduction

ENTOMOLOGISTS, BOTANISTS, and AGRICULTURISTS all have occasion to concern themselves with bees. The entomologist is fascinated by their complex behavior patterns, the botanist needs to evaluate their significance in floral biology, and the agriculturist must take them into account as vital factors in crop production. Finally, the apiculturist often wishes to extend his knowledge of bees beyond the confines of the honey bee. Recent years have seen a revival of interest in bees by all of these groups and, with it, a profusion of taxonomic and biological literature. This interest among scientists has been stimulated by exciting biological and behavioral discoveries, attempts to determine the value of biological information, and a concern in pollinator management by farmers engaged in the production of seed, fruit, and vegetable crops.

It is our hope that the following general synthesis of knowledge about bees, with special emphasis on northwestern genera, will be of general interest to many entomologists, botanists, and agriculturists and may have special value as a handbook for workers in the Northwest. The study was prepared so that it would be useful to students for class and field use, and apprise workers of the present state of knowledge in bees so that existing gaps may be more systematically filled. It has also presented an opportunity to speculate on several facets of systematics and ethology.

This work reviews present knowledge of the morphology and biology of bees in general, but emphasizes northwestern forms and, in many instances, uses them as standards of reference. No attempt is made to systematically cover morphological and biological information for each taxon, although morphological information of particular value for the separation of taxonomic groups is included. The taxonomic treatment does not extend below the generic level and is confined to northwestern forms except for a more comprehensive treatment of families. The Northwest, as here interpreted, includes the area west of the Rocky Mountains, bounded on the south by the latitude 41° N, and extending north to include British Columbia and Alaska. (See the map inside the front cover.) Several genera included in the key have not yet been taken in the above-defined area, but because they are known to occur immediately to the south or east there is a possibility that they may have escaped detection or else that they may soon become members of our bee fauna.

No species authors names are cited in the text; rather, they are included in the index at the end of this publication.

External Morphology of Bees

Adult Bees

The sections dealing with the morphological terminology used in this series of studies are presented not as definitive treatises on bee morphology, but as guides to those structures having taxonomic significance. Much of the terminology used herein is that of Michener (1944a) which has been widely accepted in apoid systematics. Our knowledge of comparative morphology in insects in general, and Hymenoptera in particular, is still woefully inadequate, and any attempt to establish a fixed general terminology for the morphologically recognizable structures in the bees would be premature. This is not to imply that absolute structural homology may not exist throughout Insecta and that our ultimate goal should not be directed towards its realization, but rather that we should adopt a standardized terminology so that one apoid taxonomist may know immediately to which structure the other is referring.

Classically, three body regions are designated among insects: the head, thorax, and abdomen. Michener (1944a) states that the use of the term mesosoma for the fused thoracic region in the Clistogastra is morphologically preferable to thorax. This region is composed of four actual segments: the prothorax, mesothorax, metathorax, and the first abdominal segment (the propodeum), which is sharply constricted posteriorly to form the petiole common to bees, wasps, and ants. Mitchell (1960) reverts to the use of the term thorax for this region, indicating that he prefers the older and more generally used term for ease of reference. We follow Mitchell's use of the term thorax even though it includes the first abdominal segment as an integral portion of that structure.

The third body region, generally referred to as the abdomen, is separated from the thorax by a very marked constriction. This has been referred to by Michener as the *metasoma,* for it consists of the second and subsequent morphological segments, the first being immovably attached to the thorax. In this bulletin the term abdomen is applied to this general body region. The term *metasomal* is used only in its adjectival sense when referring to the various abdominal terga or sterna. Thus the tergum of the second true abdominal segment is referred to as the first metasomal tergum, and the tergum of the third true morphological segment of the abdomen is referred to as the second metasomal tergum, and so on (see Fig. 1).

The following section covers the principal morphological structures employed in species discrimination among bees. The discussion of these structures includes as much comparative information as is deemed necessary for persons unfamiliar with the group. The illustrations, however, are based principally on the halictid bee, *Nomia melanderi,* as it is generally one of the most readily available species in northwestern America. Although this bee is not as "primitive" as members of the Colletidae, it is more so than *Apis* and *Anthophora,* which have been used as standards of reference in previous studies (Snodgrass, 1956; Michener, 1944a).

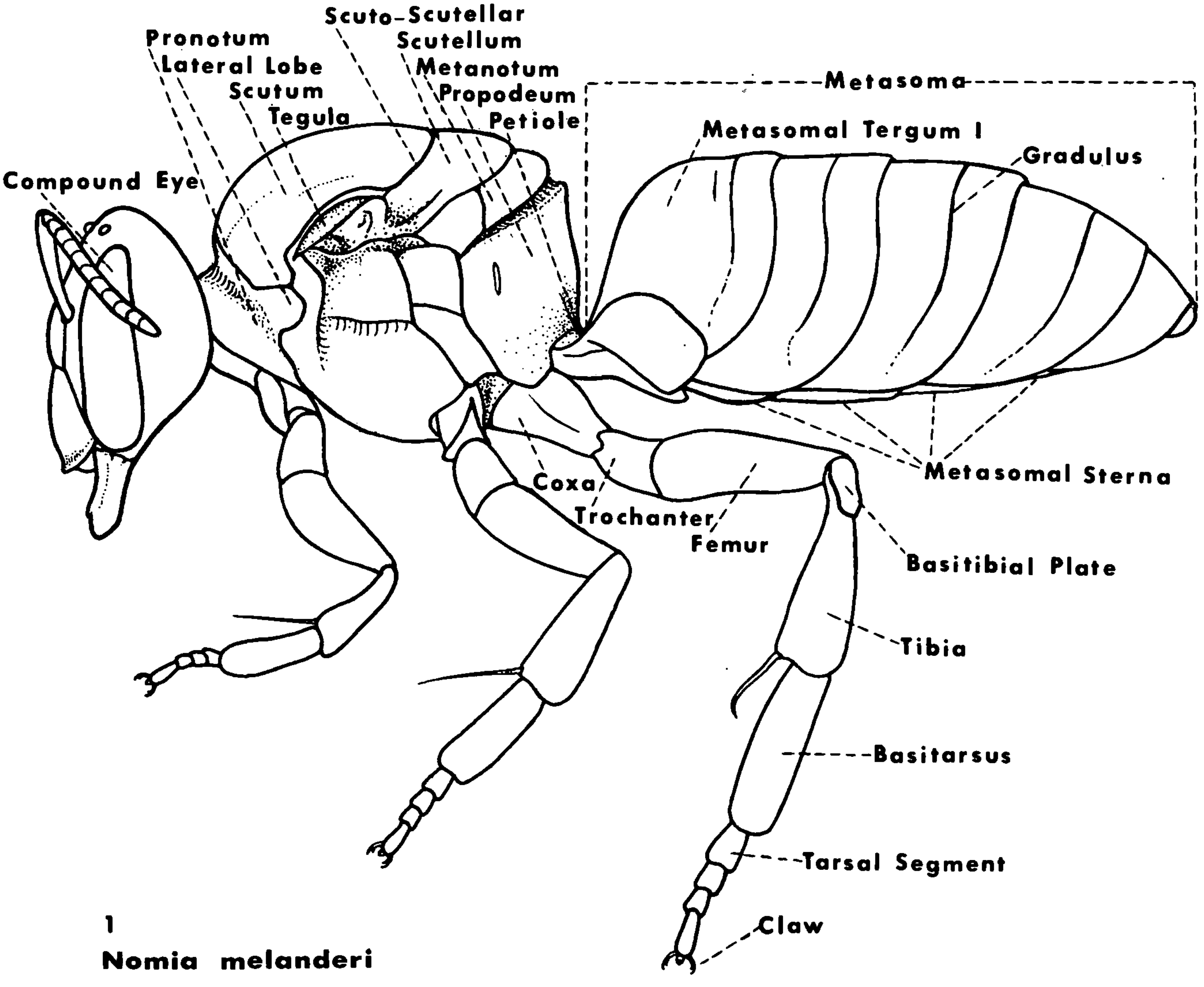
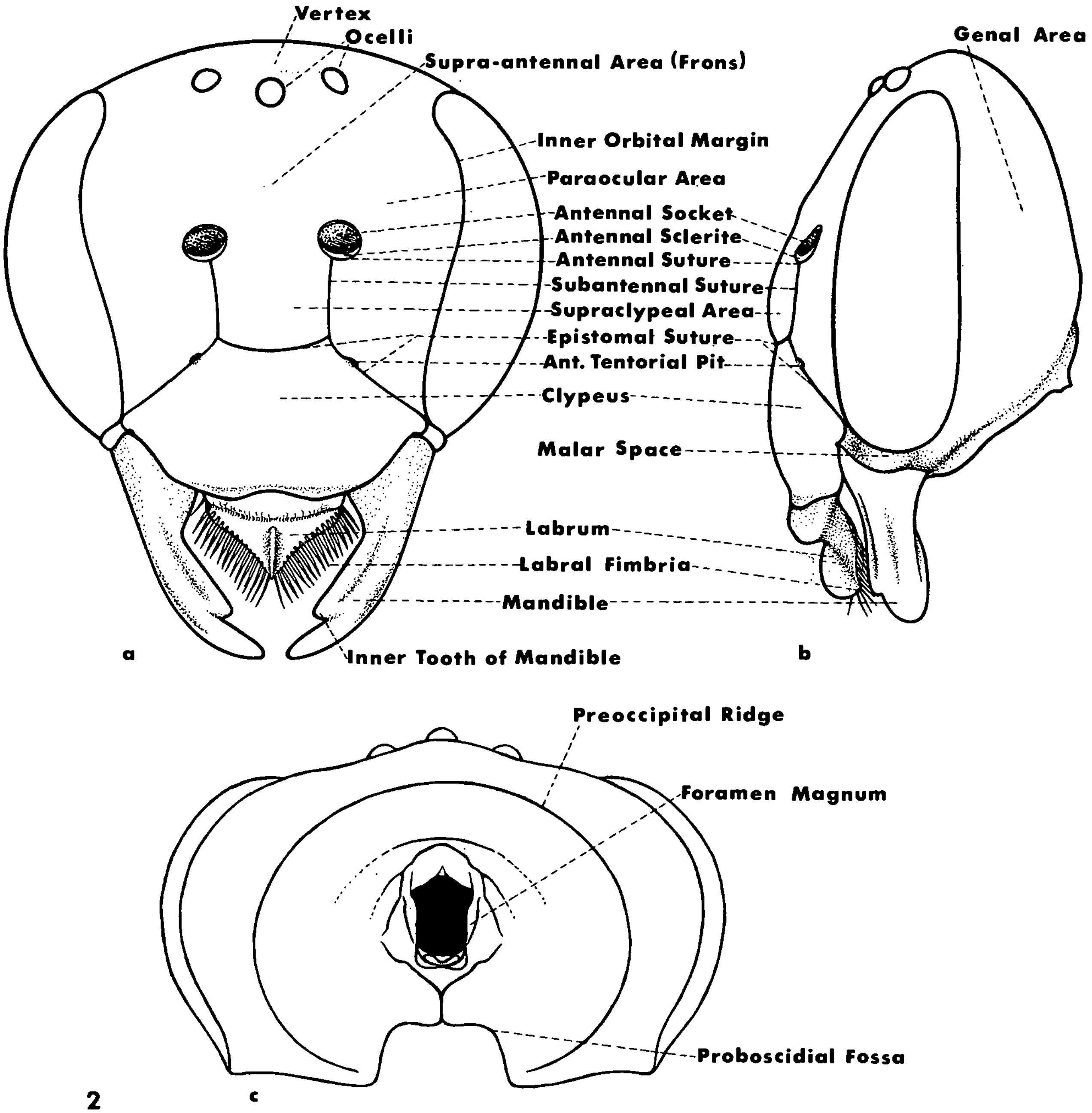


FIGURE 1. Lateral view of *Nomia melanderi* female.



2

Nomia melanderi

FIGURE 2. Frontal, lateral, and ventral views of the head of *Nomia melanderi.*

Head

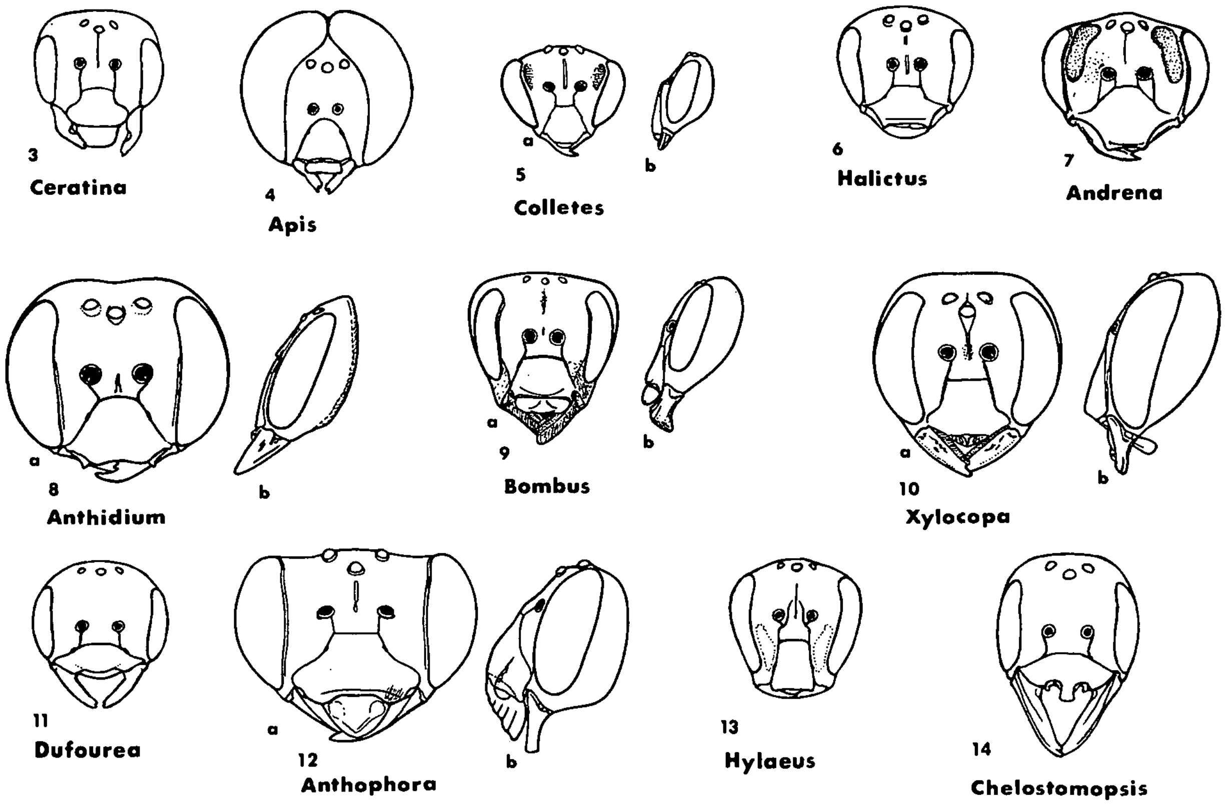
The head is hypognathous with the face perpendicular to the longitudinal axis of the body (Fig. 1). The large convex *compound eyes* occupy much of the lateral surface of the head (Fig 2a). In some genera, such as *Ceratina* (Fig. 3), the compound eyes do not nearly reach the upper margin of the sides of the head, whereas in the males of certain species of *Bombus* and *Apis* (Fig. 4) the compound eyes extend over the top of the head and meet at the mid line. The inner margins of the compound eyes, *inner orbital margins,* may converge below as in most colletids and halictids (Figs. 5, 6); may be parallel as in andrenids and megachilids (Figs. 7, 8); or more rarely diverge as in some dufoureines and andrenids. In most genera of bees the eyes are bare. However, in the American *Coelioxys, Apis,* and in the single species of *Holcopasites* that occurs in the Northwest, the eyes are densely covered with short, erect hairs.

The *vertex* is the top of the head, bounded anteriorly by an imaginary horizontal line beneath the anterior ocellus, posteriorly by the *preoccipital ridge,* and laterally by the inner margins of the compound eyes. This region of the head contains three *ocelli* of varying size (Fig. 2a). They are usually arranged in the form of a broad triangle at the summit of the vertex, but their position and size varies considerably in bees. For example, in most *Bombus* females, they are positioned in almost a linear order at the summit (Fig. 9), whereas in *Apis* and*Xylocopa* males (Fig .10) they are closely arranged well down on the face. In the nocturnal bee, *Halictus* (*Sphecodogastra*) *texanus,* they are unusually large—larger than the spaces between them.

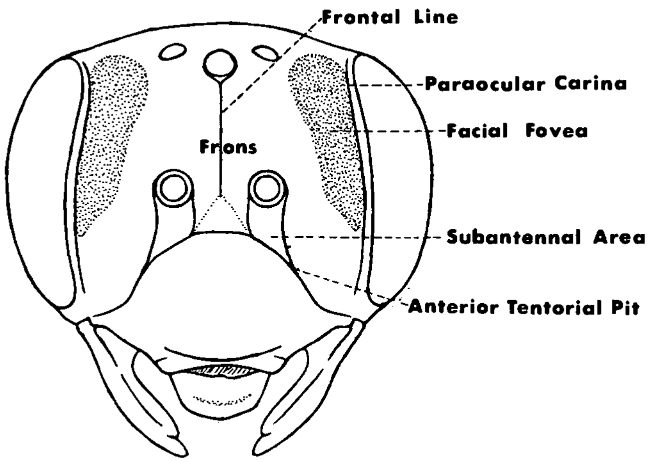
Between the imaginary line under the median ocellus and the upper margin of the clypeus lies the *frons* or frontal area. The portion of the frons lying above the antennal sockets is called the supra-antennal area. This area is bounded laterally by imaginary lines running vertically outside of the antennal sockets. In many bees a median elevated ridge or furrow extends dorsally from near the anterior ocellus to below the antennal bases. This is often referred to as the *frontal line* (*Andrena,* Fig. 15).

The *antennal bases* in *Nomia* are located about midway between the vertex and the apical margin of the clypeus. The *antennal sockets* are depressed, giving the inter-antennal area a markedly convex appearance in profile. There is a very narrow *antennal sclerite* about each antennal socket, which in turn is separated from the face by a weak *antennal suture.* The position of the antennal sockets on the face is a significant taxonomic character. The antennal sockets of most bees are located at or near the middle of the face. In many *Pseudopanurgus,* for example, they are located well above the middle of the face, whereas in other groups, such as *Dufourea* (Fig. 11), they are well below the mid line.

Extending from the base of the antennal socket to the *epistomal suture* in *Nomia* is a single *subantennal suture* (Fig. 2a). The upper end of the subantennal suture may be at the inner, mesal, or outer margin of the antennal socket, depending upon the genus of bee. Its position is highly variable and apparently is of little phylogenetic significance. Most of the bee genera have but a single subantennal suture arising from each antennal socket. However, in genera of the family Andrenidae there is usually an inner and an outer subantennal suture arising from each socket (Fig. 15). In some of the anthophorids, there is a suggestion of the upper portion of an inner subantennal suture arising from the lower inner margins of the antennal sockets.



Figures 3-14. Frontal and lateral views of heads of twelve bee genera. Figure 4 is the head of ♂ *Apis;* all others are heads of females.



15
Andrena

FIGURE 15. Frontal view of *Andrena* female head.

These partial sutures, however, are so weak that they are very unlikely to be confused with those of the andrenid bees, which are complete although sometimes difficult to discern.

That portion of the frons below the supra-antennal area and above the epistomal suture is referred to as the *supraclypeal area.* Its lateral margins are defined by the outer subantennal sutures, where only one suture arises from each antennal socket, or by the inner subantennal sutures, where two subantennal sutures arise from each socket. In the andrenid bees the area between the inner and outer subantennal sutures is referred to as the *subantennal area* (Fig. 15). In many bee genera the supraclypeal area is elevated and highly convex, often extending as a triangular piece well up into the inner antennal area. In these genera, the supraclypeal area includes the entire elevated convexity.

The clypeus is delimited above and laterally by the *epistomal suture.* In *Nomia,* as in most bees, the epistomal suture consists of a weakly defined dorsal portion extending between the dorso-lateral margins of the clypeus, plus the lateral arms which extend between the dorsal segment and the extreme lateral margins of the clypeus (Fig. 2a,b). In *Nomia* the lateral arms are weakly convex, tending to arch outward at their apices. The *lateral arms* of the epistomal suture terminate mesally from the anterior mandibular articulations, indicating that, in the bees at least, the structure has evolved secondarily to meet the demands of the mouthparts and buccal cavity. The epistomal suture is highly variable among bee genera. The dorsal arm may be horizontal (*Anthophora, Xylocopa,* Fig. 10), strongly arched (*Anthidium,* Fig. 8; *Bombus,* Fig. 9) or, as in the andrenid bees having the paired antennal sutures, the uniformity of the arch may be sharply angulate at the point where it meets the inner subantennal suture (*Andrena, Nomadopsis, Perdita,* Fig. 7). The lateral arms of the epistomal suture exhibit considerable variation among the bee genera, their contours apparently influenced by the size and shape of the clypeus. In *Colletes* and *Bombus* the lateral arms are straight throughout their entire length, whereas in the anthidiines and *Xylocopa* the arms, straight through much of their total length, curve strongly laterally to form a sharp concavity in the anthidiines (Fig. 8), and an apical convexity in *Xylocopa* (Fig. 10). In *Nomia* the lateral arms are weakly convex dorsally, but at their extremities turn sharply laterad to assume a terminally concave appearance (Fig. 2).

The anterior demarkation of the large and complex tentorium, which braces the interior of the head, is evidenced by a pair of *anterior tentorial pits* located along the epistomal suture. In *Nomia* the tentorial pits lie at the apices of the convex angles in the lateral arms of the epistomal suture (Fig. 2). The pits are located midway along the lateral arms of the epistomal suture in *Hylaeus;* near the upper extremity of the lateral arms in *Colletes, Halictus,* and *Anthidium;* and at the junction of the outer subantennal suture and the lateral arms of the epistomal suture in the andrenid bees (Fig. 15).

The clypeus is invariably convex in bees, although the extent of its convexity varies among the genera. In all bees it is produced apically over the labrum. The high degree of variability in the shape of the clypeus makes it a valuable structure for characterizing bee groups. In certain anthrophorids, such as *Anthophora* (Fig. 12a,b), and *Emphoropsis,* the clypeus is extremely protuberant at its apex and has the lateral margins bent backwards so that they are roughly parallel to the main axis of the body. In *Nomia* and *Anthidium,* the clypeus is weakly convex and its lateroapical margins are almost straight (Figs. 2b, 8b). *Xylocopa* (Fig. 10a,b), on the other hand, has the clypeus flattened so that the weakly convex apical margin is difficult to distinguish.

The dimensions of the clypeus likewise vary among the bees. In *Dufourea* (Fig. 11) and *Holcopasites* it is approximately three times as broad as long (Figs. 6, 12). The length and breadth of the clypeus in *Colletes* (Fig. 5) and *Bombus* are approximately equal, while in *Hylaeus* it is almost twice as long as broad (Fig. 13). Generally the clypeus reaches its greatest breadth at, or near, the extremities of the epistomal arms. The apical margin of the clypeus is entire in most bee genera, and it is slightly concave or straight along its apex. However, in the Megachilidae the margin of the clypeus is usually modified. Among many *Osmia* and *Megachile,* the apex may be strongly incised or lobate; in the anthidiines the margin is usually dentate; and in *Chelostomopsis* there is a long, protuberant median horn (Fig. 14).

The apex of the clypeus is defined by the *clypeolabral suture* which is hidden in most bees by the overhanging clypeus. As with the clypeus, the *labrum* is variable among bees. In most bees the labrum is subrectangular with a truncate or weakly rounded apex. It is longer than broad in *Megachile, Coelioxys,* and *Anthidium,* subquadrate in *Anthophora, Ceratina,* and *Nomada,* and approximately four times as broad as long in *Apis, Bombus* (Fig. 9), and the male *Nomia.* The labrum is subtriangular among species of *Andrena* (Fig. 15), *Colletes, Hylaeus,* and *Xylocopa.* In females of *Halictus, Nomia* (Fig. 2a,b), and *Sphecodes,* the apex of the labrum has a pointed median process, giving this structure a subtriangular appearance and making it appear longer than broad. In *Nomia* and *Sphecodes* the sides of the process are provided with a fringe, or *fimbria* (Fig. 2a).

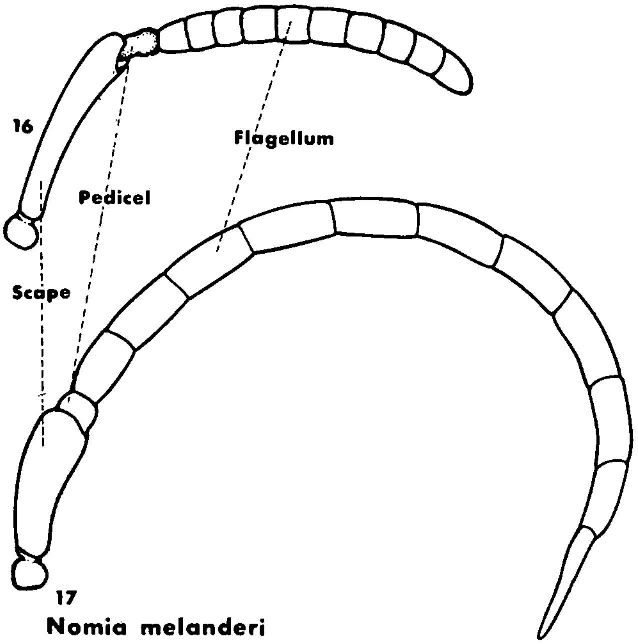
The areas on each side of the face, delimited by the compound eyes laterally, the vertex above, the supra-antennal area, supra-clypeus, and epistomal suture mesally, and the anterior mandibular articulation below, are referred to as the *paraocular areas.* These areas are simple in *Nomia* and in most bee genera. However, in *Hylaeus,* females of *Colletes,* and most andrenids, there are distinct depressions in the upper portions of the paraocular areas termed *facial foveae* (Figs. 5, 7). These depressions are most pronounced in females of *Colletes* and *Andrena,* where they are often covered with exceedingly short pile which imparts a whitish sheen to the foveae. The foveae of other andrenid bees are often indistinct and at times difficult to distinguish. This is particularly true among males. In *Hylaeus* the facial fovea consists of a narrow groove paralleling the upper, inner margin of the compound eye.

Many bee genera have an additional structure in the paraocular area, the *paraocular carina,* which closely parallels the inner margin of the compound eye. It is present in most megachilids (Fig. 8) in which it extends from the apex to near the base of the inner margin of the compound eye. In *Andrena* (Fig. 7), *Anthophora, Bombus* (Fig. 9), and several other genera, a carina similar to the paraocular carina is present, but the lower, inner margin is directed towards the anterior mandibular condyle.

Behind the compound eyes, there are large convex sclerites terminating in a distinct ridge on the back of the head. This ridge or angle, the *preoccipital ridge,* borders a sharply concave area at the back of the head which surrounds the *foramen magnum* from above, and the sharply concave *proboscidial fossa* from below (Fig. 2c). The latter fossa accommodates the proboscis, or mouthparts, of the bee when it is folded at rest. A number of sutures and sclerites of significance occur between the foramen magnum and the preoccipital ridge. However, since these are not referred to in the keys or text of this bulletin, they are not treated here. Between the compound eyes and the preoccipital ridge lie the broad, convex *genal areas* (Fig. 2b). The genal areas are variable in size among bee genera, being extremely narrow in males of *Apis* to three times the width of the compound eyes in females of certain *Osmia.*

Between the lower margin of the compound eye and the base of the mandible is an area of variable length termed the *malar space* or *malar area.* This region is generally short in most bee genera. However, in *Apis* and many species of *Bombus* (Fig. 9a) and *Colletes* (Fig. 5a), it is much longer than broad. The comparative length to breadth measurement of the malar space is arrived at by drawing a line between the anterior and posterior mandibular articulations and a parallel line at the base of the compound eye. The breadth of the malar space is measured as the distance between the anterior and posterior mandibular articulations.

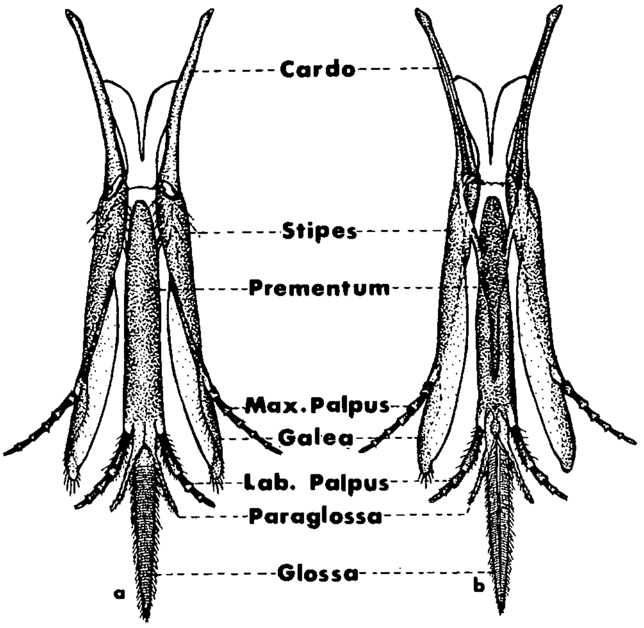
The *antenna* of *Nomia,* as in all bees, consists of a basal *scape,* a *pedicel,* and a *flagellum.* It is thought that there are only three morphologically primitive segments to the antenna, and that the segments of the flagellum are secondarily differentiated. Some authors refer to these as flagellomeres, but in this study the term *flagellar segments* is retained. The flagellum of the male is composed of 11 segments and that of the female has 10 segments (Figs. 16, 17). This sexual difference in segmentation of the flagellum is true of all northwest bees with the exception of *Neopasites* and *Holcopasites* in which it is 10-segmented in both sexes. In most bees the flagellar segments of the male are considerably longer than those of the female. This is particularly evident among the anthophorines and eucerines. The difference in length of flagellar segments is more subtle in the megachilids and andrenids, while in most of the smaller parasitic anthophorids and nomadids the flagellar segments of both sexes are of essentially the same length. The scape is usually considerably longer than broad, but in many species it is broadened and provides valuable



Figures 16-17. Antennae of *Nomia melanderi* female (16) and *Nomia melanderi* male (17).

characteristics for species discrimination. The pedicel acts as an articulatory condyle between the flagellum and the scape and is often recessed slightly into the apex of the latter structure.

Mouthparts. The *mandibles* of all bees are broadened basally and generally taper to a much more slender apex. The mandibles of *Nomia* typify this condition and, as in most bees, the females of the species possess a subapical *inner tooth* (Fig. 2a). In *Hylaeus, Xylocopa,* (Fig. 18) and the males of *Bombus,* the apex of the mandible is modified, giving an impression of a bidentate condition in which the inner tooth is slightly shorter than the outer. The males of *Apis* and both sexes of *Ceratina* have three small but distinct teeth apically, while both sexes of *Megachile, Osmia,* and *Anthidium* have the apices of the mandibles greatly broadened and possessing anywhere from two to seven teeth (Fig. 19). The number of teeth in the mandibles is used as a subgeneric and specific characteristic among many megachilids, but because of continual abrasions in constructing nesting cavities by the females, these teeth are often eroded. In some old females of this group, the apices of the mandibles appear to be edentate and, because of this condition, are difficult to identify.



20
Nomia melanderi

FIGURE 20. Mouthparts of *Nomia melanderi:* (a) anterior view; (b) posterior view.

18
Xylocopa

19
Megachile

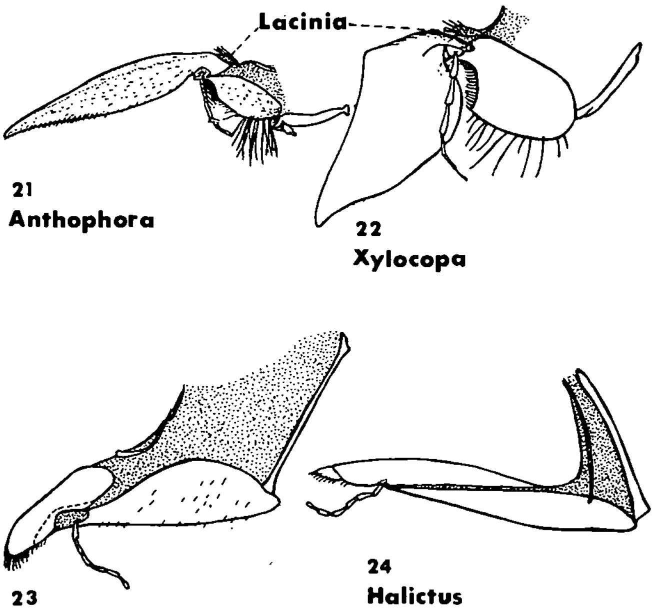
FIGURES 18-19. Bidentate mandible of *Xylocopa* (18); and multidentate mandible of *Megachile* (19).

The proboscis of bees is composed of the highly complex and modified labium and maxillae which, when extended, form the tube through which fluids are taken into the pharynx. Since this study attempts to provide the student with a means of separating the various bee genera of northwestern America, without employing characters that are normally hidden in repose, reference to the mouthparts is avoided whenever possible. For a more detailed account of bee mouthparts, the student is referred to Michener (1944a) and Snodgrass (1935).

The *maxillae* are illustrated in Figure 20, a and b. The base of the proboscis is largely membranous to permit folding and unfolding. The membrane is provided with a number of conjunctival thickenings to support and strengthen the proboscidal tube. One of the principal structures is the rod-like *cardo* (cardines) of each maxilla. The cardo is usually slender and about the same length as the *stipes* (stipites). The stipes is a flattened sclerite lying on the side of the proboscis near its base. In *Nomia* the stipes is approximately four times as long as broad and is virtually hairless. In *Xylocopa,* the stipes is less than twice as long as broad and is provided with a deep emargination subapical to the posterior margins and lined with a comb of strong bristles (Fig. 22). This subapical posterior emargination to the stipes is found in a number of genera including *Anthophora* (Fig. 21), *Bombus,* and *Diadasia,* and is more subtle in *Apis* (Fig. 25), *Nomada,* and *Triepeolus.* In the latter group of genera, only a few fine setae arise from the emargination.

The *maxillary palpus* is attached to the distal ends of segment-like palpifers which arise in membranous areas above the apical processes of the stipites. In *Nomia* the five-segmented palpus protrudes slightly beyond the apex of the lacinia (Fig. 20). The maxillary palpus undergoes great variation among the bees and varies from two to five segments even among closely related genera. It is apparent, therefore, that independent losses of maxillary palpal segments have occurred repeatedly throughout the evolutionary history of the group.

The *lacinia* in *Nomia* is extremely small and rather densely haired, and it is situated in the membrane well above the base of the galea. The laciniae in all bees are greatly reduced. They are the largest in *Megachile, Anthophora* (Fig. 21), *Anthidium,* and *Ceratina;* membranous in *Apis* (Fig. 25); and absent in *Colletes* (Fig. 23), *Halictus* (Fig. 24), and *Sphecodes.*



21 **Anthophora**

22 **Xylocopa**

23 **Colletes**

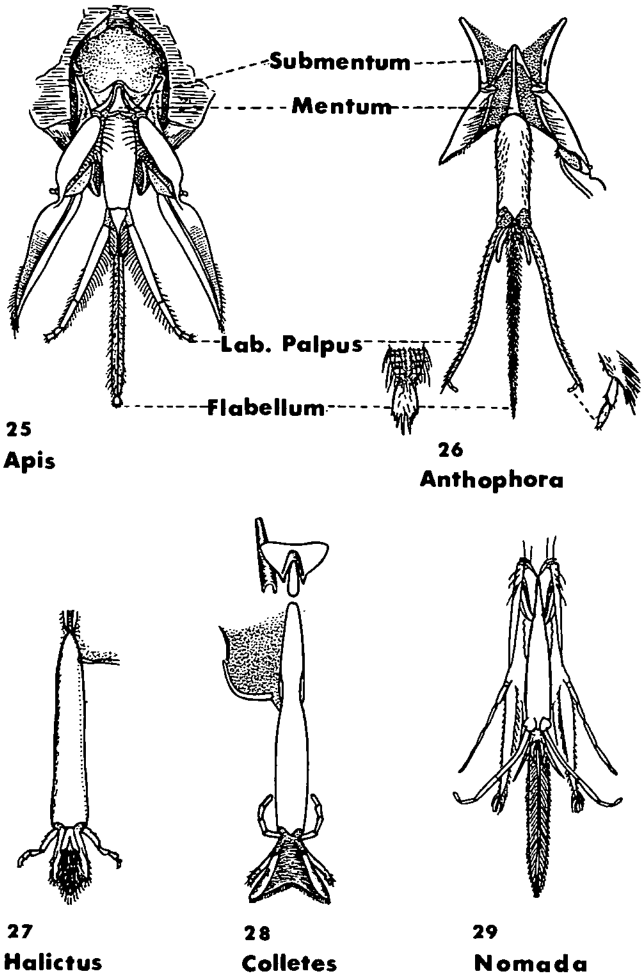
24 **Halictus**

FIGURES 21-24. Outer views of maxillae of four bee genera.

The *galea* is an elongate, blade-like structure which wraps about the outer surface of the proboscis. It, too, is variable among the bees. In *Nomia* (Fig. 20), as well as in *Andrena, Colletes,* and *Hylaeus,* the section of the galea which lies above the maxillary palpus is as long as the portion that lies below it. The prepalpal portion of the galea is about twice as long as the postpalpal portion in *Halictus* (Fig. 24) and *Sphecodes,* whereas in *Apis* (Fig. 25), *Bombus, Anthophora* (Fig. 21), and *Megachile,* the postpalpal portion is about as long as or longer than the prepalpal portion, the stipes, and the cardo combined.

Labium. The labium is the innermost structure of the proboscis and, like the maxilla, has undergone remarkable change in the bees. *Nomia* completely lacks the submentum and the mentum, and the membranous area in which these structures lie in other bees tends to be slightly sclerotic in this genus (Fig. 20). The *submentum* consists of a broad, rather lightly sclerotized structure that fills much of the membranous area between the cardines in the more primitive bee genera. In *Colletes* (Fig. 28) the subtriangular *mentum* meets the cardines subapically, whereas the lower rectangular mentum of *Hylaeus* meets the cardines at their apex. *Halictus* and *Sphecodes,* like *Nomia,* lack the mentum and submentum. Most bees have a greatly reduced, V-shaped submentum with the ends of the "V" meeting the apices of the cardines, i.e., *Apis* (Fig. 25), *Bombus, Anthophora* (Fig. 26), and *Megachile.* The *mentum* is a slender, flattened sclerite that articulates with the submentum basally and the prementum apically. It is absent in *Nomia, Halictus,* and *Sphecodes,* but in most other bee genera it tends to be broadened or even bifid at its junction with the prementum.

The *prementum* is an elongated sclerite, rather uniform in shape among all bees. It is sharply concave anteriorly. This cavity is enclosed by a membrane which contains the muscles of the glossa, as well as providing continuity for food passage. The *labial palpi* arise from the conjunctival membrane at the apex of the prementum. These structures are extremely variable and of considerable diagnostic importance among the bees. In *Nomia* the palpi consist of four segments of approximately the same shape, the first as long as the second and third combined (Fig. 20). Four-segmented palpi of approximately equal length are found in *Andrena, Colletes, Halictus,* and *Hylaeus.* In *Nomadopsis, Perdita,* and *Nomada* (Fig. 29), the first segment of the palpus is considerably elongate, flattened, and longer than the



25 **Apis**

26 **Anthophora**

27 **Halictus**

28 **Colletes**

29 **Nomada**

FIGURES 25-29. Posterior views of mouthparts of *Apis mellifera* (25); posterior view of labium of *Anthophora* with enlargements of the flabellum and terminal labial palpus (26); posterior views of labia of *Halictus* and *Colletes* (27 and 28); and posterior view of mouthparts of *Nomada* (29).

three apical segments combined. Among most other bees, the first two segments are enormously distended and flattened and usually firmly attached to each other, i.e., *Megachile, Anthidium, Anthophora* (Fig. 26), *Apis* (Fig. 25), and *Bombus*. In the genus *Proteriades,* the basal two segments of the palpi and the maxillae and galeae are covered with hooked hairs, an adaptation for collecting pollen from the flowers of *Cryptantha*.

The *paraglossae* also arise in the conjunctival membrane at the apex of the prementum, mesad to the labial palpi. In *Nomia* these are slender, rather membranous structures which tend to lie on either side of the glossa.

The *glossa* also exhibits considerable variation among bees. In *Nomia* it is short and slender, about five times as long as broad, sharply pointed, and almost spatulate in form (Fig. 20). In *Andrena* and *Halictus* it is short, usually about as long as broad and terminating in a sharp point (Fig. 27). *Colletes* (Fig. 28) and *Hylaeus* have a short glossa, but the apex is distinctly bilobed. The glossa in megachilids, anthophorids, and apids is long and slender, usually subequal to or longer than the prementum (Figs. 25, 26). Members of the latter group of bees all have a small, thin plate, or *flabellum,* at the apex of the linear glossa. The flabellum is variously modified among different bee genera (Figs. 25, 26).

Thorax

In bees, as in all clistogastrous Hymenoptera, the true first abdominal segment is fused to the metathorax. This segment is sharply constricted caudally, resulting in a short, petiolate connection between the thorax and the remaining abdominal segments (Figs, 1, 30). Michener (1944a) suggests that the inclusion of the first abdominal segment with the thorax permitted a greater development of the flight muscles in the Clistogastra.

Prothorax. This first segment of the thorax is reduced in the bees. The *pronotum* in *Nomia* is slightly concave when viewed in profile, and is fused to the anterior margin of the mesoscutum. It encircles the upper anterior end of the mesothorax, and is produced on its posterolateral margin into the *lateral lobes* of the *pronotum* (Fig. 30a). The length of the pronotum varies greatly, as does the degree of concavity when viewed in profile. It may vary from highly concave in *Nomia, Halictus,* and *Colletes* to angulate in *Anthidium* and *Hoplitis* (Fig. 31), to virtually straight in *Apis* (Fig. 32), *Bombus* (Fig. 34), and *Dioxys* (Fig. 33). In *Nomia* the propleura are large, as they are in most bees. The *propleura* narrow sharply toward the coxal bases when viewed laterally, but they can be seen to extend around to the anterior face of the first thoracic segment, where they meet but apparently do not fuse. The *prosternum* is either hidden or difficult to discern without relaxing the specimen. It is hidden in part by the propleura and in part by the folded forelegs and head.

Mesothorax. This is by far the largest segment of the thorax, and in most bees it makes up well over half of this body region. The *mesonotum* in *Nomia* consists of two very distinct sclerites: the very large, subquadrangular, anterior mesoscutum, or *scutum,* and a posterior semi-lunar shaped sclerite, the *scutellum*. The two sclerites are separated by the *scuto-scutellar suture*

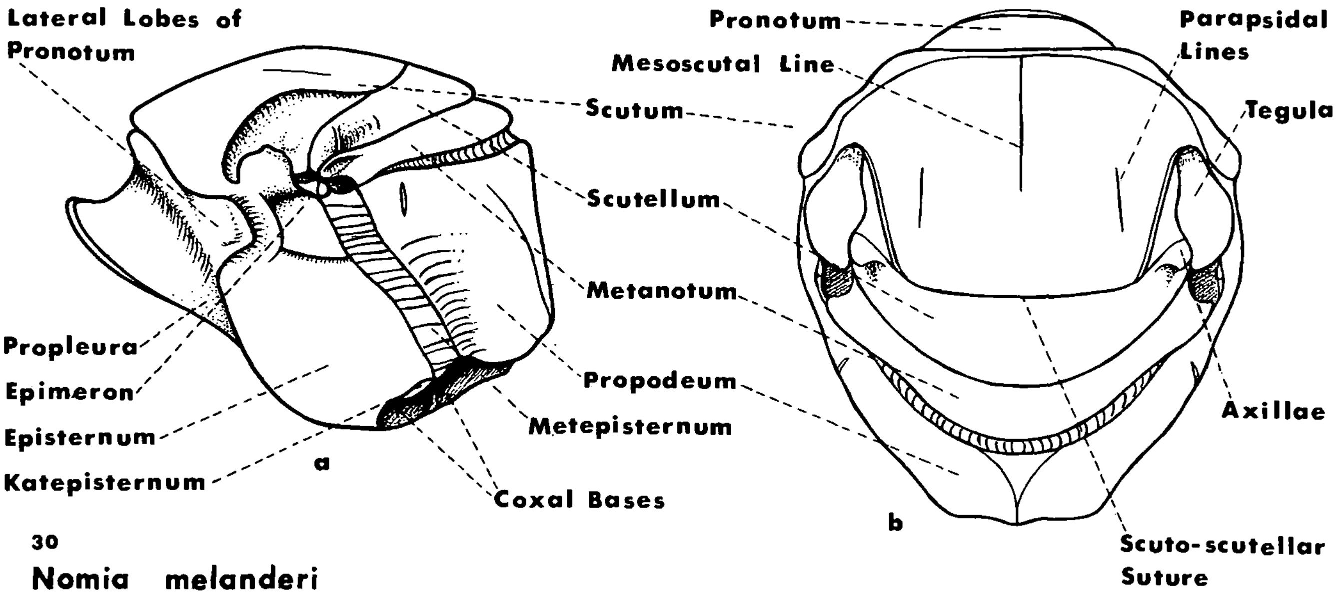
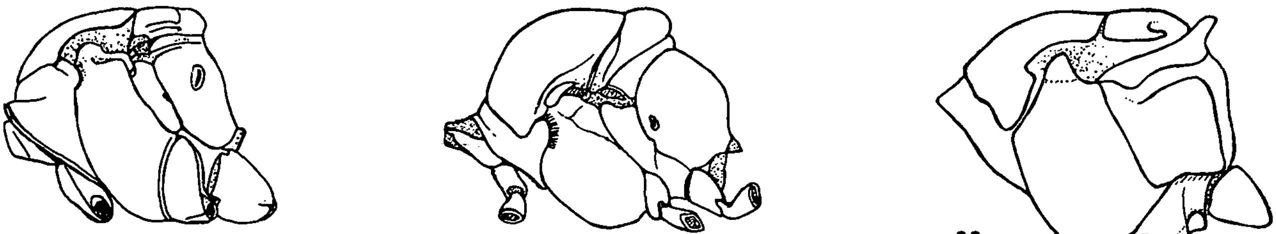


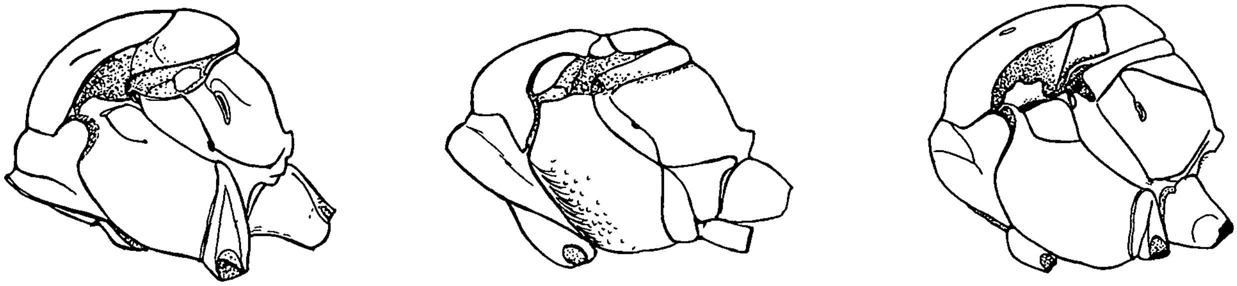
FIGURE 30. Lateral and dorsal views of the thorax of *Nomia melanderi*.



31 **Anthidium**

32 **Apis**

33 **Dioxys**



34 **Bombus**

35 **Ashmeadiella**

36 **Anthophora**

FIGURES 31-36. Lateral views of the thoraxes of six bee genera.

which extends across the caudal third of the mesonotum (Fig. 30b). A number of other sclerites make up the mesonotum, but only a few will be mentioned here. On the latero-medial margins of the scutum lie the *tegulae.* These are large, flat, disc-like structures covering the bases of the wings. In *Nomia,* as in most other bee genera, they are opaque, brownish sclerites, distinct from the melanic mesoscutal sclerites.

On either side of the postero-lateral margin of the scutum lie the *axillary sclerites,* or *axillae.* In *Nomia,* as in most of the other genera, these are functionally a portion of the scutellum, but are of scutal origin. In the parasitic genera, *Coelioxys, Dioxys,* (Fig. 33), and *Triepeolus,* the axillae are produced posteriorly as distinct spines, or teeth.

The surface of the mesonotum has several distinct sutures which are employed in taxonomic discrimination. There is a median *mesoscutal line* on the anterior half of the scutum in *Nomia,* plus two shorter impressed *parapsidal lines* lying midway between the mesoscutal line and the tegulae (Fig. 30b). The parapsidal lines are usually much less distinct than the mesoscutal line, and are often evident as slightly elevated, slightly impressed, or merely impunctate regions of the scutum. In *Nomia* the parapsidal lines are slightly impressed and quite distinct. In most other bees, these lines are readily recognizable, but, particularly in *Osmia,* the parapsidal lines are represented by a series of coarse punctures found in linear sequence in this area (Fig. 158). Consequently, the parapsidal lines in *Osmia* are termed punctiform.

The scutellum in *Nomia* is weakly rounded when viewed in profile, and its surface is essentially horizontal. This condition is also found in *Andrena, Colletes, Megachile,* and *Osmia.* In *Anthidium* (Fig. 31) and *Coelioxys* the caudal portion of the scutellum is bent sharply ventrally, whereas in *Apis* and *Bombus* (Fig. 34) the scutellum overhangs and almost conceals the metanotum. There is no evidence of a median mesoscutellar line in *Nomia,* but this suture is common to a great many bee genera.

The sclerites of the mesopleura of bees have undergone considerable modification. The *epimeron* and the *katepisternum* are reduced to two very small sclerites, the former just below the wing bases and the latter just above the coxal bases. The *episternum* is greatly expanded and occupies most of the mesopleural region. In *Nomia,* as in most other bees, the mesepisternum is weakly curved from the propleuron to the metepisternum (the pleuron of thoracic segment three) (Fig. 30). In many genera, the anterior portion of the mesepisternum curves sharply mesad to meet the propleura, and in *Ashmeadiella* (Fig. 35), *Coelioxys, Dioxys* (Fig. 33), and *Anthidiellum* this anterior face of the mesepisternum is separated from the lateral face by a distinct, raised carina.

Metathorax. The metathoracic segment like the prothorax, is reduced. It lies between the large mesothorax and the propodeum. In *Nomia* the metanotum is a narrow, horizontal sclerite lying immediately behind the scutellum and the axillae (Fig. 30). It curves towards the wing bases at its lateral margins, where it meets the metapleura. A horizontal metanotum is common also to *Andrena, Colletes,* and *Halictus,* but in *Anthophora* (Fig. 36), *Coelioxys, Megachile,* and *Osmia* the metanotum slopes sharply downward posteriorly, and in *Apis* (Fig. 32) and *Bombus* (Fig. 34) the metanotum is essentially vertical. In all northwestern bees, except *Dioxys,* the metanotum is weakly rounded or flattened, but in the latter genus there is a large posteriorly directed median tooth which overhangs the base of the propodeum (Fig. 33).

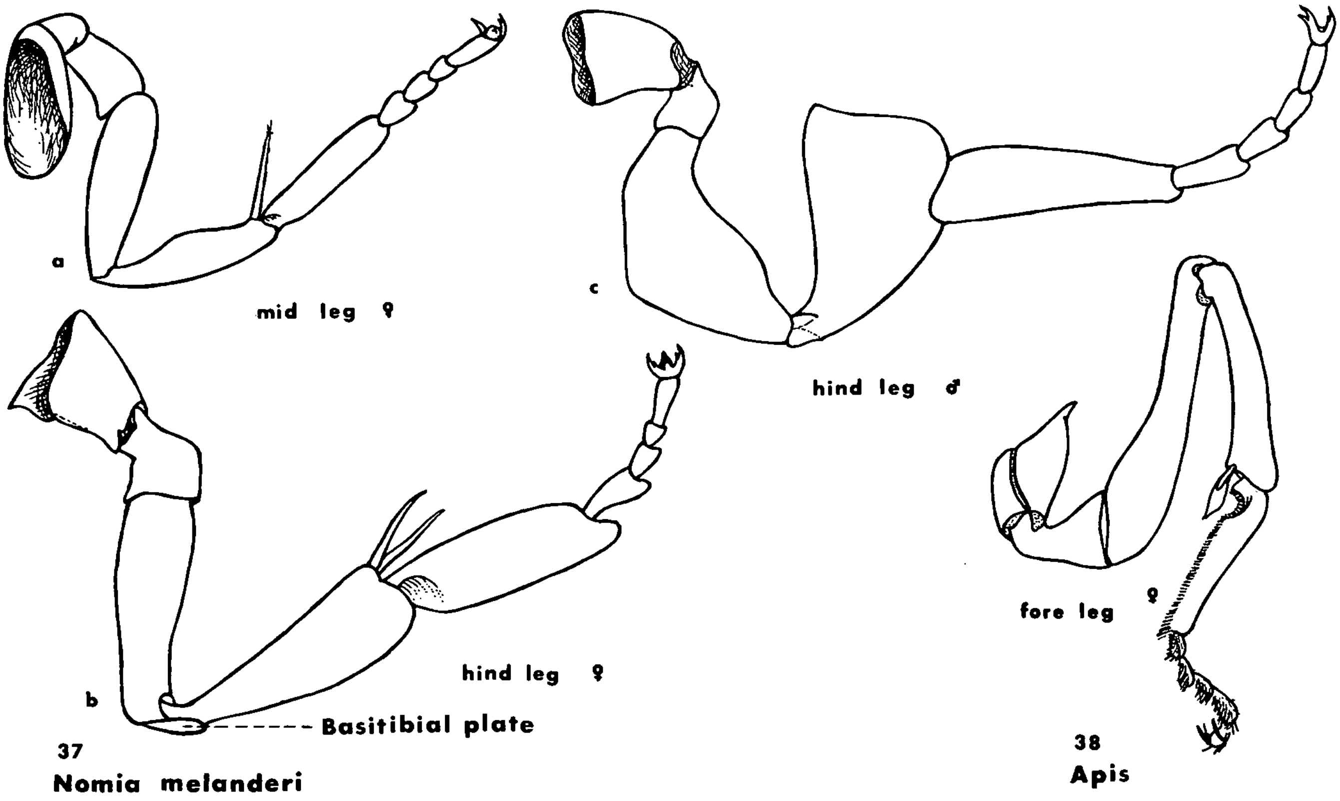
The propodeum (or true first abdominal segment) of *Nomia* has a very narrow basal area which is nearly horizontal in profile (Fig. 30). Caudad of the basal area, the propodeum slopes sharply downward towards the petiole. The horizontal or nearly horizontal basal area of the propodeum is common to *Andrena, Colletes, Halictus,* and many other primitive bee genera. The propodeum in *Megachile, Osmia, Anthophora* (Fig. 36), and in other more advanced genera, slopes sharply downward, although in some of these genera there is evidence of a very narrow horizontal area at its base. In *Apis* (Fig. 32) and *Bombus* (Fig. 34), the propodeum is vertical.

Legs. Each leg in all bees consists of a coxa, trochanter, femur, tibia, five tarsal segments, and a pair of terminal claws (Figs. 1, 37). A number of modifications of the segments of the legs occur in bees as well as a marked sexual dimorphism reaching its zenith in the anterior legs of certain species of *Megachile.*

The coxae are articulated to the lower portions of the thoracic pleura, and they vary considerably in size among the different bees. In *Nomia* they are entire and partially hidden by the legs on most mounted specimens. The anterior coxae of some species of *Colletes, Megachile,* and *Xylocopa* have a large protruding spine on their mesal margins. The midcoxae of *Anthophora* are characterized by a distant carina which extends from its pleural articulation to the anterior articulation of the trochanter.

The *trochanters* are small segments, broadened basally and tapering sharply at their apices.

The *femora* of *Nomia* are approximately as long as the tibiae. They are constricted basally in both sexes, but in the females they are sharply expanded and robust mediobasally, after which they taper slightly towards their apices.



37
Nomia melanderi

38
Apis

FIGURES 37-38. Legs of *Nomia melanderi* (37, a,b, and c); and foreleg of *Apis* (38).

The anterior and mid tibiae of the female, and all three tibiae of the male, are approximately as long as the femora and constricted sharply at their bases. There is a short robust spine on the anterior apical margin of the front and mid tibiae in both sexes of *Nomia,* termed the *tibial spine,* and on the lower inner surface of each tibia there are one or two long *tibial spurs.* The spur on the fore tibia in *Nomia,* like *Apis* (Fig. 38), forms a part of the *strigilus,* or antenna cleaner. This spur is modified to form a spine-like base or *malus* which is pointed apically and expanded into a broadened plate, or *velum,* along its inner margin. The mid tibiae each bear one elongate weakly curved spur, and each posterior tibia has two (Fig. 37). This condition exists in all northwestern bees, except that the spurs are wanting on the mid tibiae in some *Megachile* and on the hind tibiae in *Apis.* The hind tibiae of the males of *Nomia melanderi* are greatly expanded on the antero-apical margins. These nonmelanic protrusions are sufficiently large to conceal the apical spurs which lie in the convoluted underside of the apical tibial lobes (Fig. 37c).

Each posterior tibia of female *Nomia* bears a *basitibial plate* on its outer surface just below its articulation with the femur (Figs. 1, 37b). The basitibial plate is very much reduced in male *Nomia,* and can be distinguished only with difficulty. The basitibial plate is present in *Andrena, Anthophora,* and other bee genera, and is absent in both sexes of *Apis, Bombus, Megachile, Osmia,* and others. *Xylocopa* and *Ceratina* have an anteriorly directed scale-like projection in place of the basitibial plate which is much more evident in the female.

The tarsi of most bees are five-segmented, and their combined length usually exceeds that of the tibiae. The *basitarsus* is very long, exceeding the length of the following four segments combined. In *Nomia,* as in most nonparasitic bees, the hind basitarsus is proportionately broader than the fore and mid basitarsi. The second tarsal segment on the rear leg of *Nomia* is recessed into the apex of the basitarsus. Tarsal segments two to four are often referred to as the medio-tarsus, while segment five is called the distitarsus. Each of the four terminal tarsal segments are narrowed basally and broadened apically. The distitarsus is slightly emarginate at its apex, and in this emargination lies the *unguifer,* a small sclerite that serves as an articulating point for the bases of the claws (Fig. 39). The *claws* originate in the membrane at the apex of the distitarsus and are articulated to the end of each unguifer. The claws of both sexes of *Nomia* and most other bee genera are bifid, with the inner tooth of females markedly reduced in size (Fig. 39). In females of *Megachile, Osmia,* and *Chelostoma,* the claws are simple, whereas in other genera, *Melecta* and *Zacosmia,* the inner tooth is flattened and situated at the extreme base of the claw.

Arising from the membranous area between the paired claws of *Nomia,* is a large well-developed membranous extrusion termed the *arolium* (Fig. 39). The arolia in *Andrena, Apis, Bombus,* and many other genera are distinct and vary in size and shape. In *Megachile, Coelioxys,* and several other bee genera, the arolia are absent or so reduced that they are difficult to discern.

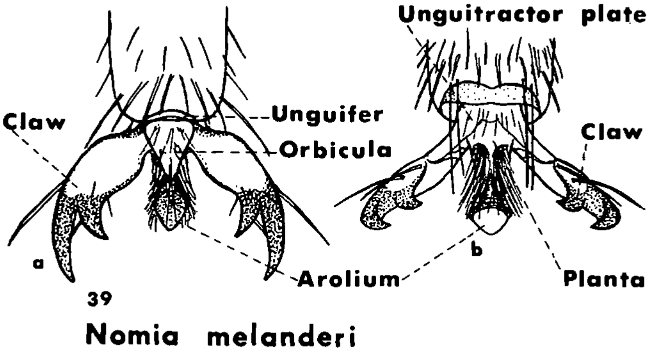


FIGURE 39. Apex of tarsus of *Nomia melanderi:* (a) dorsal view and (b) ventral view.

The pollen-collecting apparatus, or scopa, of the nonparasitic females is usually located on the posterior legs. In *Nomia* long, branched pollen-collecting hairs are found on the trochanters, femora, tibiae, and basitarsi, as well as many long-branched hairs on the under side of the abdomen which hold the pollen grains in a loose mass until they can be deposited in the cell. This rather extensive scopa on the hind legs is also common to *Andrena, Colletes,* and *Halictus.* In *Anthophora* and *Xylocopa* the scopa is restricted to a dense mass of long, simple, or highly branched hairs on the posterior tibiae and basitarsi, while in some of the smaller andrenid bees such as *Nomadopsis* and *Perdita* the hair composing the scope is restricted to the posterior tibiae. The scopa of *Apis* and *Bombus,* as well as all other nonparasitic Apidae, is modified to form a *corbicula* on the outer surface of the posterior tibia. This consists of an expanded smooth area on the outer tibial surface surrounded by a row of long incurved hairs which extend over the concave median area and serve to hold a moist pollen mass, or ball, on the hind leg.

Wings. The nomenclature applied to wing veins and cells is as proposed by Michener (1944a) and for further information on this topic, the student is advised to consult that reference. An illustration of a fore and hind wing of *Nomia* is provided with the veins and cells labeled (Fig. 40). Generic peculiarities in venation of cell structure are illustrated in the key to the bee genera of this region on pages 34-43.

Since certain features of the wings are referred to frequently in the key and since students may have difficulty in interpreting some of these couplets, the following discussion is provided.

The comparative sizes of the jugal lobe and the vannal lobe of the hind wing are referred to frequently in the generic key. The jugal is the hind lobe and the

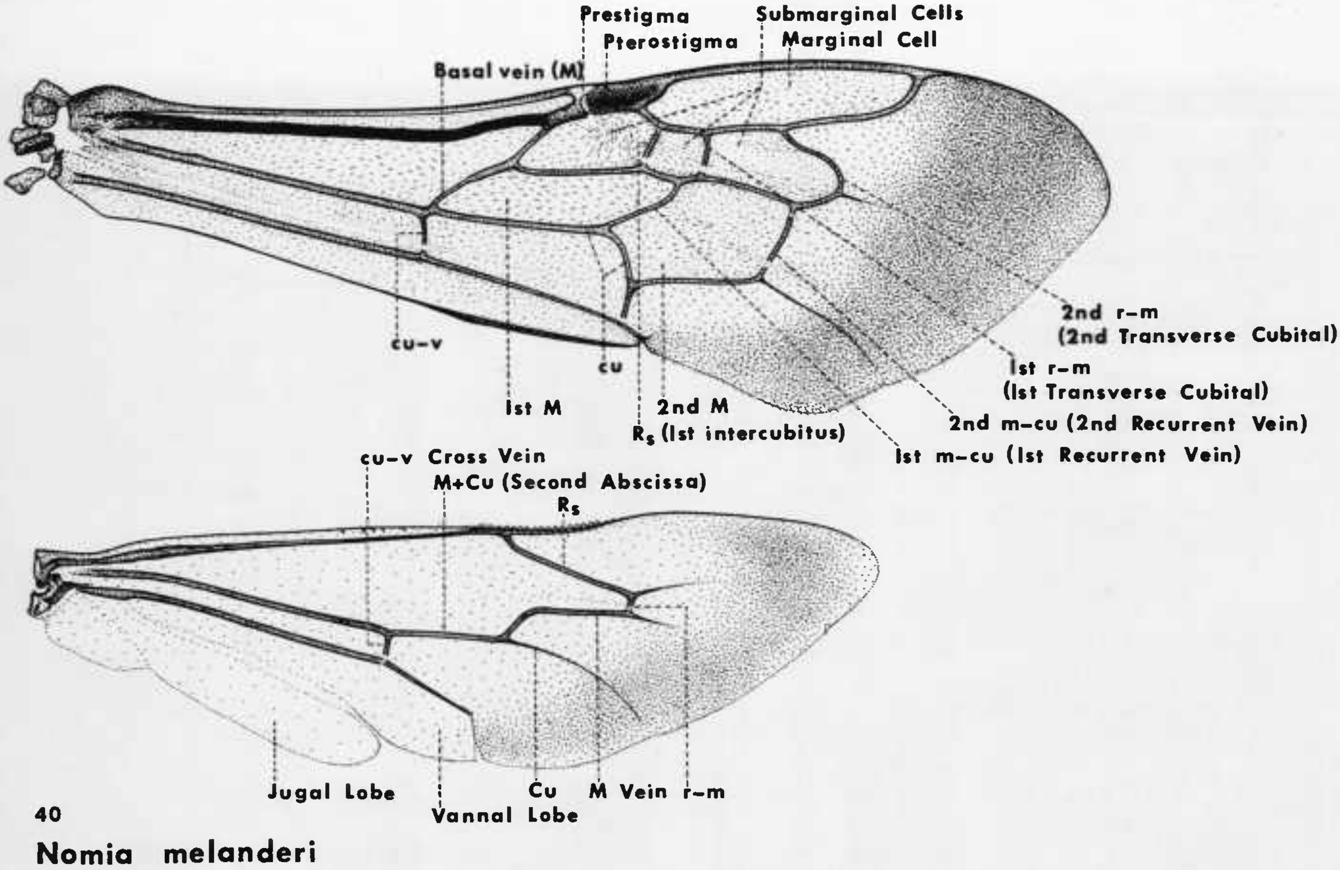


FIGURE 40. Right forewing and hind wing of *Nomia melanderi.*

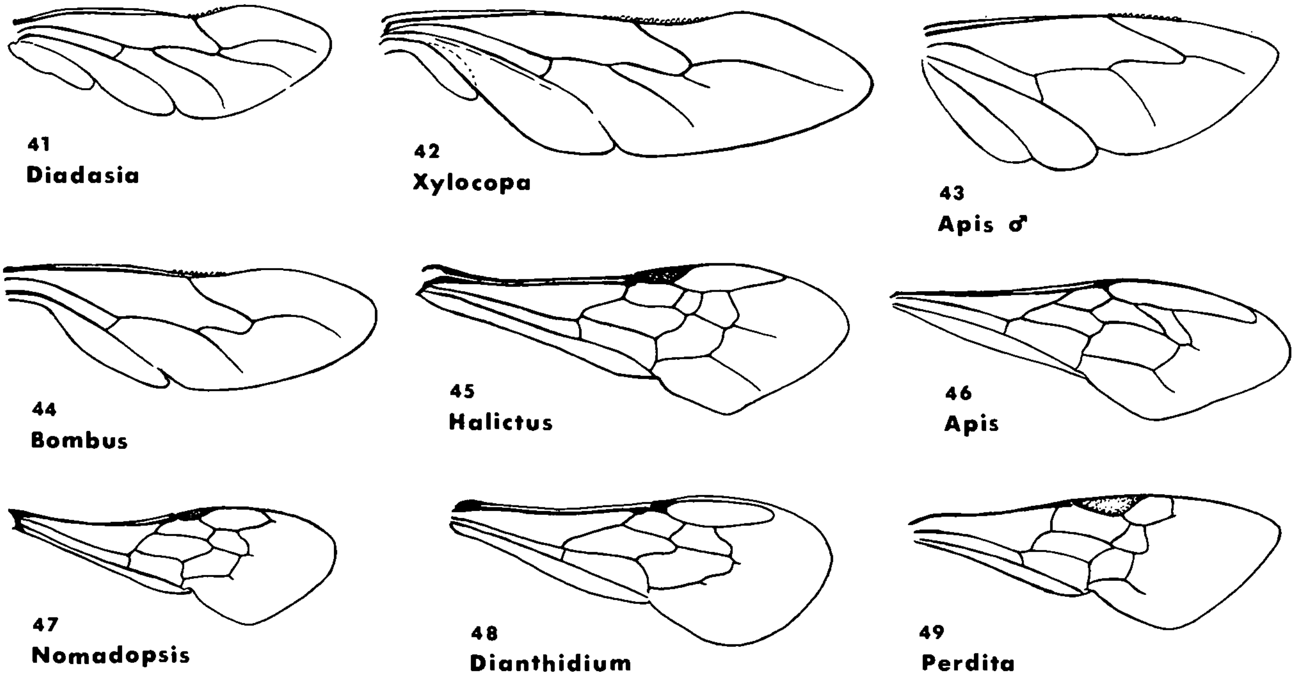
vannal is the fore lobe, and they are often hidden by the wing when it is in partial or complete repose. The jugal lobe is most difficult to see, and since comparative measurements in the length of both lobes are required, it is often necessary to rotate the specimen or at times even to straighten the wing in order to proceed. The jugal lobe in *Nomia* is approximately three fourths as long as the jugal and vannal lobes together (Fig. 40). This condition is also found in *Halictus, Colletes,* and *Apis* as well as in many other genera. In *Apis* the incision separating the jugal and the vannal lobes is minute. In many genera (*Diadasia, Nomadopsis,* and others), the jugal lobe is approximately one half as long as the vannal lobe (Fig. 41). However, in *Anthophora, Megachile, Osmia, Xylocopa* (Fig. 42), and others, the jugal lobe is one third or less as long as the vannal lobe. The jugal lobe is absent in *Bombus* (Fig. 44). In old individuals the posterior margins of the hind wings are often so frayed that the lobes cannot be made out with certainty. Choice of specimens becomes critical in this case.

Reference is also made to the comparative sizes of the *pterostigma.* The pterostigma in *Nomia* is slightly broader than the *prestigma* and is weakly convex along its posterior margin. In *Andrena, Halictus,* and *Hylaeus,* the pterostigma is large and the convex posterior margins extend well into the base of the marginal cell (Fig. 45). Its width, in these genera, is considerably greater than that of the prestigma. *Apis, Bombus, Xylocopa,* and *Megachile* have very small pterostigmata; their posterior margins are almost straight and their width never exceeds that of the prestigma (Fig. 46).

The length and the shape of the marginal cell is also used as a critical character in the generic key. The marginal cell in *Nomia* is longer than the distance from its apex to the wing tip (Fig. 40a). Its apex is pointed and located at the wing margin. In *Panurginus* and *Nomadopsis,* the apex of the marginal cell is also pointed, but the point is not on the wing margin (Fig. 47), whereas the apex is slightly rounded (Fig. 48) in *Dianthidium.* In some genera the marginal cell is extremely short (*Perdita* and *Zacosmia*) and the apex of the marginal cell may be rounded or even truncate (Fig. 49).

Metasoma

As mentioned in the discussion of the thorax, the first true abdominal segment is functionally part of the thorax, and the obvious body division between the thorax and the abdomen occurs between the first and second true abdominal segments. For this reason the first segment of the terminal body region, or metasoma,


41 Diadasia
42 Xylocopa
43 Apis ♂
44 Bombus
45 Halictus
46 Apis
47 Nomadopsis
48 Dianthidium
49 Perdita

FIGURES 41-49. Hind wings of *Diadasia* (41), *Xylocopa* (42), *Apis* (43), and *Bombus* (44); forewings of *Halictus* (45), *Apis* (46), *Nomadopsis* (47), *Dianthidium* (48), and *Perdita* (49).

in bees is actually the second true abdominal segment, or the *first metasomal segment*.

The male of *Nomia* has seven exposed metasomal segments and the female has six. Among northwestern bees, the male of *Chelostomopsis* which has only six exposed metasomal terga, is the only exception.

Each abdominal segment consists essentially of two large sclerites: a very large abdominal "tergum" which extends over the top and sides of the segment and overlaps a ventral "sternum." The sterna are much smaller than the terga in *Nomia* and are only slightly curved upwards at their lateral margins.

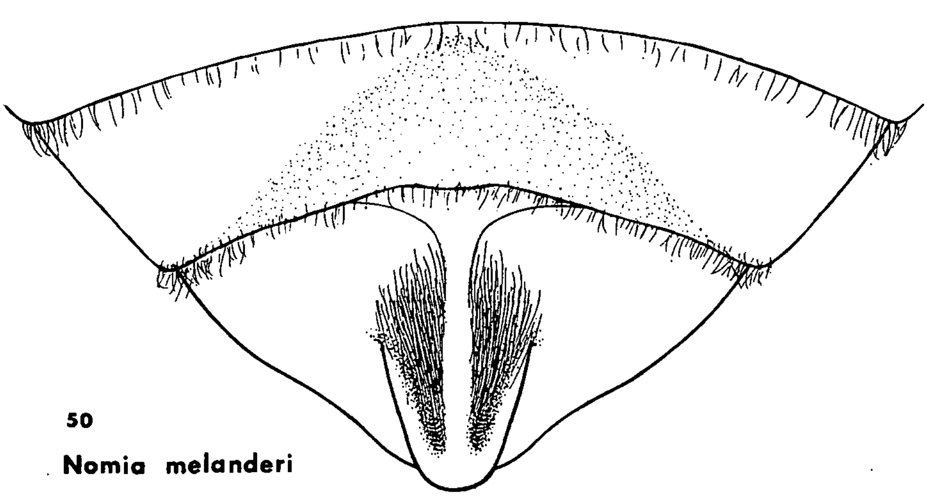
The first metasomal tergum in *Nomia* is composed of a nearly vertical anterior face which extends from near the base of the petiole to the horizontal dorsal face. In *Nomia* these two regions are very subtly differentiated by a weakly rounded angle that extends across the tergum. In many of the megachilid genera, the anterior and dorsal faces are separated by a distinct carina, and there is a marked difference in puncturation. Metasomal terga 2 to 5 in the females of *Nomia* and 2 to 6 in the males have a transverse line near their bases. This line is referred to as the *gradulus*, and it separates the tergum into a basal pregradular area and an apical postgradular area (Fig. 1).

Metasomal terga 1 through 5 in the females and 1 through 6 in the males of *Nomia* have apices which are slightly depressed, very weakly punctate, and a yellowish green color. In *Colletes, Halictus,* and certain *Megachile,* the apices of terga 1 through 5 are sharply depressed, and the depressed areas are more or less glabrous and provided with distinct apical hair bands, or *fasciae,* consisting of very dense, short, appressed pile. The fasciae in these groups may be broadly interrupted, particularly medially in older worn females.

In addition to the apical hair fasciae, many species of *Colletes, Megachile,* and others are provided with fasciae located subbasally on metasomal terga 2 through 5. The basal fasciae are usually weaker than apical fasciae, and they are often hidden when the terga are telescoped.

The halictine subgenus, *Lasioglossum,* is distinguished from the closely related subgenus *Halictus* by the presence of only basal fasciae; the apex of each metasomal tergum lacks any distinct hair banding. In *Bombus,* among others, there is neither an apical nor a basal fascia, but rather the entire tergum is covered with long erect pile. In other bee genera, including *Hylaeus, Anthidium,* and many parasitic genera, the surface of each tergum is virtually bare.

The sixth metasomal tergum of female *Nomia* is considerably modified. It is convex in its lateral aspect, except for the large flat *pygidial process* that covers the entire upper median surface and overhangs the apex of the segment (Fig. 50). The *pygidial plate* (upper surface of the pygidial process) is largely glabrous in *Nomia,* with a pair of longitudinal grooves that run much of its length. The plate is rimmed by a broad, elevated ridge that extends about the sides and the apex. The sides of the process, extending from the pygidial plate to the surface of the segment, are weakly concave and erect. Several rows of simple hairs (prepygidial fimbria) occur across the base of the pygidial plate, with the apical rows tending to be appressed to its surface. The appressed hairs are particularly evi-



50

Nomia melanderi

Figure 50. Dorsal view of fifth metasomal tergum (with pseudopygidium) and sixth (with pygidium) of *Nomia melanderi* female.

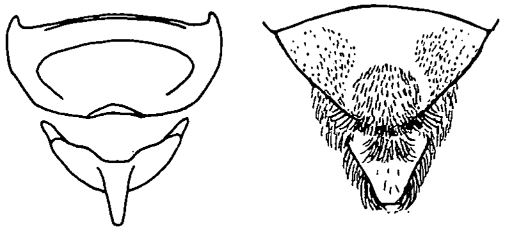
dent, and they reach their greatest apical extension along the paired longitudinal grooves of the pygidial plate.

The pygidial plate is absent in the males of *Nomia*. The seventh metasomal tergum is sharply concave in profile, and it has a broadly rounded apex with a distinct median incision.

Pygidial plates are present in both sexes of *Andrena, Anthophora,* and *Halictus,* but in most specimens it is necessary to distend the abdomen in order to expose the telescoped terminal metasomal tergum. *Anthophora,* among other bee genera, has a distinct row of simple hairs along the sides of the pygidial plate. These are referred to as the *pygidial fimbria* (Fig. 51).

Pygidial processes are absent in both sexes of *Apis, Colletes, Bombus,* and all of the megachilids.

An expanded median area extends along the posterior margin on the fifth metasomal tergum of the female and the sixth metasomal tergum of the male of some genera, resembling a pygidial area on the apical tergum. This area, the *pseudo-pygidium,* is largest and most distinct in the parasitic bee genus *Triepeolus* (Fig. 52), completely concealing the pygidium-bearing terminal segment.



51

Anthophora

52

Triepeolus

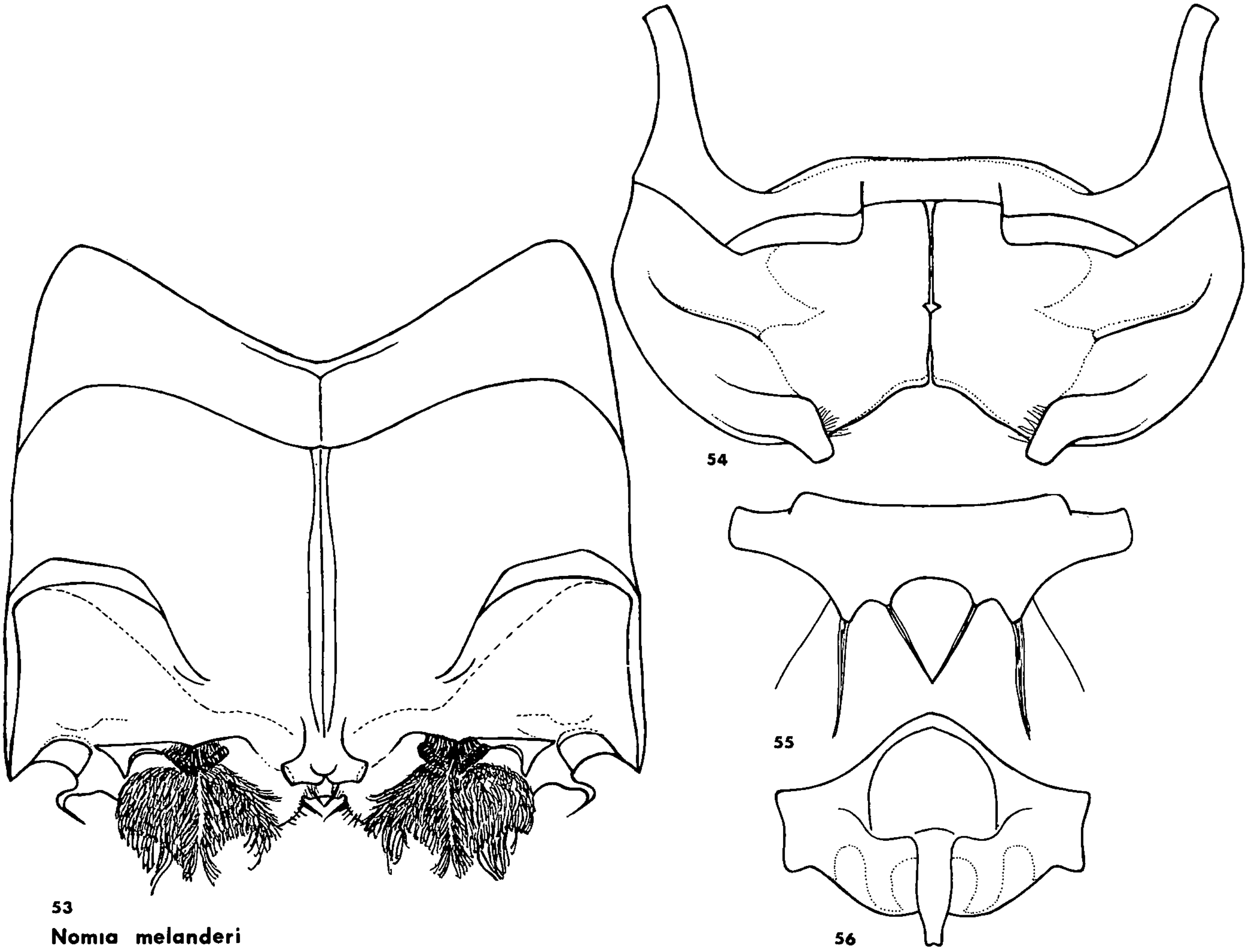
Figures 51-52. Dorsal view of fifth metasomal tergum (with pse udopygidium) and sixth (with pygidium) of *Anthophora edwardsii* female (51) and of *Triepeolus remigatus* female (52).

The metasomal *sterna* of bees lack the many distinct characteristics possessed by the metasomal terga. Among several genera, the first and the second or both of these metasomal sterna are provided with distinct processes, while in many other genera there are emarginations on the sternal apices which have generic or specific significance.

The *ovipositer* or *sting* of *Nomia,* and bees in general, consists of appendages of the seventh and eighth metasomal segments. The first and second valvifers are believed to have arisen as the coxites of the seventh and eighth metasomal segments, and the first and second valvulae are believed to have their origin in the gonapophyses. The third valvulae or gonostyli, are presumed to be the styli of the eighth metasomal segment, and those of the seventh are assumed to have been lost (Michener, 1944b). There have been no significant comparative studies in the structure of the sting among bees, and the homologies proposed by Michener are but tentative associations. As yet workers have examined stings of too few genera to permit generalization as to their specific or generic value. Most studies have indicated that the structures lack diagnostic value.

Male genitalia. The male copulatory organs of the bees are highly variable and possess an array of characteristics of diagnostic value at the generic or specific levels. Comparative genitalic studies have proved to be the only means of separating the constituent species of complexes otherwise inseparable.

The male genitalia consist of three distinct structures, the seventh metasomal sternum, the eighth metasomal sternum, and the capsule. A number of interpretations exist as to the homologies of the capsular elements, but there is little agreement as to their origin. Some workers feel that the copulatory organ consists of modified cerci or other processes of the seventh, eighth, or ninth metasomal segments. Others indicate that the structures associated with the intromittent organ or phallus have all arisen *de novo.* Another proposal



FIGURES 53-56. Ventral views of metasomal sterna of *Nomia melanderi* male: sternum V (53), VI (54), VII (55), and VIII (56).

suggests that the capsule may be composed strictly of modified true appendages, or that it may be endopodite and exopodite lobes of primitive appendages. The problem of homologizing the broadly convoluted and modified structures of the capsule is an imposing one, but until it is solved, some attempt must be made to standardize the terminology for these capsular elements so that one worker may immediately know to which character another is referring. The terms employed by Michener (1944a), even though they may imply erroneous homologies, have proved to be workable. Thus, for the purposes of this work, his terminology will be employed.

The *seventh metasomal sternum* of the male is highly variable, ranging from a narrow horizontal band in *Halictus* and *Xylocopa* (Fig. 73) to broadly bilobed seventh ventral plates in *Colletes* (Fig. 58) and a large weakly sclerotized plate in *Bombus* (Fig. 76).

The eighth metasomal sternum likewise undergoes considerable variation among bee genera. The shape is generally characteristic for each genus, and within each genus the species invariably display modifications and variations within the bounds of generic latitude. Some indication of the variability of the eighth metasomal sternum can be seen in Figures 59, 62, 65, 68, 71, 74, 77, and 80.

The primary copulatory organ, the capsule, is a highly complex structure consisting of several distinct sclerites having specific and generic significance. The variety of names applied to each of these sclerites has created considerable nomenclatorial confusion. The structural nomenclature (see Snodgrass, 1941, 1957; Michener, 1944a, 1944b) adopted here is in general usage in bee taxonomy and is presented below along with the more common synonyms for each of the major sclerites. This nomenclature is not intended to reflect structural homologies.

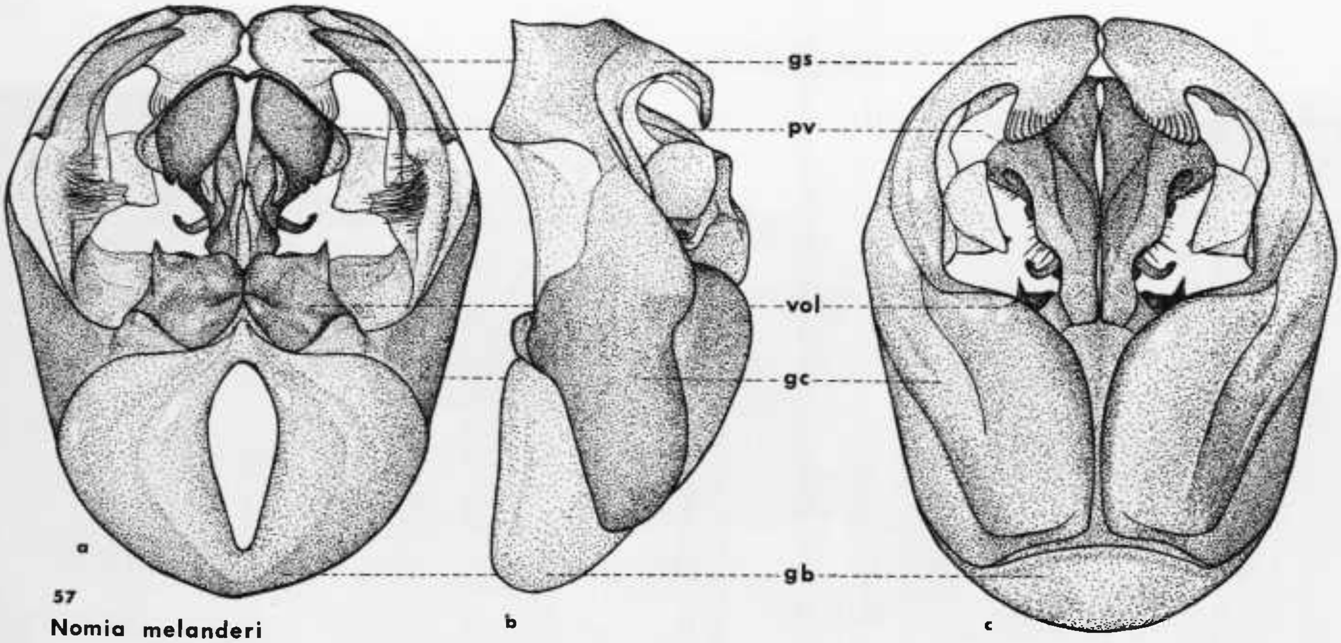


Figure 57. Genital capsule of *Nomia melanderi* male: (a) ventral view, (b) lateral view, and (c) dorsal view (gb = gonobase; gc = gonocoxite; gs = gonostylus; pv = penis valve; and vol = volsella).

Gonobase (gb.). Synonyms: basal ring, cardo, gonocardo, and lamina annularis.

The annular sclerite surrounding the foramen of the capsule, through which pass the ducts, nerves, and so forth from the body cavity. The gonobase is present in all bees except *Apis* (Fig. 82), *Trigona,* and the panurgines of the Andrenidae (Figs. 66, 69). It is present as a separate but very weak sclerite in *Melipona* (Fig. 81).

Gonocoxite (gc). Synonyms: basimere, basipatamere, coxopodite, gonostipes, lamina paramerale, parameral plate, and stipes.

Elongate, entire sclerites which are usually firmly attached to the gonobase and united with the base of the penis proximally. In *Nomia* there is a subapical plate-like endite on each gonocoxite.

Gonostylus (gs). Synonyms: apical segment of stipes, forceps, harpes, lacinia, paramere, squama, stylus, telomere, and valva externa.

Situated at the apex of each gonocoxite, the gonostylus may be elongated and flexible as in *Melipona* (Fig. 81); weakly fused to, but distinct from, the gonocoxite as in *Nomia* (Fig. 57); or completely fused to the gonocoxite as in *Andrena* (Fig. 63). They are usually simple and slender, but in certain genera such as *Nomia* and *Bombus* (Fig. 78) they may be variously modified.

Gonoforceps (fg). Synonyms: claspers and paramere.

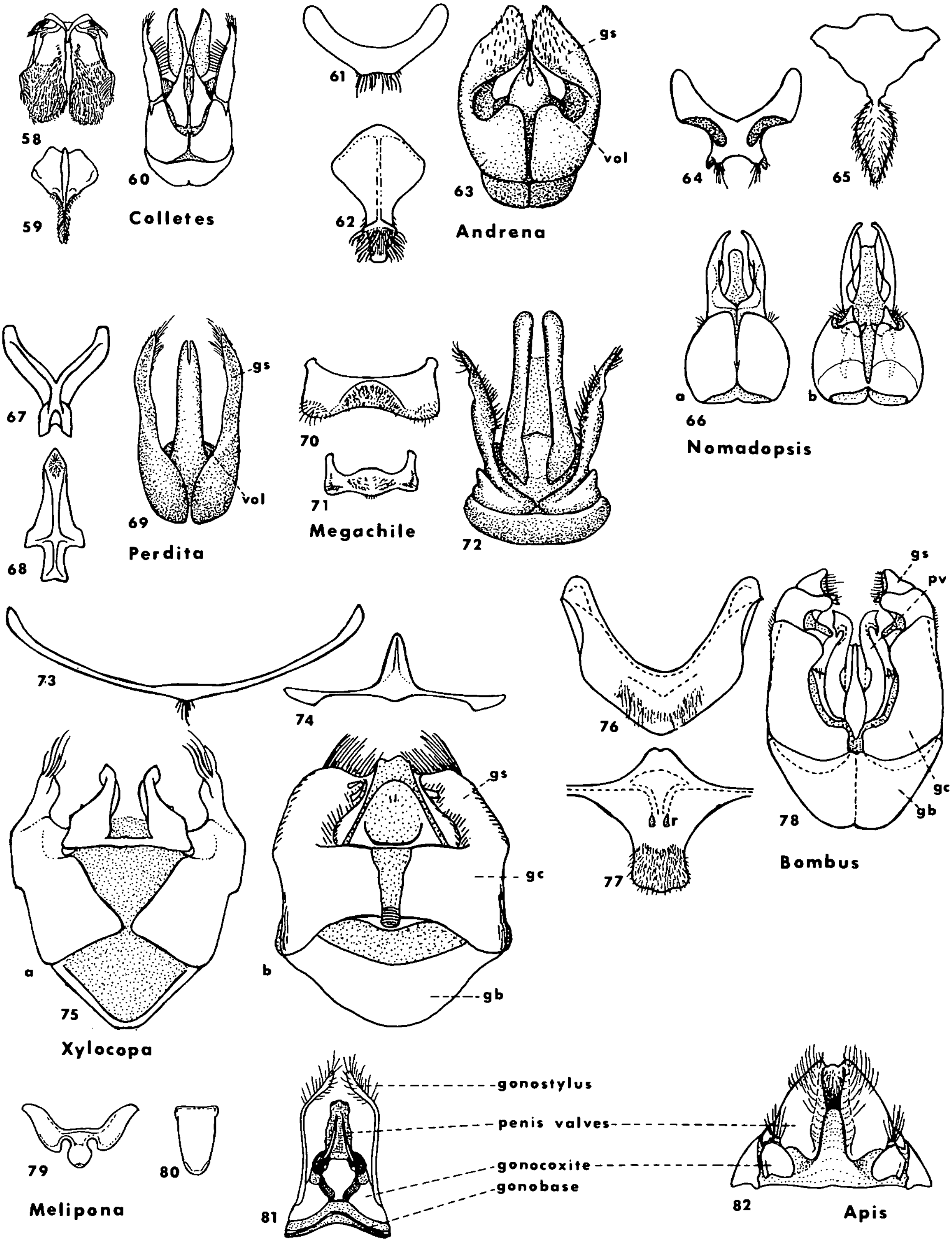
The combined gonocoxite and gonostylus. This term is applied principally but not exclusively when the two structures are fused so completely that their juncture is not discernible (*Andrena* and *Perdita*) (Figs. 63, 69).

Volsellae (vol). Synonym: valvae internal.

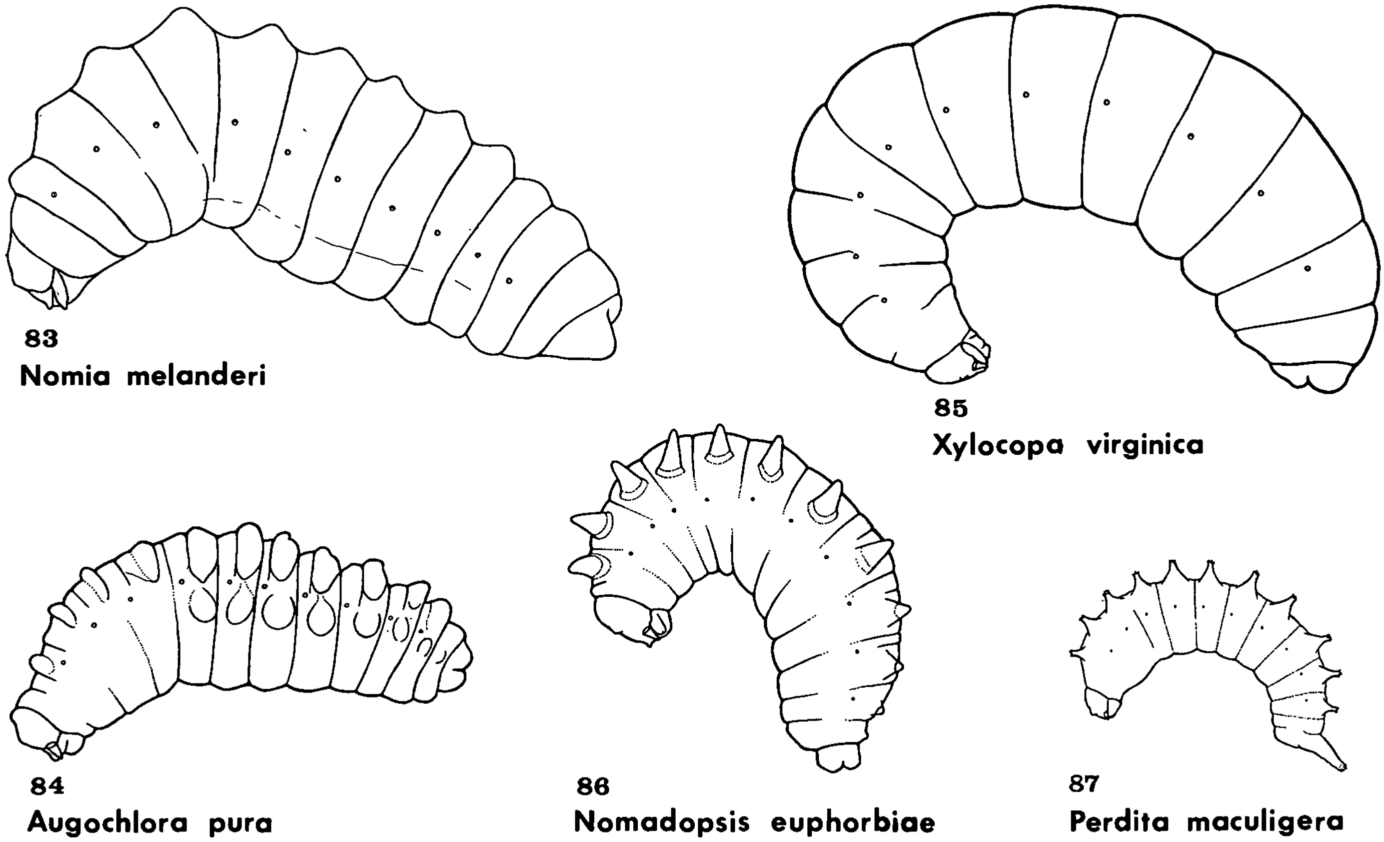
Aedeagal elements that are peculiar to the Hymenoptera. In the lower Hymenoptera they are modified apically into a lateral cuspis and a medial digitus, which are used to assist in copulation. The volsellae are small in the genera *Nomia, Andrena,* and *Colletes,* and are apparently absent in *Apis* (Fig. 82), *Bombus* (Fig. 78), and *Megachile* (Fig. 72).

Penis valves (pv). Synonyms: parameres, sagittae, and sagittal rods.

Sclerotized rods located between the gonocoxites and the membraneous penis with their apices generally projecting beyond the penis and often modified. The penis valves may be independent of each other (*Apis,* Fig. 82); united at their bases by a median plate or bridge (*Xylocopa,* Fig. 75); or fused through much or all of their length (*Andrena,* Fig. 63). In *Melipona* (Fig. 81) they consist of simple rods, whereas in *Nomia* (Fig. 57) and other genera they may be greatly modified.



FIGURES 58-82. Metasomal sterna VII and VIII and dorsal views of male genital capsules of *Colletes* (58, 59, 60), *Andrena* (61, 62, 63), *Nomadopsis* (64, 65, 66), *Perdita* (67, 68, 69a dorsal, 69b ventral), *Megachile* (70, 71, 72), *Xylocopa* (73, 74, 75a ventral, 75b dorsal), *Bombus* (76, 77, 78), and *Melipona* (79, 80, 81); and genitalia of *Apis* (82).



83
Nomia melanderi

85
Xylocopa virginica

84
Augochlora pura

86
Nomadopsis euphorbiae

87
Perdita maculigera

FIGURES 83-87. **Prepupae of five bee species, illustrating the variation in body tuberculation.**

Bee Larvae

Studies on the biology and morphology of the immature stages of bees have lagged considerably behind those of the adult. Students interested in accounts of comparative studies of hymenopterous larvae should consult papers by Michener (1953) and Grandi (1961). There is ample reason for the paucity of publications on immature stages of bees since the pollen masses, eggs, and larvae are always concealed in habitats where observation can be made only with difficulty. The only bee larvae adapted for moving along the cell walls or burrowing through the pollen are the early instars of most parasitic bees and the later instars of the Allodapini. The early stages of all bee larvae except the Allodapini and some *Bombus* are individually enclosed in a cell which offers protection to the developing young.[1] Provision of a larval habitat that supplies all the food needed for development, as well as protection against extremes of environmental stress, has evolved slow moving, poorly sclerotized forms.

Apparently, when Hymenoptera changed from the active larval life characteristic of the Chalastogastra to the more sedentary, protected existence characteristic of the Clistogastra, there was an accompanying loss of legs, vision, and sclerotization and a development of other less obvious adaptations. The larval habits of aculeates represent only a slight departure from those of parasitoids such as chalcids and ichneumonids, which are supposedly ancestral to them. As might be expected, their larvae are likewise similar. Although the diet of bee larvae has changed from that of its supposed aculeate wasp ancestors, larval environment and activities have changed very little.

Most of the published information on larval structure is based on mature forms which have finished defecation and have assimilated all of their food. There are distinct differences in body conformation between immature and mature bee larvae. Immature larvae can be readily recognized if they are exhumed while still feeding on the remnants of a pollen mass. In the early part of the last instar, the larvae have a body conformation similar to that of previous instars in that their heads are weakly sclerotized and their bodies are smooth and glistening. The fat bodies and contents of the hind gut are evident through the very thin cuticle. Once the food has been assimilated by the last instar larva, there is a marked increase in head-capsule sclerotization and a change in color of body cuticle from translucent white to opaque pasty white or pale yellowish brown. In this condition the larva may undergo a long dormant period (in diapause) or it may quickly undergo physiological changes leading to pupation. This latter stage is re-

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[1] Several eggs are often placed in the host cell by parasite bees (usually by different individuals). The larvae may co-exist for a short period but invariably only one reaches maturity.

ferred to as the prepupa in bees. It is not a distinct instar, for there is no molt between the shiny larva of the last instar and the prepupa, nor is there any change in the size of the head capsule. The term prepupa is thus a relative one, signifying that the larva has undergone a transition from the delicate feeding type to the durable overwintering form. In much of the literature, the prepupa has been referred to as the postdefecating form and all of the earlier stages as predefecating. Since the larvae of a number of species begin defecating long before they have finished feeding, the terms predefecating and postdefecating cannot be applied universally.

Most bees overwinter as prepupae, but certain ones, *Emphoropsis miserabilis, Bombus, Apis,* some *Andrena,* most *Osmia,* some *Megachile,* and Halictinae overwinter as adults. Such bees have the typical prepupal stage described above, but its duration is much shorter. The shortened period is also characteristic of those species which pass through multiple generations.

Techniques of preservation

Many fluids are used as preservatives for larvae. Certain materials better maintain gross body shape, while others assist in preserving muscles and internal organs. Alcohol alone tends to make the cuticle very brittle after prolonged periods of preservation, particularly if the specimens are dropped into it alive. In addition, alcohol becomes diluted if a number of specimens are placed in a single vial, thus necessitating a periodic renewal of fluid.

The following methods of preservation have been used with success by different workers in this country. [Students should consult Peterson (1962) for additional preserving compounds and suggestions as to their applicability.]

- Drop the live larva into water near the boiling point for a couple of minutes, then transfer it to 70% ethyl alcohol. Killing in boiling water appears to prevent any major distortion in body shape.
- Drop the live larva into one part glacial acetic acid and three parts 90% ethyl alcohol for one week, then transfer to 70% alcohol. This preservative does not appear to cause any major change in body conformation.
- Dietrich's solution: Drop the live larva into 5 parts glacial acetic acid, 30 parts 95% ethyl alcohol, 10 parts formalin, and 55 parts distilled water. After three days transfer the larva to 70% alcohol. This material is particularly valuable as a fluid for preserving internal musculature and other internal body organs. It may be necessary to slit the body wall of large larvae to permit the fluid to reach the internal organs before decomposition occurs.
- KAAD: Place the larva in 1 part kerosene, 8 parts ethyl alcohol, 2 parts glacial acetic acid, and 1 part dioxane. After three days transfer the larva to 90% ethyl alcohol. This fixative is inclined to inflate larvae and pupae. It does not seriously affect the body shape of large bee larvae, but it may distort or split the cuticle of small larvae or early instars or larger forms. A smaller quantity of kerosene in the formulation alleviates much of the distortion and splitting of the cuticle in small larvae.
- If larvae are to be preserved for histological examination, prepare two solutions of: (1) 4 g. chromium potassium sulfate, 25 ml. formalin concentrate, 2 ml. glacial acetic acid, and enough distilled water to fill 300 ml.; (2) and 100% ethyl alcohol. Just prior to fixing larvae, mix the two solutions (1:1) and pour the mixture into a series of small containers. Place each clean larva into each container for no more than one and one-half hours. Wash twice in 95% alcohol and preserve the material in fresh 95% alcohol.[2]

It is necessary to change the final preservation at least once, a few weeks after the specimens have been treated. This is essential where a number of larvae are maintained in a small vial, for the body fluids dilute the concentration of the preservative, leading to a deterioration of the specimens. Storage vials must be tightly sealed to avoid evaporation. Stoppers of neoprene are more satisfactory than those of cork or any of the rubber that deteriorates in alcohol.

Examination of specimens. Morphological studies of larvae require examination of gross body structure, for which a lateral view of the specimen is generally presented, plus detailed studies of the structures of the head capsule and the spiracles. Before the head capsule can be studied in detail, it should be removed from the body and separated from the appended tissue by gently boiling it in a 15% solution of sodium hydroxide ($NaOH$). The head capsule is very lightly sclerotized and caution should be taken not to overboil. It has also been found that simmering the head capsule in a 10% nitric acid solution for 15 to 30 seconds permits the muscular tissues to be teased away very easily from their points of attachment. Nitric acid is preferable to sodium hydroxide since it softens but does not quickly clear the weakly sclerotized portions of the head capsule. The head capsule may then be immersed in glycerine or placed in a watch glass on a piece of cotton in a weak alcohol solution for microscopic examination. The presence of the cotton prevents the head capsule from floating freely and permits prolonged examination at any particular angle. The mandibles are usually removed from the head capsule in order to view their inner surfaces. They are generally the most heavily sclerotized portion of the head capsule and will stand prolonged boiling in either $NaOH$ or nitric acid without losing their original form.

The spiracles may be removed with some of the adjacent tissue and examined under a high-powered dissecting microscope or a low-powered compound mi-

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[2] This solution was formulated by Bronte J. Gatenby and H. W. Beana, (The Microtomist Vade-Mecum, London: J. and A. Churchill, 1950), and modified by N. Youssef, Utah State University.

croscope. The surface view of the spiracle presents all depths of the atrium when viewed through the atrial opening. A lateral view, or longitudinal section, of the spiracle exposes the subatrium as well as the attachment of spines when they are present (Fig. 98).

Larval morphology

The larvae of clistogastrous Hymenoptera are not well known, principally because of the paucity of collected material, much of which is poorly preserved. A notable exception is the comparative morphological study of bee larvae by Michener (1953a) in which he describes all of the larval material available to him at that time. His work precipitated the interest of a number of workers throughout the country, and some excellent descriptive and illustrative works on bee larvae have appeared since.

Entire bee genera still exist for which the larvae are unknown, and many other large genera are known only by the larvae of a single species or specimen. This section is included in the hope that it may provide impetus to workers in the Northwest to collect bee larvae whenever they are available.

Some precautions should be observed before nesting sites are exhumed. It is desirable to mark the nesting site and record as much adult behavioral data as possible. Daily records of activity can be used as a criterion for estimating the number of cells that have been completed and for indicating when mature prepupae are present. The latter point is particularly important, for most comparative studies of bee larvae have been based on prepupae. Premature exposure of a newly found nesting site often reveals only pollen balls with eggs or immature larvae, which are difficult to rear to maturity. Fortunately, bee larvae mature rather rapidly, and most northwestern species reach larval maturity from 10 days to 3 weeks after egg deposition. Development is slower in species that are active in the early spring and late fall, and it is most rapid in the mid-summer forms. If the nesting site is extensive, an indication of larval maturity may be gained by examining nesting females. The prevalence of older females, as indicated by loss of tergal pubescence and tattering of the wings, indicates that the site contains both mature and immature larvae. One or more adults of the nesting species as well as early instar larvae should be preserved to make certain of the larva-adult association.

The external morphology of the alkali bee is presented here in some detail as a guide for those interested in accumulating morphological information on unknown or poorly known larval forms.

Alkali bee larvae can be obtained in most alfalfa seed producing areas in the northern part of the Great Basin; or representative specimens can be obtained by contacting any of the state universities in this area that are engaged in bee research.

When there is a wide variation in certain diagnostic characters among bee larvae, morphological comparisons are made with larvae of other bee genera. Comparisons are made with those bee genera which are most readily available to workers in the Northwest, particularly *Apis, Bombus,* and *Megachile,* but reference to other genera is sometimes necessary. Where *Nomia* represents an intermediate condition in the expression of a certain characteristic, genera are compared in which that characteristic is either poorly developed or highly elaborated.

Body

The prepupa of *Nomia* is grub-like in that it lacks legs and has no separation between thorax and abdomen. The prepupa tends to be weakly "7" shaped at maturity with the dorsum of each segment weakly tuberculate. Behind the head there are 3 thoracic and 10 abdominal segments. The mesothorax and metathorax and the first eight abdominal segments bear strongly sclerotized spiracles laterally (Fig. 83). The tergal region of each abdominal segment is weakly divided into a *cephalic* and a *caudal annulet* by a weak transverse furrow that can be seen only upon close examination. The dorsal and caudal annulets are distinct in the genus *Augochlora* (Fig. 84), whereas *Xylocopa* shows no evidence of segmental annuletation (Fig. 85). In many species the caudal annulets are distinctly produced to form *dorso-lateral tubercles.* These are weak in *Nomia,* distinct in *Augochlora,* and produced as sharp conical projections in *Nomadopsis* (Fig. 86) and *Perdita* (Fig. 87). Some bee genera have a series of sharply projecting tubercles immediately below and caudad from the spiracles. These *ventrolateral tubercles* are most evident on the mid-abdominal segments of *Augochlora* (Fig. 84) but are absent in *Nomia.* The *anal opening* is found on the terminal abdominal segment and may be located at the extreme apex of the segment as in *Nomia,* dorsally as in *Exomalopsis,* or ventrally from the apex.

Head

The head capsule of *Nomia* consists of a rounded, weakly sclerotized, and multilobate structure fused to the membranous anterior margin of the first thoracic segment throughout its length. It is bounded on its posterior margin by a narrow chitinized band which expands into a broader *hypostomal thickening* at the *posterior tentorial pits.* The hypostomal thickening continues as a broadened cuticular expanse along the lateral margin of the head capsule to the *posterior mandibular articulation* and extends dorsally and medially above the *mandibular corium* as the *pleurostomal thickening.* It meets an expanded internal ridge at the *anterior mandibular condyle* which is indicated externally by the *epistomal suture* on the face. The combined hypostomal and pleurostomal thickenings are referred to by Michener as the *marginal thickening* of the head capsule (Fig. 88).

In most bee genera there is a distinct *cleavage line* or *epicranial suture* that runs from the middle of the vertex of the head capsule, ventrally toward the epistomal suture. This is absent in *Nomia,* present in *Apis* as a straight unbranched suture (Fig. 89), and repre-

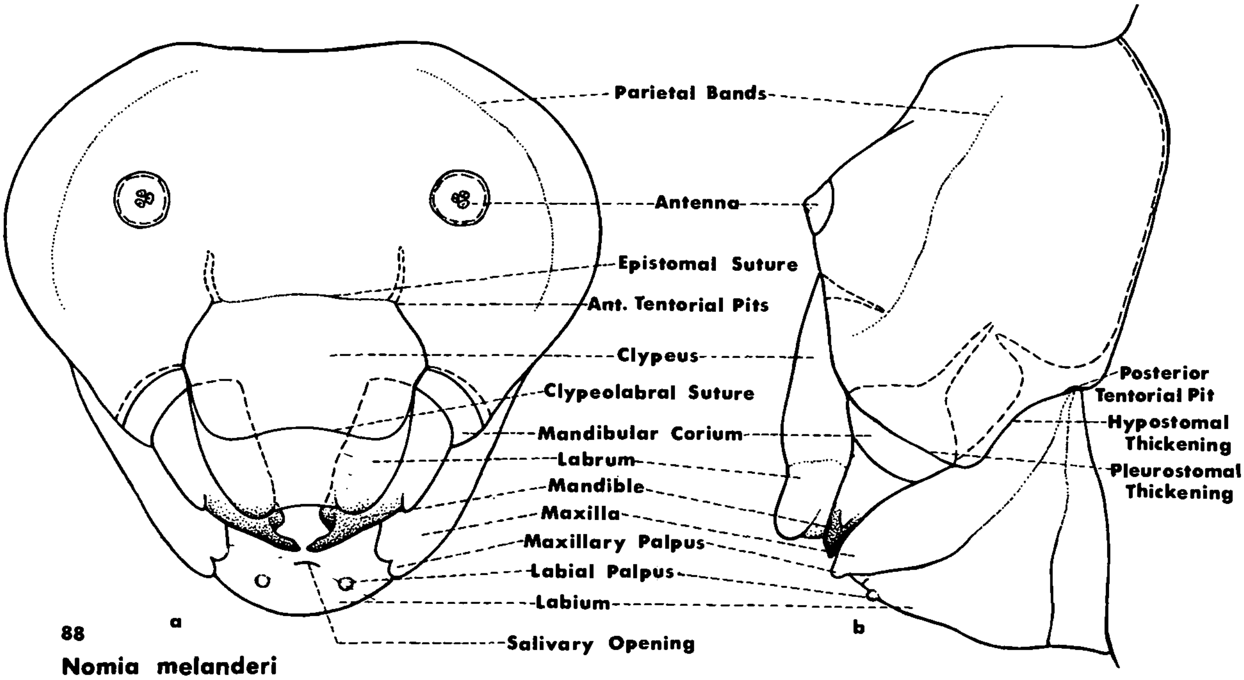
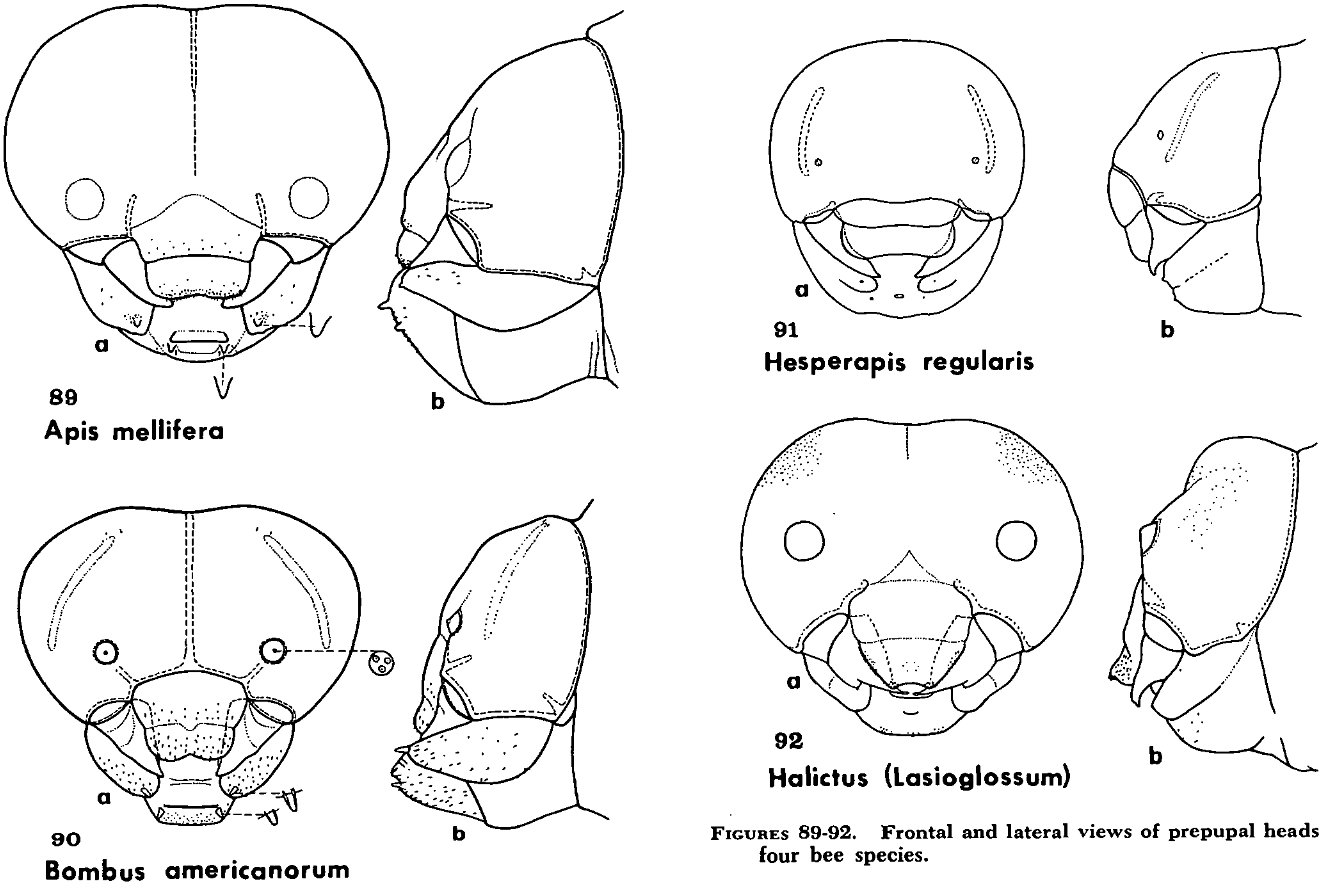


FIGURE 88. Frontal and lateral views of the head of *Nomia melanderi* prepupal larvae.



FIGURES 89-92. Frontal and lateral views of prepupal heads of four bee species.

sented in *Bombus* as paired sutures that extend to the epistomal suture (Fig. 90). The presence of the cleavage lines, their length in relation to their extension towards the epistomal suture, and the degree of terminal branching on the middle of the face are good diagnostic characters in certain taxa. The *antennae* of *Nomia* are distinct and conical and each has a weak papilla. In *Apis* the antennae are present merely as weakly rounded convexities lacking papillae (Fig. 89b), whereas in *Bombus* (Fig. 90b) the papillae are more distinct than those of *Nomia* (Fig. 88b). The *parietal bands* are weakly defined in *Nomia,* extending about the sides of the antennal papillae; in *Bombus* they are much more distinct and broader (Fig. 90), and in *Apis* (Fig. 89) the parietal bands are absent. The *epistomal suture* is weakly developed in *Nomia,* and it is defined as a shallow transverse depression between the *anterior tentorial pits*. The epistomal suture is absent in *Apis* (Fig. 89) but distinct in *Bombus* (Fig. 90). This suture is marked by a distinct internal ridge extending laterally and fusing with the pleurostomal thickening at the anterior mandibular condyle. The *clypeolabral* suture is weak in *Nomia* and *Apis* (Fig. 89) but much more distinct than the epistomal suture. In *Bombus* the epistomal suture is more clearly defined than the clypeolabral suture (Fig. 90). *Apis* is peculiar in having the clypeolabral suture strongly inflexed. The apex of the fleshy, very weakly lobed labrum in *Nomia* overhangs the mouth, which in turn leads into the fore gut. The mouth is difficult to see unless the labrocypeal lobe is moved. Below the mouth there is a distinct convex area termed the *hypopharynx,* and towards the apical extremity of this lobe is located the *salivary opening*. In *Nomia* this is evident as a distinct slit which extends for a short length between the bases of the labial palpi and lacks protective lips (Fig. 88). In *Bombus* the salivary slit is protected by weakly sclerotic lips (Fig. 90), whereas in *Apis* the lips are large and protruding (Fig. 89).

The lower appendages of the head, including the hypopharynx and the labium, and in some genera even the maxillae, are often represented among bee larvae as a complex of structures that have undergone partial or complete fusion. Thus, it is impossible to distinguish the suture which normally delimits the hypopharynx from the prementum of the labium, and in some genera (*Hesperapis*) the maxillae and the labium are difficult to separate because of extensive fusion (Fig. 91b). For this reason Michener (1953) suggests that the term "labial lobe" be used for descriptive purposes when referring to the area including the hypopharynx, salivary slit and lips, and labium.

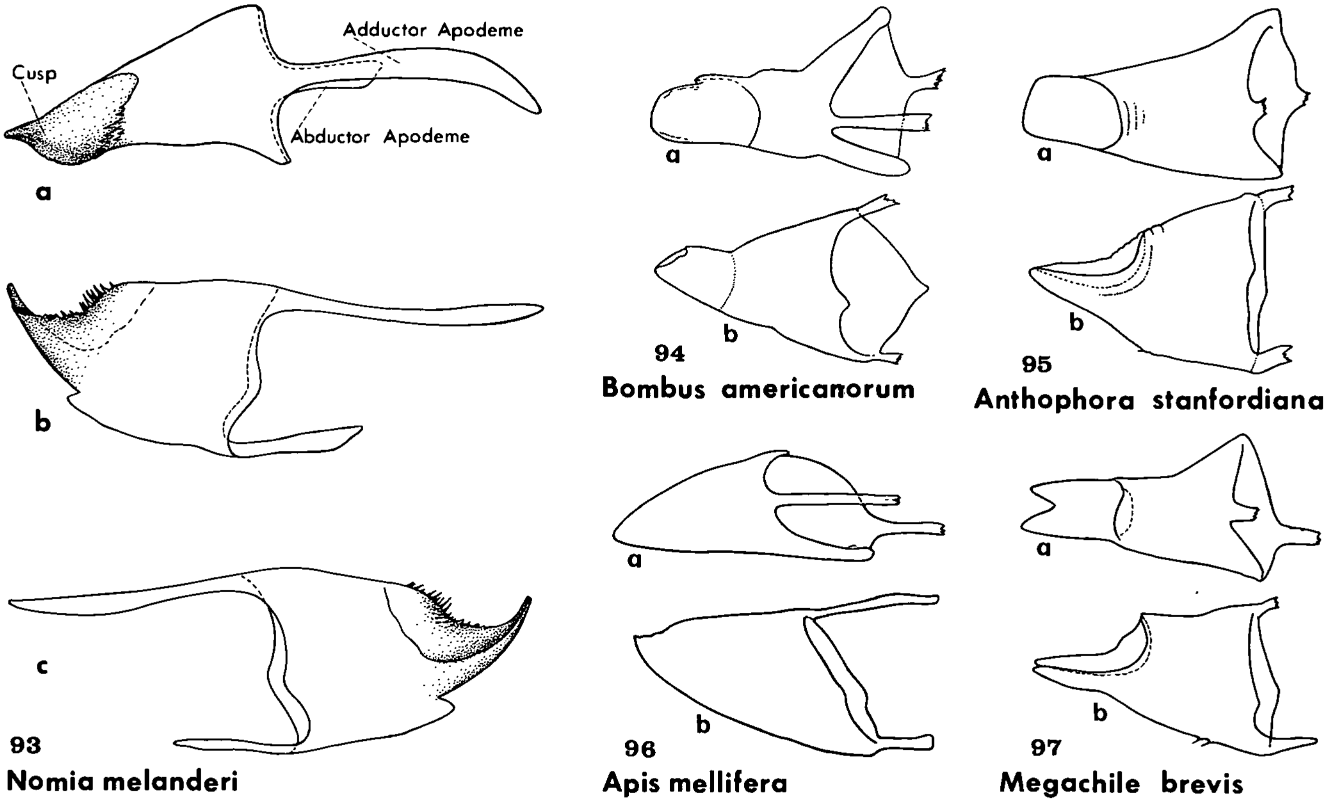
The *mandibles* of bee larvae offer many important characters that appear to have both generic and specific value. They differ from most other hymenopterous larvae in that their apices never have more than two distinct teeth. The mandibles are the most highly sclerotized structures on the head. Each mandible of *Nomia* terminates in a single strongly sclerotized, pointed tooth (Fig. 93), whereas the mandible of *Bombus* terminates in two teeth, one large and apical, the other smaller and subapical (Fig. 94a). The mandibles of *Apis* are subtriangular and can be considered to terminate in a single tooth (Fig. 96).

Many genera of bees have variously shaped mandibular projections located along the inner surface, termed the *cusp*. It is usually delimited by bands of numerous small teeth that extend along the upper margins of the mandibles. The bands may also extend beyond the cusp towards the mandibular apex. In addition to the cusp, *Nomia* is one of several genera with the area beyond the cusp hollowed slightly and delimited by a distinct ridge (Fig. 93a). The mandibles of *Nomia* are peculiar in that they possess a single large tubercle on their outer surfaces (Fig. 93b). The mandibles of *Bombus* lack the teeth of the cusp as well as the small teeth on the upper surface (Fig. 94b). In *Apis* both the cusp and the concave mandibular apex have been lost (Fig. 96b). The mandibles of many bee genera, such as *Anthophora* and *Diadasia,* terminate in a blunt, subquadrate apex which is considered to be a modification of a two-toothed condition (Fig. 95a). Typically bidentate mandibular apices are common to most of the megachilidae (Fig. 97a). In this group the teeth are subequal in length, the mandible thus tapering to a bifid apex.

Two large mandibular apodemes, the abductor and adductor, extend into the head. In *Nomia* the adductor apodeme is twice the length of the abductor, whereas in *Apis* the apodemes are subequal in length (Figs. 93, 96). A broad membranous area, the *mandibular corium,* lies between the bases of the mandibular articulations and the base of the head (Fig. 88b). The width and shape of the corium is variable as shown in the accompanying diagrams.

The *maxilla* of bee larvae is a highly specialized lobate structure representing the stipes, lacinia, cardo, and galea. In most bee genera these structures are fused, but in some encerines and centridines the stipes, cardo, and galea are distinct. The only obvious appendage to the maxilla is a one-segmented palpus. In some bee genera (*Bombus*), there is a weakly sclerotized region near the base of the maxilla which Michener (1953) considers to be the remnant of the cardo. The maxilla may be distinct from the labium (*Apis* and *Bombus*) or partially fused with it (*Nomia*). The length of the maxillary palpus is highly variable. In *Nomia* the apex of the maxilla is weakly bilobed; the outer lobe represents the maxillary palpus (Fig. 88b). The maxillary palpus is distinct and almost twice as long as broad in *Bombus* (Fig. 94b), whereas in *Halictus* s.s. and *H.* (*Lasioglossum*) the maxillary palpus is absent (Fig. 92b).

The *labium* forms the under surface of the head in bee larvae. It is lightly sclerotized, and (as indicated above) it is often indistinguishable from the hypopharynx and may be fused in its entirety to the maxillae (*Hesperapis*) (Fig. 91b). In *Bombus* (Fig. 90b) and *Apis* (Fig. 89b), the labium is separated into a post-



FIGURES 93-97. Prepupal mandibles of *Nomia melanderi:* (a) inner view, (b) outer view, and (c) ventral view (93); prepupal mandibles of four bee species: (a) inner views and (b) outer views (94-97).

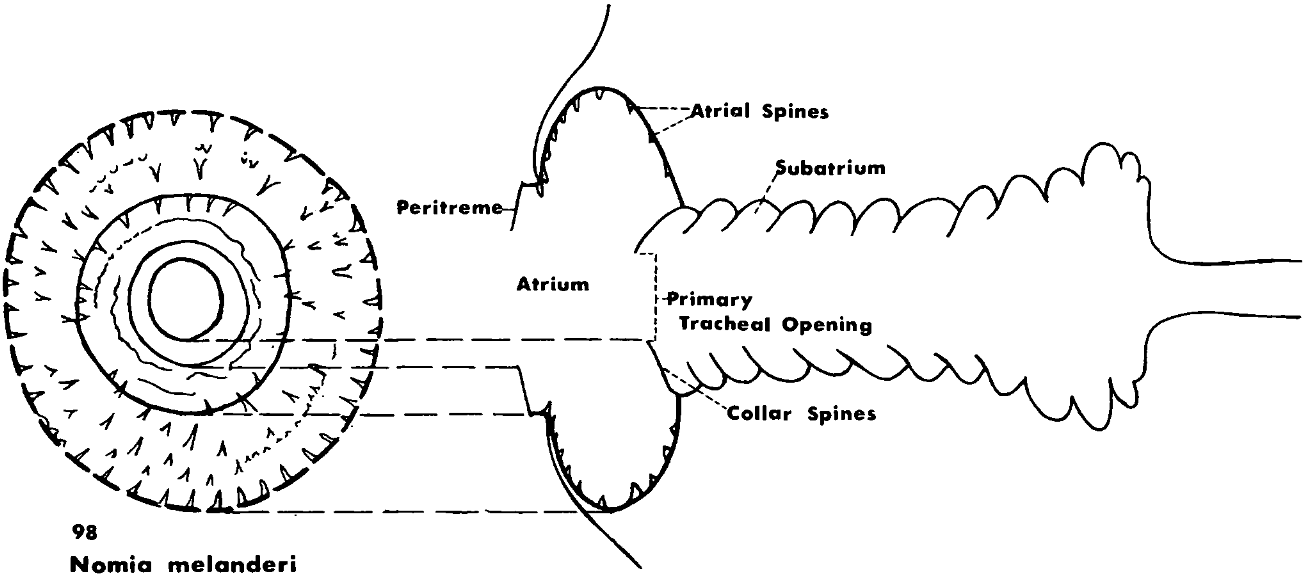
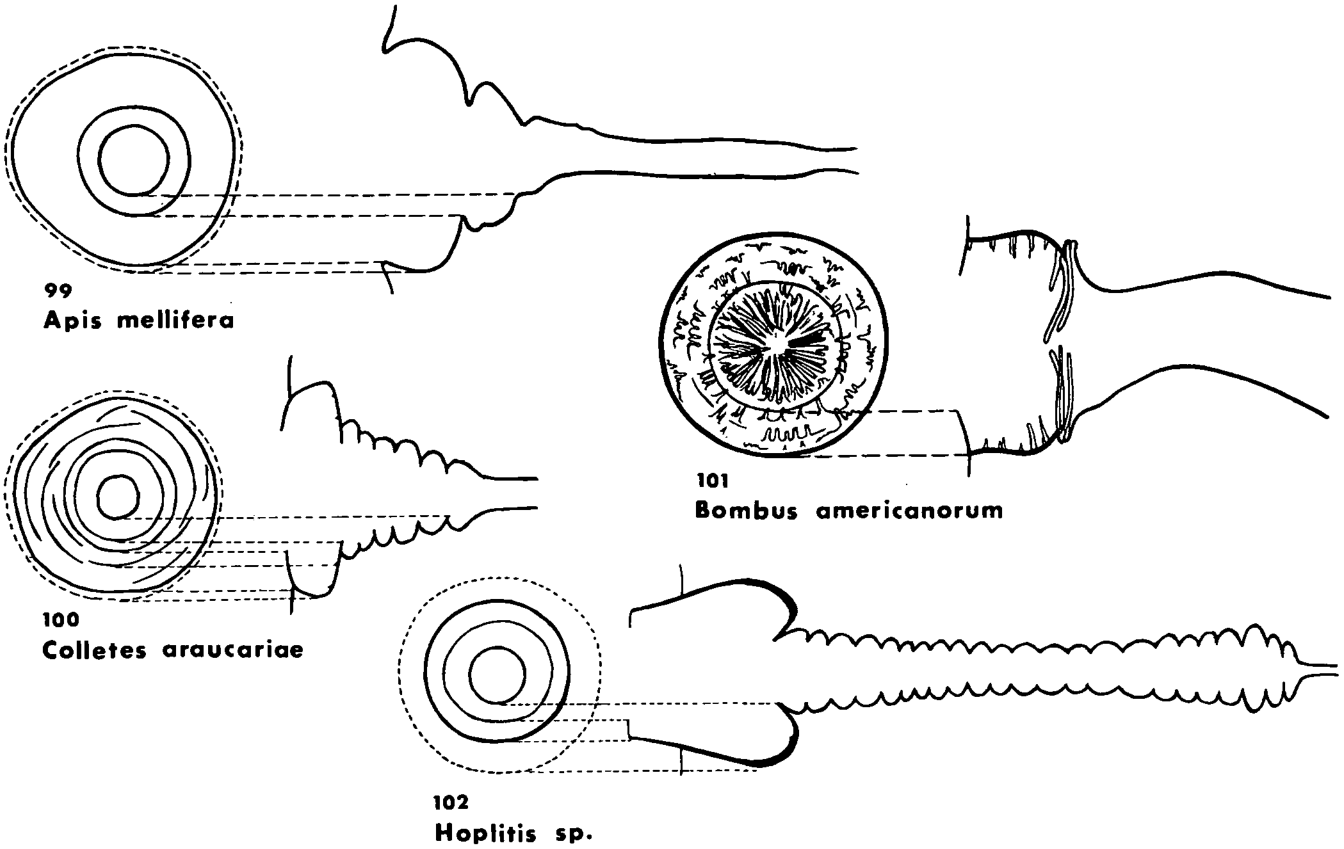


FIGURE 98. Spiracles of *Nomia melanderi* prepupa: surface view (left) and longitudinal sectional view (right).



99
Apis mellifera

100
Colletes araucariae

101
Bombus americanorum

102
Hoplitis sp.

FIGURE 99-102. Surface and longitudinal sectional views of prepupal spiracles of four bee genera.

mentum and a prementum by a distinct transverse furrow, whereas in *Nomia* the furrow separating these two structures extends only part way towards its anterior margin. In various other genera (*Halictus* (*Lasioglossum*), *Hesperapis,* and *Diadasia*), the labium is entire and there is no evidence of segmentation. The apical margin of the labium is provided with a pair of small tubercles situated on either side and below the salivarium. These structures, considered to be homologous with the labial palpi, vary in shape and size among bee larvae. In *Nomia* they are broader than long (Fig. 88b), whereas in *Apis* and *Bombus* they are considerably longer than broad (Figs. 89b, 90b). The larvae of *Halictus* and *Sphecodes* lack labial palpi (Fig. 92b).

The positions of the anterior and the posterior tentorial arms are indicated in the figures of the heads. As can be seen, there is considerable variation in their size and shape. However, their value as a diagnostic character among bee larvae has not been fully exploited.

The spiracle of *Nomia melanderi* consists of an invaginated cuticular *atrium;* the upper lips of this atrium protrude beyond the body wall. The upper margin of the atrial wall is flared to form a rim from which a transparent lip or *peritreme* extends inward, its apical margins designating the circumferal limits of the atrial opening (Fig. 98). The atrium may be flush with the body wall as in *Apis* and *Bombus* (Figs. 99, 101), and the peritreme may be large (*Colletes,* Fig. 100), small (*Hoplitis,* Fig. 102), or even absent (*Apis,* Fig. 99). The atrium in *Nomia melanderi* is provided with several rows of sharp spines which line the inner wall. The form and position of the *atrial spines* are usually species-specific characteristics. In many species the spines are long and densely clothe the atrial wall, whereas in others the spines are wanting (*Apis,* Fig. 99). In *Nomia* and *Bombus* there are series of longer modified atrial spines termed *collar spines* which surround and cover the *primary tracheal opening* (Figs. 98, 101). The primary tracheal opening begins at the base of the collar spines or, in species where collar spines are absent, at the point where the heavy cuticular atrial wall meets the membranous *subatrium.* The subatrium in *Nomia* is distinctly annulated, whereas in *Bombus* and *Apis,* it is smooth and tapering (Figs. 98, 99). Beyond the subatrium, the trachea becomes progressively narrower and minutely branched.

The spiracles in some genera offer excellent diagnostic characters at the species level. Ritcher (1933) was able to distinguish between the species of *Bombus* larvae by using spiracular differences. However, an examination of the spiracles of other bee larvae indicates that they may vary significantly among congeneric species. Two of the species of the genus *Nomia,* for example, are separable on the basis of the presence or absence of atrial spines, the shape of the atrium and the primary tracheal opening, as well as differences in other minor structures.

From the foregoing discussion, it is apparent that the head, mouthparts, and general body conformation of prepupal bees are rather homogeneous among all the genera. Although the magnitude of intergeneric differences does not approach that of the adults, the more subtle differences exhibited by the larvae are consistent at both the specific and generic levels.

Exceptions to the general character homogeneity noted among bee larvae are strikingly evident in the first (and sometimes second) instars of parasitic bees. Unfortunately, first instars of only a few parasitic species have been illustrated or described, and comparative studies of this stage would be premature. The first instar larva of *Triepeolus remigatus* is provided to illustrate larval modifications associated with the parasitic mode of life (Figs. 103, 104). Both the thorax and (particularly) the abdomen are provided with enormously expanded ventro-lateral tubercles which provide the larva with a means of locomotion to seek and destroy the host larva and to locate provisions. The head capsule is highly modified, dorso-ventrally flattened, and equipped with enormous, strongly sclerotized mandibles. The capsule and the mandibles are sparingly covered with short hairs. The clypeolabral suture is distinct, and a large, weakly sclerotized, bilobed labrum protrudes anteriorly between the mandibles. The maxillae are reduced to simple elongate sclerites on the lower margins of the head capsule and the maxillary palpi have been lost. The labium is largely membranous medially, and it bears two very long one-segmented palpi.

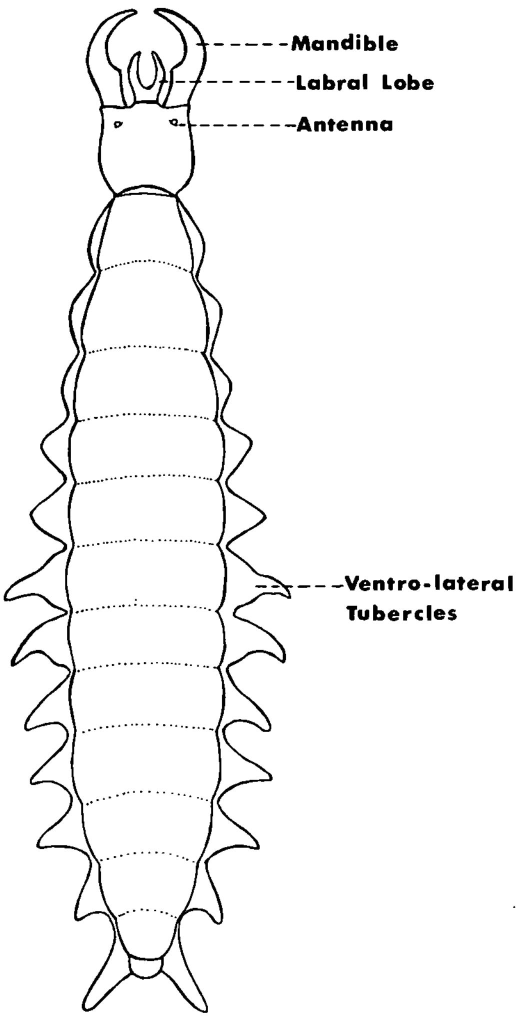


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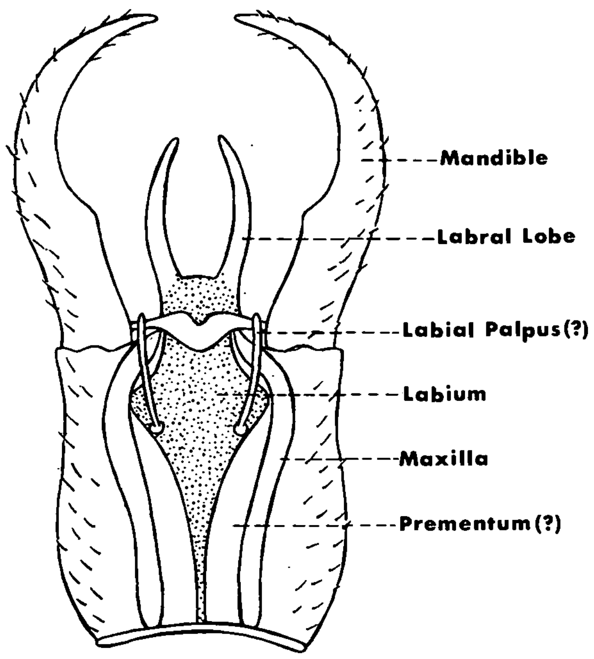
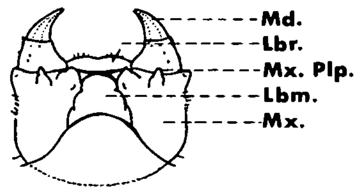
Figure 103. Dorsal view of first instar larva of *Triepeolus remigatus*.



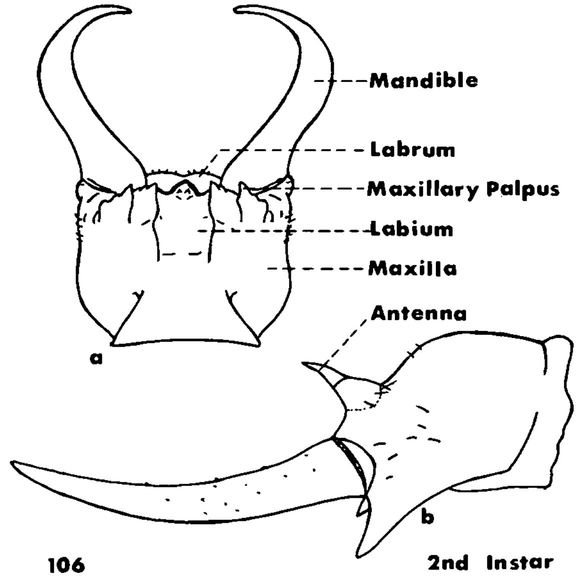
104

Figure 104. Ventral view of the head of first instar larva of *Triepeolus remigatus*.

Not all first instar larvae of parasitic bees are as obviously modified as those of *Triepeolus.* First instar larvae of *Coelioxys* and *Stelis* (Fig. 107) exhibit no extensive elongation of the mandibles or adaptation in general body conformation for locomotion. The mandibles are short and robust (Figs. 105, 108), and they do not differ greatly from those of nonparasitic bees of the same stadium. In the second instar, the head structures undergo slight change, but there is an enormous increase in mandibular size (Fig. 106).



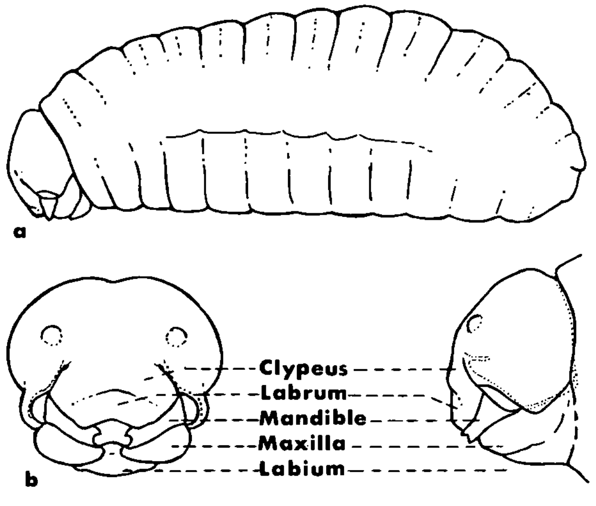
105 **1st Instar**



106 **2nd Instar**

Coelioxys 8-dentata

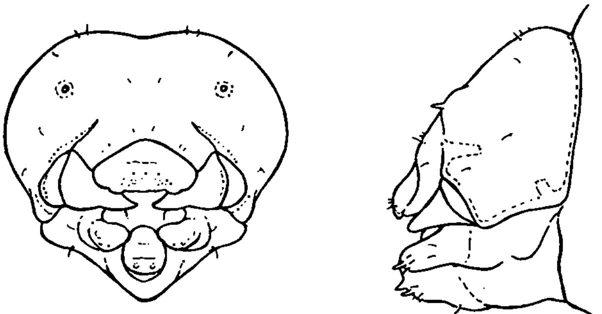
FIGURES 105-106. Ventral view of the head of first instar larva of *Coelioxys 8-dentata* (105); and two views of the head of second instar larva of *Coelioxys 8-dentata*—ventral view (106a) and lateral view (106b).



107 **1st Instar**

Stelis bilineolata

FIGURE 107. Lateral view of first instar larva (107a); and frontal and lateral views of the head of *Stelis bilineolata* (107b).



108

Stelis lateralis **Mature Larva**

FIGURE 108. Frontal and lateral views of the head of *Stelis lateralis* prepupae.

Bee Pupae

So little informaion is available on details of pupal structure among bees that any comparative studies on their morphology are premature. Michener (1954), upon examination of pupae of available genera, presented a series of pupal characters (consisting principally of spines and projections) that he considered to have some generic significance. Most of the spines and projections appear to offer accommodation to spines or hairs of the adult, and in most instances the latter are visible through the lightly sclerotized projections. However, the presence of hair-accommodating spines and projections on many of the hairless parasitic bees suggests that these structures may be retained long after they have served their original function. Their potential value in determining relationships among bee genera justifies the description of these structures whenever material becomes available. Recently Yager and Rozen (1966) provided a more comprehensive study on the pupae of the Andrenidae. On the basis of 17 species in 6 genera, they concluded that there were consistent specific and generic differences among the pupae examined, but that patterns of relationship were not obvious.

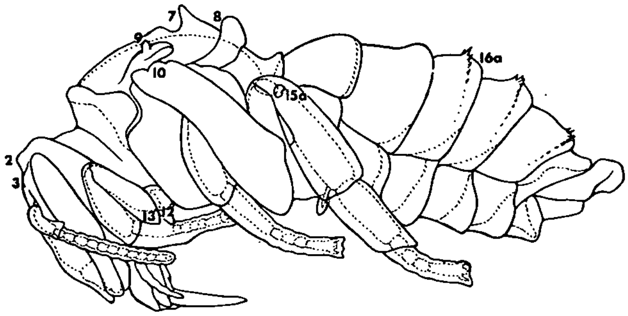
Pupae are more difficult to obtain than larvae since the pupal stage is of shorter duration. Species that overwinter in the prepupal stage sometimes require a period of cold conditioning before they will pupate. Those species that overwinter as adults pass rapidly through the pupal stage during the late summer or early fall. It is, therefore, usually advisable to hold prepupae in the laboratory until they pupate rather than attempt to be on hand for the brief pupal period in the field. Pupae may be fixed, preserved, and examined in the same manner as larvae (see pages 22 and 23).

Michener (1954) points out that certain adult spines appear to have arisen independently in a number of unrelated bee genera. On the other hand, anterior coxal spines are present on virtually all bee pupae and usually contain only hair. The universality of coxal spines on the pupae of bees suggests that this may well be a primitive character common to the progenitors of this group.

The following list of apparently significant spines and protuberances is adapted from Michener (1954), and it is presented as a guide for future comparisons. Figure 109, the pupa of *Nomia melanderi,* illustrates the position of many of the structures referred to, but the student should recognize that no known pupa contains all of the features cited.

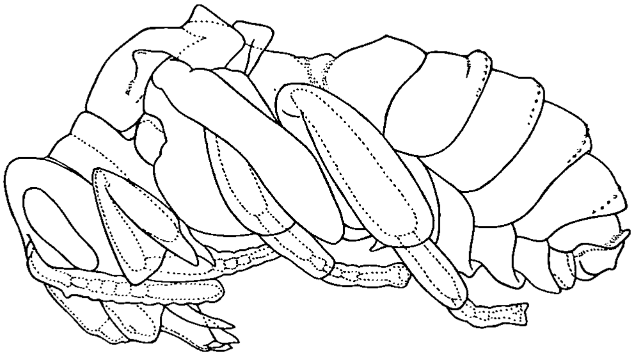
1. Scape:
   a. The antennal scape has a small median tubercle in some bee genera, i.e., *Augochlora.* It is absent in *Nomia.*
   b. There is a distinct protuberance on the outer surface near the juncture of the scape and the flagellum. This has been seen only in *Andrena viburnella* (Fig. 110).
2. Vertex: There is a pair of small protuberances in the proximity of the lateral ocelli on the vertex of *Nomia,* the halictines, one of the colletids, *Policona,* and *Perdita maculigera maculipennis.* These are not found in any other known apoids.
3. Frons: A pair of small protuberances is found mesad from the summits of each eye in some halictines, as well as in *Nomia.*
4. Lateral angles of pronotum: These angles are produced to spines in *Colletes,* but are normal in all other known bee genera.
5. Posterior lobes of pronotum: These lobes are markedly produced in *Colletes, Diadasia, Emphoropsis,* and *Anthophora.* They are normal in *Nomia.*
6. Mesoscutum: There are one or two pairs of weak tubercles near the mid-line of the mesocutum in some bee genera. These are absent in *Nomia.*
7. Scutellum: The scutellum is provided with a pair of large vertical spines in colletids, in *Nomia,* in other known halictids, and in *Emphoropsis.* A pair of smaller, anteriorly directed spines are found in this region in some anthrophorids (*Anthophora, Diadasia*).
8. Metanotum: There is a strong median protuberance on the metanotum of *Nomia,* all known halictids, colletids and *Andrena viburnella* Graen. It has not been noted on any other bee genera.
9. Tegulae: A distinct tubercle on each tegula is evident in *Nomia, Halictus, Emphoropsis, Policona,* and *Andrena.*
10. Wings: *Nomia* and known halictines have a small tubercle located medially on the forewing in addition to a basal tubercle; *Peponapis, Melissodes,* and *Exomalopsis* possess only the basal tubercles.
11. Coxae: The fore, mid, and hind coxae of all known bee genera each bear an inner apical spine. The length of the spine varies from the "average" length in *Nomia* to very long in *Colletes* and *Xylocopa.*
12. Trochanters: As with the coxae, all pupae bear a spine on each of the fore, mid, and hind trochanters. They are of "average" length in *Nomia,* long in *Colletes* and *Xylocopa,* and very long only on the fore trochanters of *Apis.*
13. Fore femora: *Nomia* and most other bee genera have a distinct protuberance on the underside of each fore femur near its base. This protuberance is long and spine-like in *Colletes* and *Anthophora.*
14. Mid femora: Protuberances located in the same position as those on the fore femora are found on the mid femora of *Nomia, Apis,* and *Andrena.* These are absent in most other genera, but in *Anthophora* they are long and spine-like.
15. Hind tibiae:
   a. *Nomia, Augochlora,* and *Halictus* (*Lasioglossum*) have a sharp spine on the outer margins of each hind tibia near its base. This spine is located approximately at the end of the basitibial plate of the adult. *Halictus* has a weak protuberance in this position, but in all other known bee genera this area is not modified.
   b. There is an outer apical spine on the hind tibia of *Halictus.* This spine is unknown in any of the other bee genera examined.
16. Tergal spicules:
   a. There is a subapical row of spicules on the median tergal segments of most bees. In *Nomia* the spicules are found on metasomal terga III through V, but in most other genera they are found on terga II through V or VI. *Halictus, Augochlora,* and *Emphoropsis miserabilis* have them on the first segment as well. There is no evidence of spicules on *Colletes* or *Apis,* and on *Hylaeus* the spicules are minute.
   b. Spicule size: The spicules vary from barely discernible in *Hylaeus,* to exceptionally long in *Halictus.*
17. Body setae: Certain species of *Megachile, Coelioxys,* and *Lithurgus* have long setae over the vertex, mesoscutum, and metasomal terga (Fig. 111).
18. Terminal spine: The last metasomal tergum is produced as an elongate spine in several genera. It is very long and pointed in *Perdita* (Fig. 112), long and rounded in *Nomadopsis.*

The diagram of the pupa of *Nomia melanderi* (Fig. 109) is labeled numerically, with the numbers corresponding to the structures indicated above. It is suggested that students collect series of pupae where possible, and that the examination for spines and tubercles be conducted on specimens that have just begun to darken. The contrast of the translucent structures against the darkened adult exoskeleton beneath facilitates their detection.



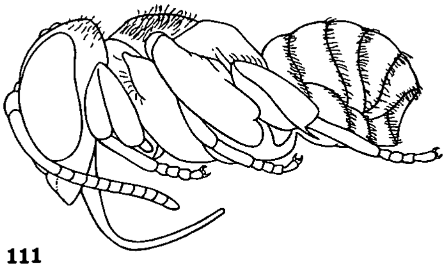
109

Nomia melanderi



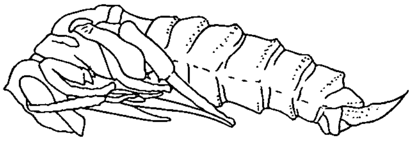
110

Andrena viburnella



111

Megachile rotundata



112

Perdita lingualis

FIGURES 109-112. Pupa of *Nomia melanderi* (109)—numbers refer to spines and tubercles cited in the text; pupae of *Andrena viburnella* (110), *Megachile rotundata* (111), and *Perdita lingualis* (112).

Systematic List of Included Taxa

(Northwest genera indicated by *)

Superfamily: APOIDEA

Family: COLLETIDAE

Colletinae	
Caupolicanini	_Caupolicana_
	Ptiloglossa
Colletini	_Colletes_*
Paracolletini	_Eulonchopria_
Hylaeinae	_Hylaeus_*
	Meroglossa
Chilicolinae	_Chilicola_
Diphaglossinae	_Policana_

Family: HALICTIDAE

Halictinae	_Agapostemon_*
	_Augochlora_*
	Augochlorella
	Augochloropsis
	Corynura
	_Halictus (sensu lato)_*
	Megalopta
	Megommation
	Neocorynura
	Nomioides
	Paragapostemon
	Paroxystoglossa
	Pseudagapostemon
	_Sphecodes_*
Nomiinae	_Nomia_*
Dufoureinae	_Conanthalictus_*
	_Dufourea_*
	_Micralictoides_*
	Protodufourea
	Systropha

Family: ANDRENIDAE

Andreninae	_Andrena_*
	Ancylandrena
Panurginae	
Melitturgini	_Camptopeum_
	Melitturga
Panurgini	_Perdita_*
	_Nomadopsis_*
	_Calliopsis_*
	Hypomacrotera
	Panurgus
	_Panurginus_*
	_Pseudopanurgus_*
	Psaenythia

Family: OXAEIDAE	_Oxea_
	Protoxea

Family: MELITTIDAE

Melittinae	_Melitta_
Dasypodinae	_Dasypoda_
	_Hesperapis_*
Macropidinae	_Macropis_*

Family: FIDELIIDAE

Family: MEGACHILIDAE

Lithurginae	_Lithurgus_
Megachilinae	
Anthidiini	_Heteranthidium_*
	Trachusa
	Archianthidium
	_Paranthidium_*
	_Anthidium_*
	_Callanthidium_*
	_Dianthidium_*
	_Anthidiellum_*
	_Dioxys_*
	_Stelis_*
	Heterostelis
	_Protostelis_*
	Bothranthidium
Megachilini	_Megachile_*
	_Chelostomoides_*
	Chalicodoma
	_Coelioxys_*
	_Chelostoma_*
	_Chelostomopsis_*
	_Heriades_*
	_Ashmeadiella_*
	_Hoplitis_*
	_Proteriades_*
	_Anthocopa_*
	_Osmia_*

Family: ANTHOPHORIDAE

Anthophorinae	
Exomalopsini	_Exomalopsis_*
	Ancyloscelis
Emphorini	_Diadasia_*
	Melitoma
	Ptilothrix
Eucerini	_Melissodes_*
	_Tetralonia_*
	_Svastra_*
	_Anthedonia_*
	_Xenoglossodes_*
	_Peponapis_*
	Xenoglossa

Anthophorini	_Anthophora_* _Emphoropsis_*
Centridini	_Centris_*
Melectini	_Zacosmia_* _Xeromelecta_* _Melecta_*
Ericrocini	_Ericrocis_
Nomadinae	
Ammobatini	_Oreopasites_* _Parammobatodes_
Biastini	_Neopasites_*
Epeolini	_Epeolus_* _Epeoloides_ _Odyneropsis_ _Triepeolus_*
Holcopasitini	_Holcopasites_*
Neolarrini	_Neolarra_*
Nomadini	_Nomada_* _Hexepeolus_
Protepeolini	_Isepeolus_ _Protepeolus_
Townsendiellini	_Townsendiella_
Xylocopinae	
Ceratinini	_Ceratina_* _Allodapula_ _Allodape_ _Eucondylops_ _Exoneura_ _Exoneurula_ _Inquilina_
Xylocopini	_Xylocopa_* _Proxylocopa_
Family: APIDAE	
Apinae	
Apini	_Apis_*
Meliponini	_Melipona_ _Trigona_ _Lestrimelitta_ _Dactylurina_
Bombinae	
Bombini	_Bombus_* _Psithyrus_*
Euglossini	_Aglae_ _Euglossa_ _Eulaema_ _Euplusia_ _Exaerete_

Key to the Genera of Northwestern Bees

The following key is artificial in that it uses convenient characters rather than those grouping the genera into higher taxa. Difficult-to-see and hidden characters requiring special mounting techniques were avoided whenever possible. Since some genera were found to be variable with respect to certain characters used (for example, the number of submarginal cells in *Andrena*), it was expedient to have them key out in more than one place. A number of genera exhibit great morphological variability. Thus, for the sake of simplicity, we used a few characteristics that are valid only for northwestern forms. By selecting characters as indicated above and by using illustrations approximately opposite each couplet, we have sought to make the key useful to laymen, students, and entomologists alike. Users of the key should refer to the illustrated drawings in the adult morphology section for glossary information.

A word of warning or explanation may be needed for some of the characters used in the key. The length of the jugal and vannal lobes of the hind wing is compared in several couplets. Although these lobes are differentiated nearly to the wing base, we decided that for purposes of the key it would be best to measure them along the lower wing margin to the tips of the lobes. For some bees in which the jugal lobe tends to fold under, it may be necessary to use a probe, or to remove one hind wing, before the lobes can be seen clearly. Since the jugal and vannal lobes often become tattered in old individuals, young specimens should be chosen for keying. A similar warning applies to the use of mandibular characters.

It is often difficult to see both subantennal sutures in the Andreninae. It may be helpful to scrape some of the hair away and adjust the lighting to achieve maximum suture definition. The facial foveae of the Andreninae are sometimes hard to distinguish, especially in the males where they are very broad and shallow with little other differentiation. In the Panurginae the foveae are more sharply defined, but they may be quite small.

Boundaries of the stigma and prestigma are sometimes difficult to define without the use of transmitted light. In differentiating *Melissodes* from other eucerines on the basis of the tegulae, it is often necessary to scrape away some of the hair from the tegula base.

To avoid confusion in counting abdominal segments, we have used the term "metasoma" where specific segments are mentioned. For the measurement of cells and veins, we are using minimal dimensions (excluding the thickness of the boundary veins). Comparative measurements should be made with an eyepiece micrometer, especially when the indicated differences are small.

1 Forewing with three submarginal cells (Fig. 113) 40

Forewing with one or two submarginal cells (Fig. 114) 2

2(1) Arolia absent (Fig. 115) 3

Arolia present (Fig. 116) 8

3(2) Abdominal terga with distinct yellow or white integumental markings 4

Abdominal terga lacking yellow or white markings 5

4(3) Sixth metasomal tergum of female with a large median emargination at least one half as wide as distance from emargination to lateral angle (Fig. 117); male with penis valves having recurved extensions clearly visible ventrally on undissected specimens .... *Callanthidium*

Sixth metasomal tergum of female not emarginate medially or with a small median notch less than one fifth as wide as distance from notch to lateral angle (Fig. 118); male with penis valves normal, not visible on undissected specimens (Fig. 118) .... *Anthidium*

5(3) Axilla produced to strong acute projection on each side of scutellum (Figs. 119, 120) 6

Axilla uniformly rounded (Figs. 121, 122) 7

6(5) Eyes bare; metanotum with median spine (Fig. 119) .... *Dioxys*

Eyes hairy; metanotum without median spine (Fig. 120) .... *Coelioxys*

7(5) Females with mandible having beveled area (cutting edges) at base of or interspaces between one or more teeth; males with metasomal sternum IV not retracted, well sclerotized, and dark colored .... *Megachile*

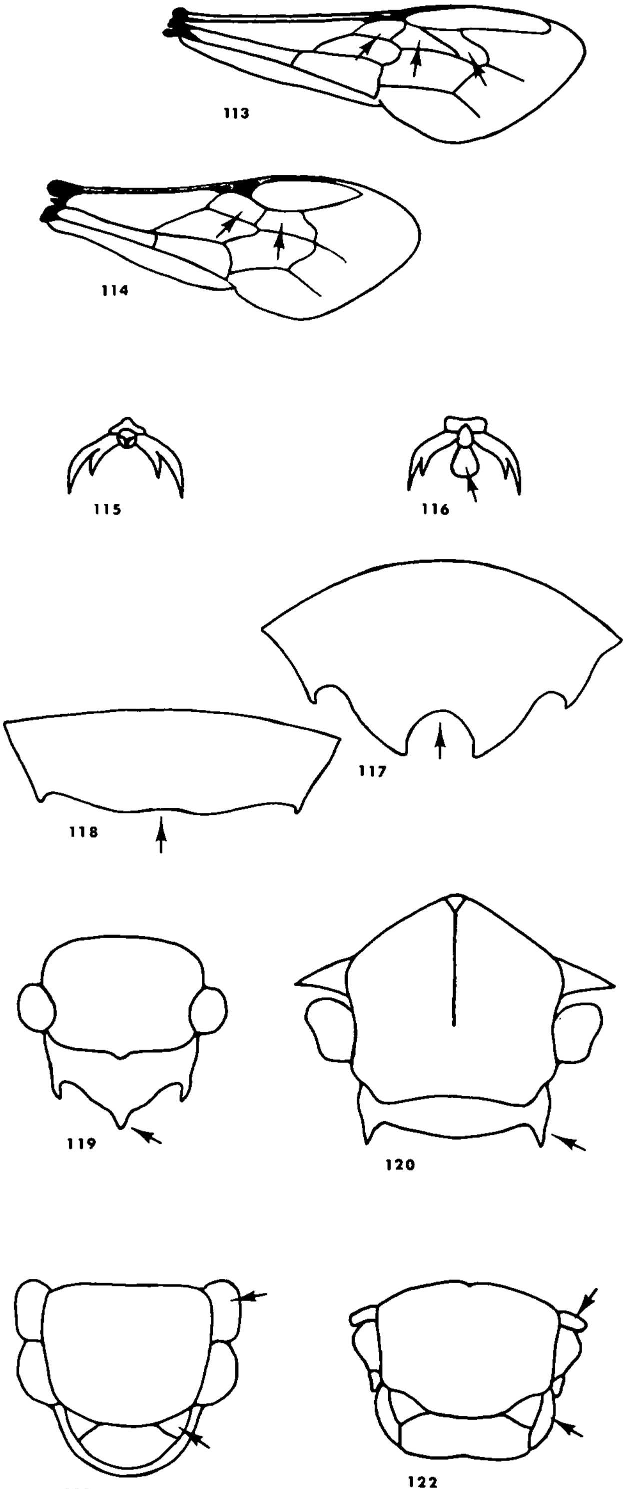
Females with mandible having simple edges, without beveled areas; males with fourth metasomal sternum retracted, weakly sclerotized, light brown in color .... *Chelostomoides*

8(2) Abdominal terga with sharply defined yellow or white integumental markings 9

Abdominal terga without white or yellow integumental markings; metasoma black, red, or with intergrading black and red; colors usually not distinctly delimited within a segment 17

9(8) Scutellum produced to a broad truncation (Fig. 122); subantennal sutures arcuate (Fig. 123) .... *Anthidiellum*

Scutellum rounded (Fig. 121); subantennal sutures nearly straight (Fig. 124).. 10



Figures 113-122

10(9) Stigma short, less than one fourth the length of marginal cell (Fig. 125) 11
Stigma long, more than one half as long (usually much longer) than marginal cell (Fig. 126) 15

11(10) Pronotal lobe with large transparent lamella extending forward on each side to a line anterior to fore margin of mesoscutum (Fig. 121) .... *Dianthidium*
Pronotal lobe with lamella very small or absent (Fig. 122) 12

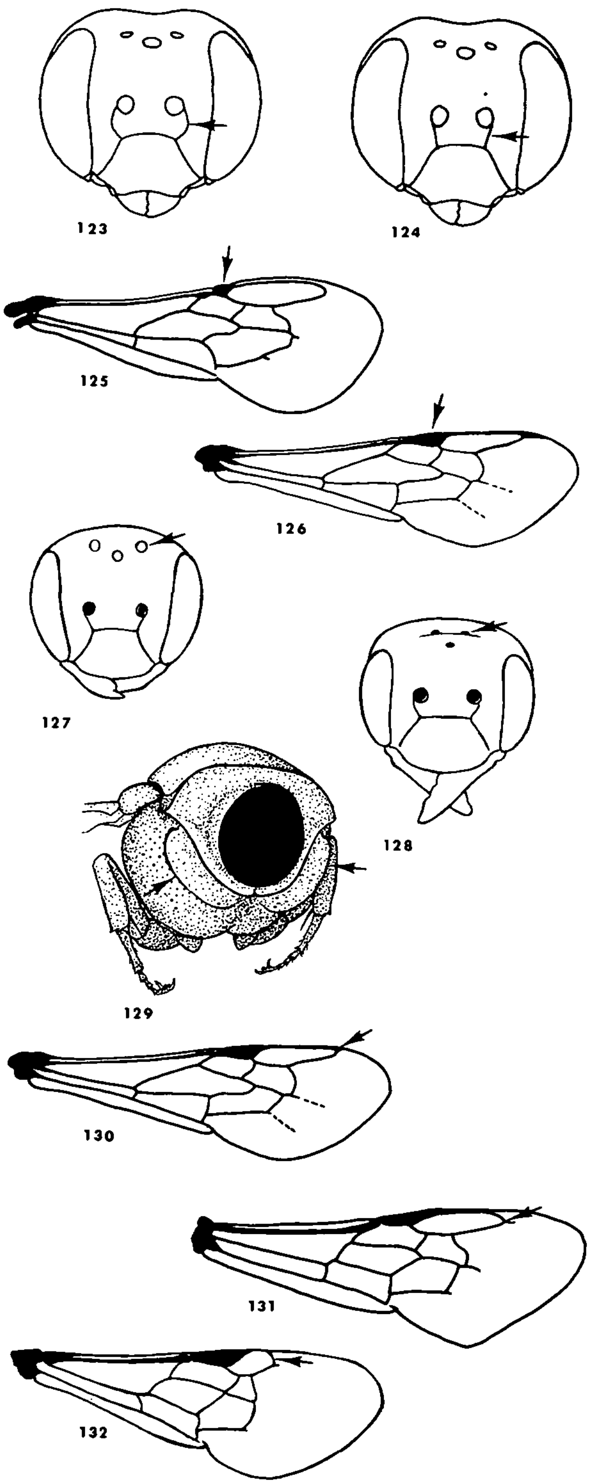
12(11) Females with dense abdominal scopa; males with basal two thirds or more of outer surface or mandible yellow or creamy 13
Females lacking scopa; males with mandibles dark or with pale maculation occupying less than one half of outer surface .. 14

13(12) Ocelli normal in size, well elevated above head surface, located entirely anterior to posterior margin of compound eye (Fig. 127); males without comb on metasomal sternum IV .... *Heteranthidium*
Ocelli unusually small and set in depressions, posterior pair not entirely anterior to posterior compound eye margin (Fig. 128); males with comb on metasomal sternum IV .... *Paranthidium*

14(12) Mesepisternum with anterior face separated from lateral face by a distinct carina (Fig. 129); males with comb of metasomal sternum IV represented by a pair of long finger-like projections .... *Protostelis*
Mesepisternum with anterior face rounded into lateral face, no evidence of a carina; males with comb composed of several to many fine teeth .... *Stelis**[3]

15(10) Apex of marginal cell terminating on wing margin (Fig. 130); females lacking scopa on hind legs .... *Nomada**
Apex of marginal cell terminating away from wing margin (Fig. 131); females with dense scopa on hind legs 16

16(15) Marginal cell truncate apically; portion of marginal cell on margin of wing shorter than stigma (Fig. 132) .... *Perdita**
Marginal cell pointed apically; portion of marginal cell on margin of wing longer than stigma (Fig. 131) .... *Nomadopsis*



FIGURES 123-132

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[3] Genera marked by asterisks appear in the key more than once (separate keying of sexes is not so designated).

17(8) Jugal lobe over one half (usually 3/4) as long as vannal lobe (Fig. 133) 18

Jugal lobe less than one half (usually less than 1/3) as long as vannal lobe (Fig. 134) 27

18(17) Marginal cell truncate, subtruncate, or strongly diverging from wing margin apically (Fig. 135) 19

Marginal cell pointed or weakly rounded apically, usually terminating on or near wing margin (Fig. 136) 22

19(18) Stigma as long as greatest length of marginal cell (Fig. 135) ....*Perdita**

Stigma distinctly shorter than greatest length of marginal cell 20

20(19) Inner subantennal sutures shorter than, or at most as long as, width of subantennal areas (Fig. 137) .... *Calliopsis*

Inner subantennal sutures longer than width of subantennal areas (Fig. 138) 21

21(20) First recurrent vein approximately interstitial with (sometimes basad of) first transverse cubital (Fig. 139) .... *Panurginus*

First recurrent vein much distad of first transverse cubital (Fig. 140) *Pseudopanurgus*

22(18) Antennae inserted conspicuously below middle of eyes (viewed from side) (Fig. 141); clypeus nearly as short as labrum; labrum broader than long 23

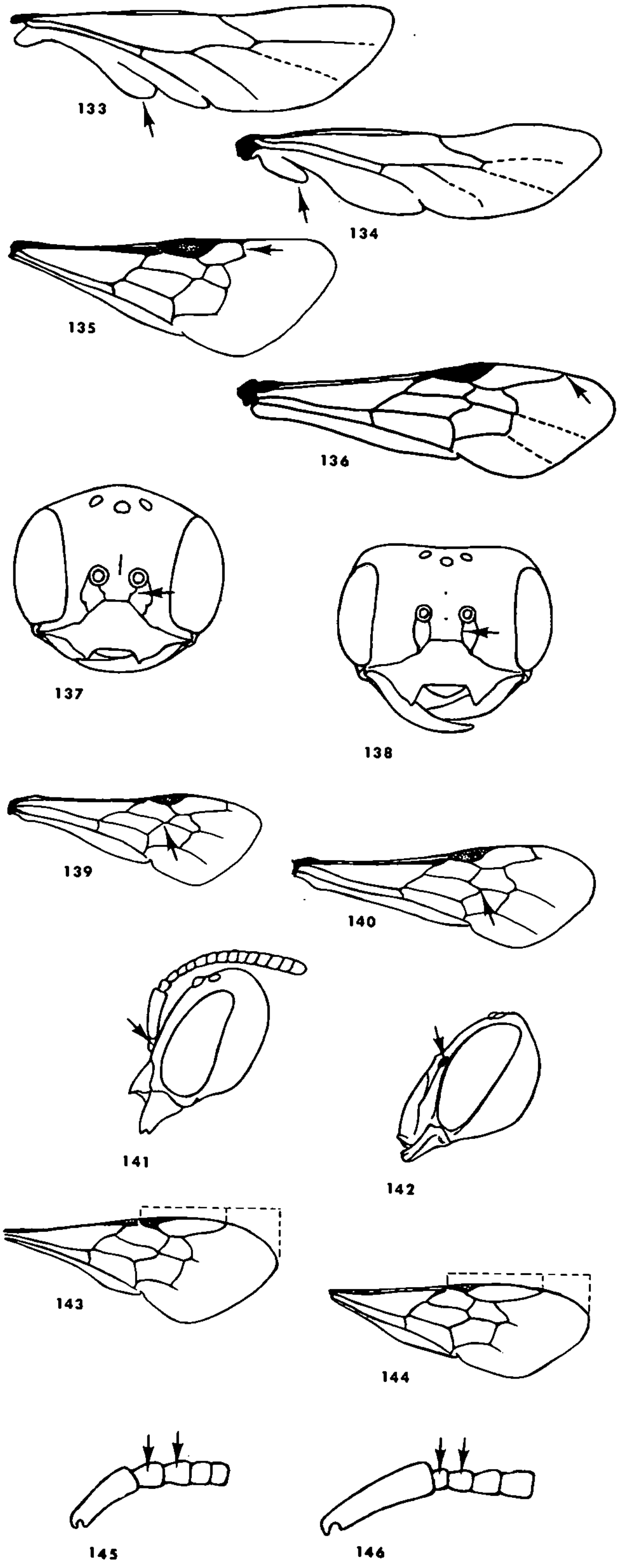
Antennae inserted at or above middle of eyes (viewed from side) (Fig. 142); clypeus considerably longer than labrum, or labrum considerably longer than broad.. 24

23(22) Forewing with distance from base of stigma to tip of marginal cell from one half to three fifths the distance from base of stigma to wing tip (Fig. 143); body without metallic reflections; males with pedicel longer than flagellar segment II (Fig. 145); hind basitarsus light brown, much paler than femur .... *Micralictoides*

Forewing with distance from base of stigma to tip of marginal cell about two thirds or more the distance from base of stigma to wing tip (Fig. 144); or body with metallic reflections; male with pedicel shorter than flagellar segment II (Fig. 146); hind basitarsus dark brown to nearly black .... *Dufourea*

24(22) Posterior basitarsus of female broader than posterior tibia; posterior basitarsus of male less than one half the length of tibia .... *Macropis*

Posterior basitarsus of female narrower than posterior tibia; posterior basitarsus of male more than one half the length of tibia 25



Figures 133-146

25(24) Dark bees, almost devoid of hair, usually with yellow integumental markings restricted to head and thorax; mesepisternal suture present (Fig. 147) .... *Hylaeus*
Bees without integumental markings; body densely pubescent; mesepisternal suture absent (Fig. 148) 26

26(25) First submarginal cell one and a third times longer than second submarginal cell when measured along posterior margin (Fig. 149); facial foveae absent....*Hesperapis*
First submarginal cell shorter, or subequal to second submarginal cell when measured along posterior margin (Fig. 150); facial foveae present (Fig. 174) .... *Andrena**

27(17) Mandibles slender, narrowed apically, and terminating as a single tooth; inner tooth, if present, at least one fourth the distance from apex to base of mandible 28
Mandibles usually broad throughout, terminating as two or more teeth, the inner tooth (or teeth) only slightly more basal than the outer 32

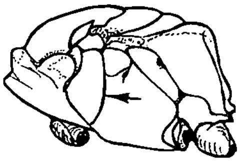
28(27) Labrum one and a half times as long as broad, usually quadrate and truncate apically 29
Labrum as broad as long, pointed or rounded apically 30

29(28) Marginal cell subtruncate (Fig. 150); males with 13 antennal segments; metasomal tergum V of female without median ridge .... *Oreopasites*
Marginal cell rounded apically (Fig. 151); males with 12 antennal segments; metasomal tergum V of female with median ridge .... *Holcopasites*

30(28) Marginal cell much smaller than first submarginal cell; second submarginal cell less than one half as long as first submarginal cell or absent (Fig. 152) .... *Neolarra*
Marginal cell larger than first submarginal cell; second submarginal cell two thirds as long as first submarginal cell (Fig. 153).. 31

31(30) Scape, excluding basal bulb, less than twice as long as broad; abdomen usually red; antennae of male 12 segmented; female without pygidial plate .... *Neopasites*
Scape, excluding basal bulb, more than twice as long as broad; abdomen never red; antennae of male with 13 segments; female with pygidial plate .... *Epeolus**

32(27) Females without abdominal scopa; males with metasomal sternum IV having apical comb composed of slender black teeth .. *Stelis**
Females with abdominal scopa; males lacking comb on metasomal sternum IV .. 33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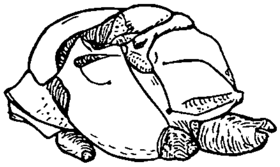
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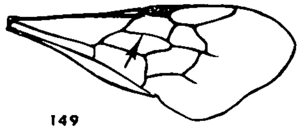
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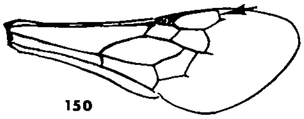
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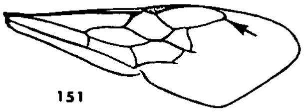
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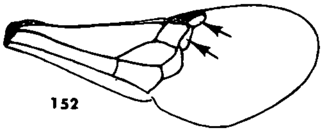
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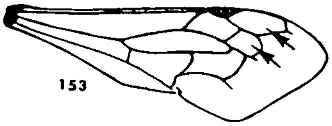
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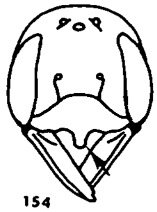
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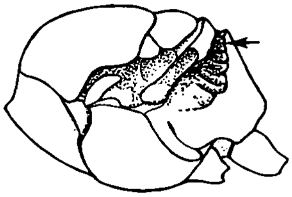
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Figures 147-155

33(32) Males with six exposed metasomal terga; females with apical, medial spatulate process on clypeus (*Chelostomopsis,* Fig. 154) or with sharply defined horizontal area of propodeum bearing a transverse row of deep pits (*Heriades,* Fig. 155) 34

Males with seven exposed metasomal terga, sometimes with only edge of tergum VII visible when in ventral view; females without spatulate process on clypeus and without transverse row of deep pits on propodeum (if pits present, shelf poorly defined medially) 35

34(33) Base of propodeum bearing transverse row of deep quadrate pits (Fig. 155) .... *Heriades*

Base of propodeum without defined row of deep pits (Fig. 160) .... *Chelostomopsis*

35(33) Anterior face of metasomal tergum I broadly concave, punctate dorsal face sharply separated from impunctate anterior face by distinct carina (Fig. 156) 36

Anterior face of metasomal tergum I not separated from dorsal face by distinct carina, often somewhat convex except for median impressed line (Fig. 157) 38

36(35) Parapsidal lines punctiform (Fig. 158); metallic blue or blue-black forms .... *Osmia*

Parapsidal lines linear (Fig. 159); rarely metallic forms 37

37(36) Anterior face of mesepisternum shiny impunctate, separated from coarsely punctate lateral face by a fringed carina (Fig. 160); metasomal tergum VII of males quadridentate apically .... *Ashmeadiella*

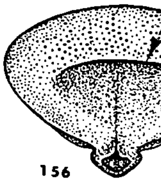
Anterior face of mesepisternum not separated from lateral face by a carina or marked change in punctation (Fig. 161) metasomal tergum VII of males not quadridentate .... *Anthocopa*

38(35) Maxillary galea and first two segments of labial palpi with stiff hairs whose tips are hooked or wavy (Fig. 162); proboscis unusually short, scarcely reaching beyond proboscidial fossa in repose .... *Proteriades*

Maxillary galea and labial palpi without specialized hairs; proboscis reaching well beyond proboscidial fossa in repose 39

39(38) Propodeum with a horizontal basal zone, always black; marginal cell with not more than one tenth of its length conspicuously diverging from costal margin (Fig. 165).. .... *Chelostoma*

Propodeum with a slanting basal zone, if nearly horizontal, then brilliant metallic; marginal cell with at least one fifth of its length diverging from costal margin (Fig. 164) .... *Hoplitis*



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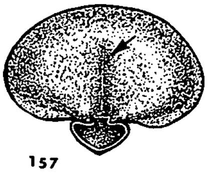

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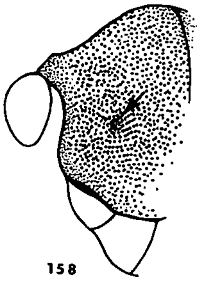

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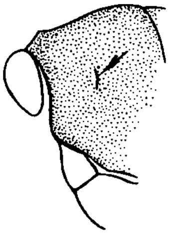

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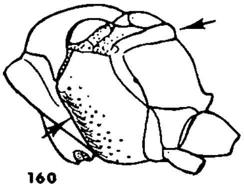

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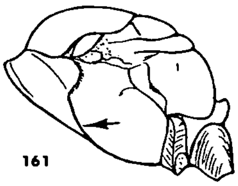

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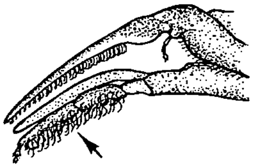

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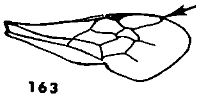

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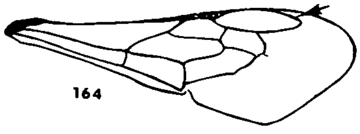

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Figures 156-164

40(1) Head and thorax brilliant metallic green; basal vein strongly arcuate; galea much darker than genal areas 41
Head and thorax never brilliant metallic green, usually black; sometimes having weak to moderate brassy reflections; galea as dark as or lighter than genal areas 42

41(40) Posterior tibiae as long or longer than first four tarsal segments; first recurrent vein basad of second transverse cubital by more than a vein width (Fig. 165) .... *Agapostemon*
Posterior tibiae shorter than first four tarsal segments; first recurrent vein interstitial, distad, or basad of first transverse cubital by less than a vein width (Fig. 166) .... *Augochlora*

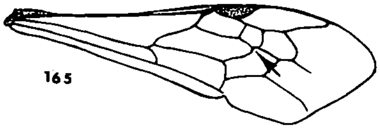
42(40) Forewing with first r-m meeting marginal cell near its midpoint (Fig. 167) .... *Centris*
Forewing with first r-m meeting marginal cell at about its basal one third (Fig. 168).. 43

43(42) Jugal lobe less than two thirds as long as vannal lobe (jugal lobe absent in *Bombus*) (Fig. 169) 51
Jugal lobe at least two thirds (usually 3/4) as long as vannal lobe (Fig. 170) 44

44(43) Tibial spurs absent on hind legs; first recurrent vein short, never as long as vein first r-m (Fig. 171) .... *Apis*
Tibial spurs present on hind legs; first recurrent vein long, twice as long as first r-m (Fig. 172) 45

45(44) Second recurrent vein strongly arcuate outward posteriorly (Fig. 172) .... *Colletes*
Second recurrent vein straight or weakly curved (Fig. 173) 46

46(45) Third submarginal cell subequal to first when measured along posterior margin (Fig. 173) 47
Third submarginal cell less than three fourths as long as first when measured along posterior margin (Fig. 178) 48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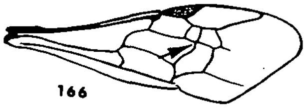
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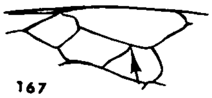
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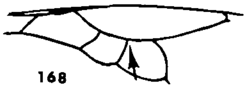
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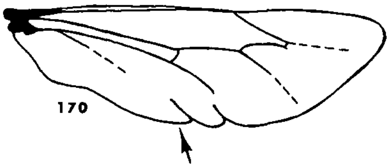
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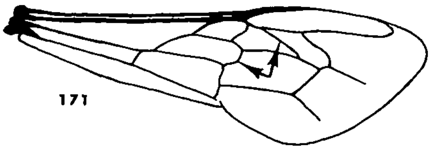
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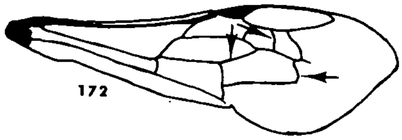
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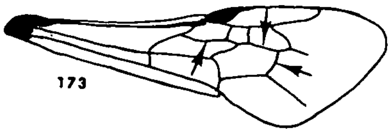
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Figures 165-173

47(46) Two subantennal sutures present on each side, but often difficult to detect; pronotum in profile with only shallow depression at middle; females with distinct facial foveae (Fig. 174) .... *Andrena**

One subantennal suture; pronotum in profile deeply depressed at middle and sharply elevated toward posterior margin; females lacking facial foveae (Fig. 175) .... *Nomia*

48(46) Antennae inserted below middle of face, at lower one third of compound eyes (Fig. 176); clypeus short, only slightly longer than labrum .... *Conanthalictus*

Antennae inserted well above lower third of compound eyes (Fig. 175); clypeus much longer than labrum 49

49(48) Basal vein strongly arcuate; facial foveae absent; face with one subantennal suture on each side (Figs. 177, 175) 50

Basal vein straight or weakly curved; facial foveae present; face with two subantennal sutures (often difficult to detect) (Figs. 178, 174) .... *Andrena**

50(49) Abdominal terga coarsely punctate and sparsely pubescent; propodeum and thoracic pleura strongly rugose; abdominal integument with usually some reddish color; females lacking scopae .... *Sphecodes*

Abdominal terga weakly punctate, usually with dense basal and/or apical pubescence; propodeum and thoracic pleura finely striate; females with dense scopae on hind legs .... *Halictus*

51(43) Second abscissa of vein M+Cu of hind wing at least one and a half times as long as vein cu-v, and at least two thirds as long as vein M (Fig. 179) 57

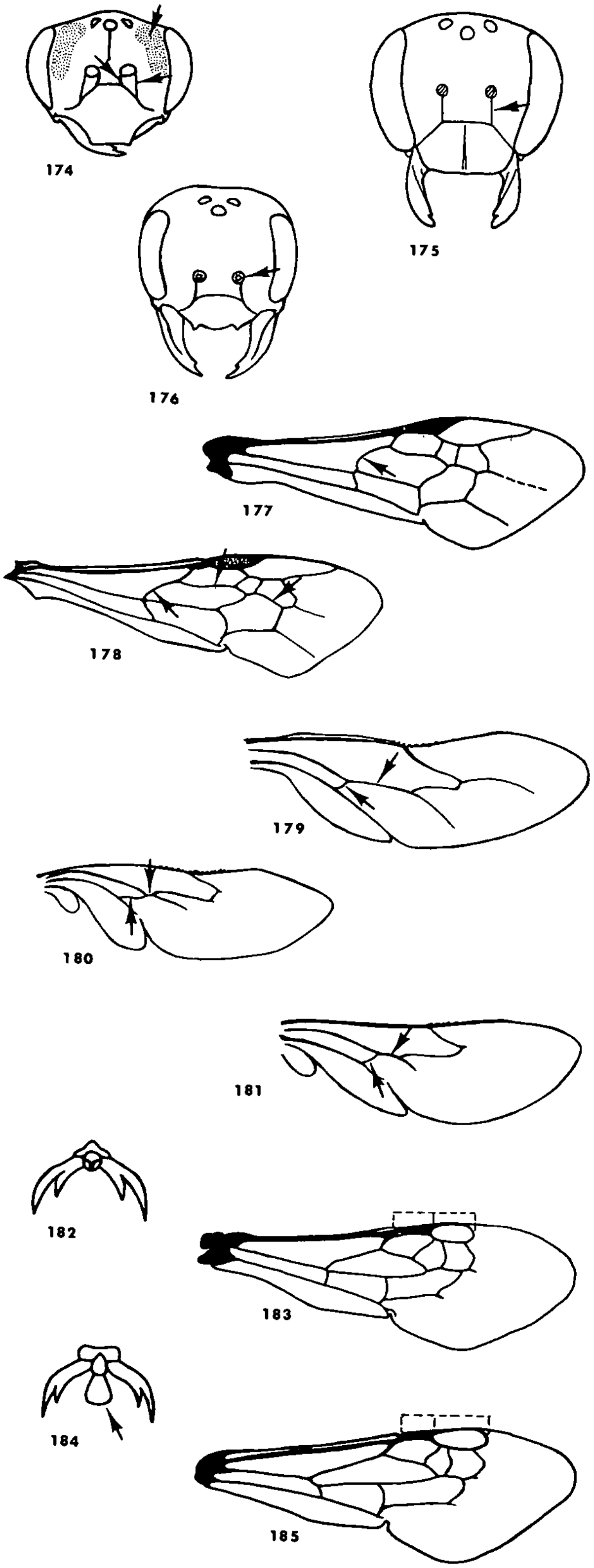
Second abscissa of vein M+Cu of hind wing at most slightly longer than vein cu-v, and less than half as long as vein M (Figs. 180, 181) 52

52(51) Second abscissa of vein M+Cu of hind wing one half or less as long as cu-v vein (Fig. 180) 53

Second abscissa of vein M+Cu and cu-v vein of hind wing subequal in length (Fig. 181) 55

53(52) Arolia absent; marginal cell about as long as pterostigma (Figs. 182, 183) ...... *Zacosmia*

Arolia present; marginal cell slightly longer than pterostigma (Figs. 184, 185).. 54



Figures 174-185

54(53) Apex of inner ramus of mid- and posterior tarsal claws broad and lobe-like (Fig. 186) .... *Xeromelecta*
Apex of inner ramus of mid- and posterior tarsal claws acute, usually long (Fig. 187) .... *Melecta*

55(52) Jugal lobe one half or more as long as vannal lobe (Fig. 188) .... *Diadasia*
Jugal lobe one third or less as long as vannal lobe (Fig. 189) 56

56(55) Third submarginal cell much narrower at marginal cell than along posterior margin (Fig. 190) .... *Emphoropsis*
Third submarginal cell approximately of equal length along anterior and posterior margins (Fig. 191) .... *Anthophora*

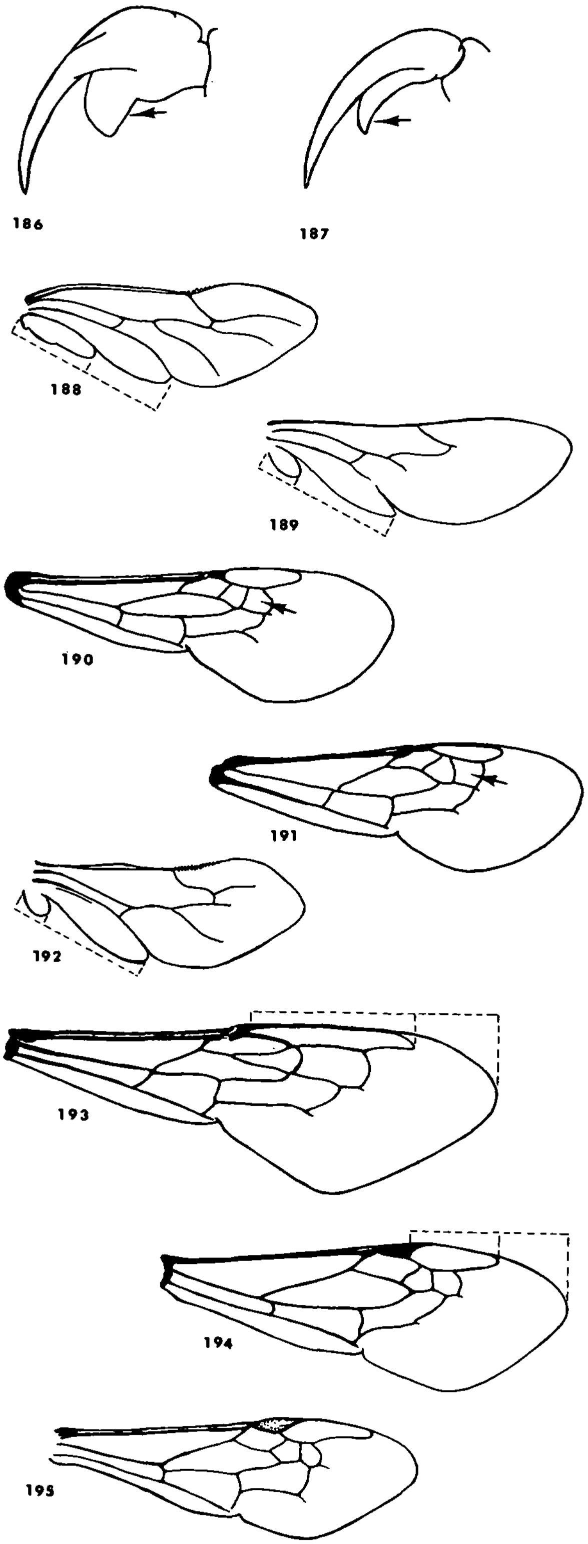
57(51) Jugal lobe one fourth or less as long as vannal lobe (Fig. 192) (jugal lobe absent in *Bombus, Psithyrus*) 58
Jugal lobe at least one third as long as vannal lobe (Fig. 188); or small, naked, dark metallic colored bees 63

58(57) Jugal lobe absent 59
Jugal lobe present, sometimes a small circular disc 60

59(58) Females with posterior tibia convex and hairy; males with hind tibia less than one fourth as wide as long .... *Psithyrus*
Females with posterior tibia having a large, concave, shiny corbiculum surrounded by long lateral hairs; males with hind tibia more than one fourth as wide as long .... *Bombus*

60(58) Marginal cell at least one and a half times as long as distance from its apex to wing tip (Fig. 193) 61
Marginal cell not more than one and a third times longer than distance from its apex to wing tip, usually less (Fig. 194).. 62

61(60) Marginal cell at least eight times as long as wide (Fig. 193); large, black bees; females with tibial scopae .... *Xylocopa*
Marginal cell no more than four times as long as wide (Fig. 195); medium to small species, never black; females without scopae .... *Nomada**



Figures 186-195

62(60) Pseudopygidial area of female transverse, clothed with short silvery pubescence; pygidial area of male short and broad with sides straight or convex (Figs. 196, 197) .... *Epeolus**

Pseudopygidial area of female at least half as long as broad and having dark pubescence; pygidial area of male elongate with sides gently concave, concavity sometimes hidden by apical margin of preceding segment (Figs. 198, 199) .... *Triepeolus*

63(57) Bees naked, metallic, slender .... *Ceratina*

Bees hairy and robust, not metallic 64

64(63) Area between ocelli and upper margin of compound eye flat, or nearly so, and polished; males with flagellum slightly, if any, longer than width of face .. *Exomalopsis*

Area between ocelli and upper margin of compound eye conspicuously concave, not distinctly polished; males with flagellum much longer than width of face 65

65(64) Some spatulate hairs on first two metasomal segments, more numerous on first segment (45X or higher) (Fig. 200) 66

Abdominal fascial bands without spatulate hairs (Fig. 201) 67

66(65) Females with scopal hairs simple; males with flagellar segment I subequal in length with flagellar segment II; last antennal segment acuminate (Figs. 202, 204) .... *Anthedonia*

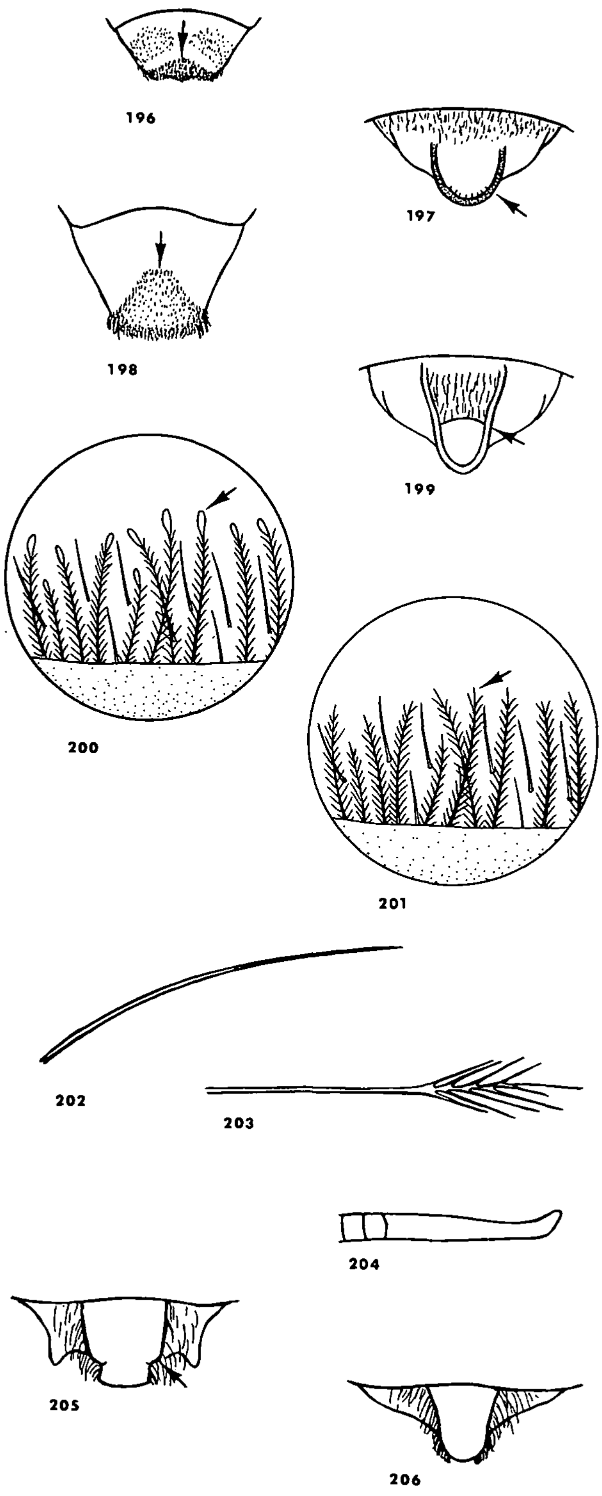
Females with scopal hairs plumose (Fig. 203); males with flagellar segment I less than half as long as flagellar segment II; last antennal segment normal, not acuminate .... *Svastra*

67(65) Without scopae and with 13 antennal segments (males) 68

With scopae and with 12 antennal segments (females) 71

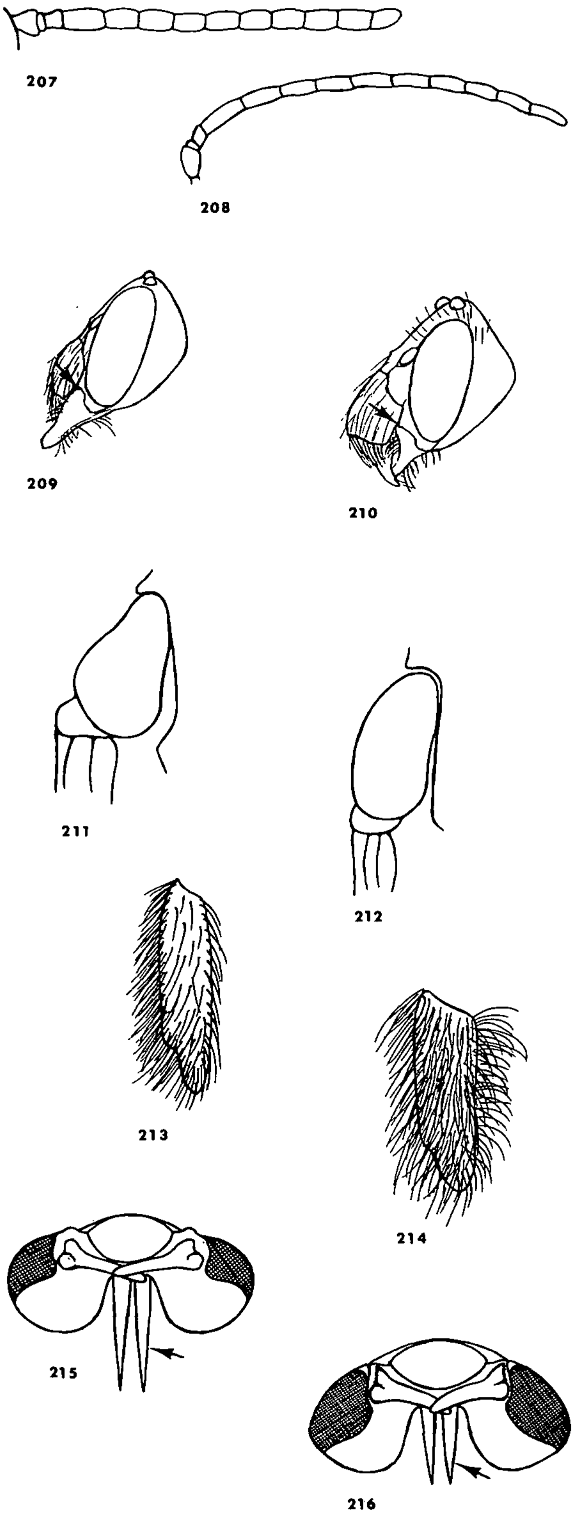
68(67) Pygidial plate with a tooth or strong angle on each side (Fig. 205) .... *Melissodes*

Pygidial plate without teeth on lateral margins (sometimes metasomal sternum VI possesses lateral teeth which can be seen from above and confused with tergal teeth) (Fig. 206) 69



FIGURES 196-206

69(68) Median flagellar segments less than one and a half times as long as wide (Fig. 207) .... *Peponapis*
Median flagellar segments more than twice as long as wide (Fig. 208) 70
70(69) Compound eye slightly wider above than below when viewed in profile; anterior mandibular articulation located slightly in front of inner orbital margin; malar space about a fourth as long as broad (Fig. 210); mandibles weakly bidentate apically, clypeus greatly protuberant .... *Tetralonia*
Compound eye as wide below as above when viewed in profile; anterior mandibular articulation located behind a line drawn along inner orbital margin; malar space linear (Fig. 209); mandibles with apex entire .... *Xenoglossodes*
71(67) Tegula with anterior one third narrowed (Fig. 211) .... *Melissodes*
Tegula not narrowed anteriorly (Fig. 212) 72
72(71) Posterior basitarsus with hairs of inner surface sparse except for a narrow band of dense hairs near posterior margin (Fig. 213) .... *Peponapis*
Posterior basitarsus with inner surface uniformly densely haired (Fig. 214) 73
73(72) Distal portion of galea as long or longer than compound eye; apex of mandible weakly bidentate (Fig. 215) .... *Tetralonia*
Distal portion of galea shorter than compound eye; mandible with apex simple (Fig. 216) .... *Xenoglossodes*



Figures 207-216

Characterizations of the Bee Taxa

The following characterizations are intended to give a comprehensive, phylogenetic view of the genera of the Northwest and their groupings into tribes, subfamilies, and families. The foregoing key, by using many convenient characters that do not indicate relationships, is not adequate for this purpose. In addition we have made a few general statements concerning the relationships of each group; and for each genus we have provided an estimate of the number of species in North America and the Northwest.

The following statements emphasize macroscopic, general characteristics which might be termed the "personalities" of the groups involved. In some cases, exceptions to these characters exist. The charted information following the general statements summarizes many of the diagnostic characters for each group as represented in the Northwest. Many of the characters used in this section are of phylogenetic value but were not used in the key because they are normally hidden, difficult to discern, or hard to express in unequivocal, diagnostic terms.

SUPERFAMILY: APOIDEA

Bees are usually robust and pilose, although most parasitic forms and a few nonparasitic genera are relatively bare and slender like many sphecoid or vespoid wasps. The presence of pollen-transporting scopae or corbiculae on the posterior tibiae, or of scopae on other parts of the body, is characteristic of females of most nonparasitic forms. *Hylaeus* and *Lestrimelitta* are exceptions in that they carry pollen in the honey stomach. Bees can often be distinguished from otherwise similar appearing sphecoids by the absence of metallic-colored pile, especially on the face. Bees can also be distinguished from most vespids by their unfolded wings. Exceptions to both of these criteria occur among certain tropical bees: some *Amegilla* have metallic body and fascial hairs; and *Eulonchopria* fold their wings in vespid fashion.

The most diagnostic feature of bees is the presence of at least slightly plumose hairs on various parts of the body. The most consistent areas to examine are near the thoracic spiracles and the sides of the propodeum. Sometimes high magnification (70X or higher) is required to see plumosity. Broadened posterior tibiae and metatarsi are obvious characteristics of the genera that transport pollen. Even the genera that carry it elsewhere usually have broader tibiae and metatarsi than are found on wasps.

Apoidea has been variously divided into families. Many European authors have considered all bees as belonging to the single family, Apidae. From the standpoint of expressing a parallel with the family Sphecidae, this concept has considerable merit. We are following the lead of Michener (1944a) in compromising between the single family concept and the many family concept of the early American hymenopterists. We depart from Michener (1944a) by elevating his subfamily Anthophorinae (Apidae) to full family status. Mouré and Michener (1955) elevated Fideliinae (Apidae) to family rank; in our opinion, these three groups are roughly comparable to the other families as used by Michener (1944a). In addition, we are following Rozen (1965a) in recognizing Oxaeidae as a distinct family rather than a subfamily of Andrenidae.

The families of Apoidea are characterized in the following list.[4] Fideliidae and Oxaeidae, although not represented in the Northwest, are included since they are the only other recognized families of bees in the world.

Family: COLLETIDAE

1. One subantennal suture.
2. Subantennal suture directed to inner side of antennal socket.
3. Facial foveae usually present.
4. Labrum broader than long, subtriangular or broad-oval.
5. Tip of glossa bilobed or truncate.
6. Flabellum absent.
7. Galea short prepalpally and postpalpally.
8. Labial palpi four-segmented, segments subequal, subcylindrical.
9. Pre-episternal suture complete.
10. Basitibial plate absent.
11. Scopa present or absent on tibia, absent on abdominal sterna (except *Chilicola*).
12. Mid or posterior portion of second recurrent vein usually arcuate outwardly.
13. Pygidium absent.
14. Jugal lobe at least half as long as jugal and vannal together measured along wing margin.
15. Arolia well developed in both sexes.
16. Marginal cell normal; stigma large, elongate.

Family: ANDRENIDAE

1. Two subantennal sutures.
2. Inner subantennal suture directed to inner side of antennal socket.
3. Facial foveae present, but difficult to see in some males.
4. Labrum broader than long, subtriangular or broad-oval.
5. Tip of glossa acute or rounded.
6. Flabellum absent.
7. Galea short prepalpally and usually short postpalpally.
8. Labial palpal segments subequal, subcylindrical (Andreninae); first segment elongate or flattened (Panurginae).
9. Pre-episternal suture present below scrobal suture, or absent.
10. Basitibial plate present in female.
11. Scopa present on tibia, absent on abdominal sterna.
12. Mid or posterior portion of second recurrent vein not arcuate outwardly.
13. Pygidium present in females, rarely in males.
14. Jugal lobe at least three fourths as long as jugal and vannal together measured along wing margin.
15. Arolia well developed in both sexes.
16. Marginal cell normal; stigma large, elongate.

Family: MEGACHILIDAE

1. One subantennal suture.
2. Subantennal suture directed to outer side of scrobe.
3. Facial foveae absent.
4. Labrum longer than broad, subquadrangular.
5. Tip of glossa acute or rounded.
6. Flabellum present.
7. Galea short prepalpally—long postpalpally.
8. Labial palpi with first two segments elongate and flattened.
9. Pre-episternal suture absent.
10. Basitibial plate absent.
11. Scopa present on abdominal sterna, absent on tibia.
12. Mid or posterior portion of second recurrent vein not arcuate outwardly.
13. Pygidium absent.
14. Jugal lobe nearly half as long as jugal and vannal together (Megachilinae), more than half (Lithurginae), measured along wing margin.
15. Arolia present or absent at generic level.
16. Marginal cell normal; stigma short to moderate, subquadrangular.

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[4] The characteristics for each of the taxa in these lists are numbered to facilitate direct comparison.

Family: HALICTIDAE

1. One subantennal suture.
2. Subantennal suture directed to inner side of scrobe.
3. Facial foveae absent.
4. Labrum broader than long, subtriangular or broad-oval.
5. Tip of glossa acute or rounded.
6. Flabellum absent.
7. Galea usually longer prepalpally than postpalpally.
8. Labial palpal segments usually subequal, subcylindrical.
9. Pre-episternal suture nearly complete.
10. Basitibial plate present; ill defined in *Sphecodes*.
11. Scopa present on tibia, nearly always absent on abdominal sterna.
12. Mid or posterior portion of second recurrent vein not arcuate outwardly.
13. Pygidium present, often retracted.
14. Jugal lobe more than half as long as jugal and vannal together measured along wing margin.
15. Arolia well developed in both sexes.
16. Marginal cell normal; stigma large, elongate.

Family: OXAEIDAE

1. Two subantennal sutures.
2. Inner subantennal suture directed to inner side of antennal socket.
3. Facial foveae present on females as broad, flat areas.
4. Labrum slightly longer than broad, viewed from in front.
5. Tip of glossa acute.
6. Flabellum present.
7. Galea short prepalpally and postpalpally.
8. Labial palpal segments short and subcylindrical, but first distinctly longer than the others.
9. Pre-episternal suture absent.
10. Basitibial plate present in female.
11. Scopa present on tibia and second abdominal sternum.
12. Mid or posterior portion of second recurrent vein not arcuate outwardly.
13. Pygidium strong on female, weak on male.
14. Jugal lobe at least three fourths as long as jugal and vannal together measured along wing margin.
15. Arolia absent in female, present but small in male.
16. Marginal cell very slender, elongate; stigma nearly absent.

Family: ANTHOPHORIDAE

1. One subantennal suture.
2. Subantennal suture directed to inner side of scrobe.
3. Facial foveae absent (except in some Exomalopsini).
4. Labrum broader than long except *Oreopasites* and *Holcopasites*.
5. Tip of glossa acute or rounded.
6. Flabellum usually present.
7. Galea short prepalpally—long postpalpally.
8. Labial palpi with first two segments elongate, flattened.
9. Pre-episternal suture absent below scrobal suture, present above it.
10. Basitibial plate present, at least in nonparasitic forms.
11. Scopa present on tibia, absent on abdominal sterna.
12. Mid or posterior portion of second recurrent vein not arcuate outwardly.
13. Pygidium present in at least one sex, absent in *Ceratina*.
14. Jugal lobe variable.
15. Arolia present to absent.
16. Marginal cell normal, but shortened in some parasitic forms, and elongate in *Xylocopa;* stigma short to elongate, except nearly absent in *Xylocopa*.

Family: MELITTIDAE

1. One subantennal suture.
2. Subantennal suture directed to inner side of scrobe.
3. Facial foveae absent.
4. Labrum broader than long, subtriangular or broad-oval.
5. Tip of glossa acute or rounded.
6. Flabellum absent.
7. Galea usually short prepalpally and short to moderately short postpalpally.
8. Labial palpal segments subequal, subcylindrical.
9. Pre-episternal suture usually absent; sometimes present above scrobal suture.
10. Basitibial plate present in female.
11. Scopa present on tibia, absent on abdominal sterna.
12. Mid or posterior portion of second recurrent vein not arcuate outwardly.
13. Pygidium present.
14. Jugal lobe variable.
15. Arolia well developed in both sexes.
16. Marginal cell normal; stigma large, elongate.

Family: FIDELIIDAE

1. One subantennal suture.
2. Subantennal suture directed to inner side of scrobe.
3. Facial foveae absent.
4. Labrum longer than broad.
5. Tip of glossa acute or rounded.
6. Flabellum present.
7. Galea short prepalpally—long postpalpally.
8. Labial palpi with first two segments elongate, flattened.
9. Pre-episternal suture absent below scrobal suture, present above it.
10. Basitibial plate present, at least in female; weakly developed.
11. Scopa present on both abdominal sterna and tibia.
12. Mid or posterior portion of second recurrent vein not arcuate outwardly.
13. Pygidium present in both sexes, sometimes ill defined.
14. Jugal lobe about two thirds as long as jugal and vannal together measured along wing margin.
15. Arolia present.
16. Marginal cell normal; stigma well developed.

Family: APIDAE

1. One subantennal suture.
2. Subantennal suture directed to inner side of scrobe.
3. Facial foveae absent.
4. Labrum broader than long.
5. Tip of glossa acute or rounded.
6. Flabellum present.
7. Galea short prepalpally—long postpalpally.
8. Labial palpi with first two segments elongate, flattened.
9. Pre-episternal suture absent below scrobal suture, present above it.
10. Basitibial plate absent.
11. Scopa replaced by corbiculum on hind tibia; scopa absent on abdominal sterna.
12. Mid or posterior portion of second recurrent vein not arcuate outwardly.
13. Pygidium absent.
14. Jugal lobe absent (Bombinae) or half as long as jugal and vannal together measured along wing margin.
15. Arolia present or absent.
16. Marginal cell normal to elongate; stigma variable.

COLLETIDAE

Subfamily: Colletinae	Subfamily: Hylaeinae
1. Three submarginal cells.	1. Two submarginal cells.
2. Basal vein not more than one and one-half times as long as Rs (first intercubitus).	2. Basal vein at least twice as long as Rs (first intercubitus).
3. Scopa present.	3. Scopa absent.
4. Body hairy, usually with well-defined metasomal hair bands.	4. Body with short, inconspicuous pubescence.
5. Body entirely black.	5. White or yellow maculations usually present.
6. Tentorial pits well above middle of lateral arms of epistomal suture.	6. Tentorial pits at or below middle of lateral arms of epistomal suture.

Family: **COLLETIDAE**

Colletidae includes six subfamilies of which only two, Colletinae and Hylaeinae, occur in North America. Since the other four subfamilies are confined to South America or Australia, the distributional pattern indicates an ancient origin for the family. This is supported by many morphological characteristics as well, although considerable specialization has occurred in the various subfamilies. More primitive characteristics (those shared by many sphecid wasps) are found in this family than in any other. According to Michener (1944a) all of the other bees could have been derived from a colletid ancestor.

The wide separation between *Colletes* and *Hylaeus* has caused some to suggest independent origins for the Holarctic subfamilies, and even an independent origin of Hylaeinae from a sphecid ancestor. However, several Australian genera in various subfamilies bridge most of the gaps and indicate that Colletidae is a natural grouping.

The most distinctive feature of the family is the short, bilobed glossa, although in some Australian genera it is merely rounded. The bilobed glossa appears to be used in the shaping of transparent, cellophane-like brood cells characteristic of colletid nests. The arcuation of the posterior part of the vein m-cu of the forewing toward the wing apex is another distinctive characteristic of most members of the family.

Subfamily: Colletinae

Colletinae is a world-wide subfamily including three tribes of which only Colletini is found in the Northwest. Females of this subfamily have a scopa and construct burrows in the soil. In the Northwest they are easily distinguished from Hylaeinae by their abundant pubescence.

Tribe Colletini. Colletini is primarily a Holarctic tribe apparently containing only the genus *Colletes*. Paracolletini is pan-austral and Caupolicanini is Neotropical, but at least a few species of each are found in the southwestern states. The absence of a pygidial plate separates Colletini from Paracolletini, and the arcuation of m-cu in the forewing separates it from Caupolicanini.

Genus *Colletes* Latreille: *Colletes* is a large genus with about 115 North American species and 21 northwestern species. It extends into South America and Africa but is not found in Australia. Bees in this genus are moderate in size, with entirely black integument, and usually with well-defined abdominal hair bands. They can be distinguished from andrenids and melittids, which they superficially resemble, by the arcuate m-cu of the forewing.

Subfamily: Hylaeinae

Hylaeinae is a world-wide subfamily represented by six or more genera which are not usually grouped into tribes. Only the genus *Hylaeus* occurs in North America. The subfamily is characterized by the absence of external pollen-transporting structures; the pollen is mixed with the nectar in the honey stomach. Most members of this subfamily are small and all species are nearly hairless.

Although wasp-like in appearance and lacking a scopa, it is believed that these are specialized characteristics and do not represent direct links with sphecid ancestors.

Genus *Hylaeus* Fabricius: *Hylaeus* is a world-wide genus with about 50 species in North America, of which at least 20 occur in the Northwest. Although varying somewhat in size and extent of yellow maculation, members of this genus are so distinct from other North American bees that there is never a problem in distinguishing them. The jet black, nearly naked body, the triangular face with a long clypeus, the light maculations (in nearly all species), the two submarginal cells of which the second is much smaller than the first, and the absence of a scopa and a pygidium make a highly characteristic combination of characters.

Family: **HALICTIDAE**

Halictidae is composed of three subfamilies which are very distinctive but have enough in common to form a clearly recognizable unit. They share long prepalpal parts of the galeae and absence of mentum and submentum; have complete or partial pre-episternal sutures; and lack facial foveae. The jugal lobes of the hind wings are long, and the hypostoma is fused with the tentorium.

The family has several features in common with Colletidae and could have diverged from one of the more primitive forms of that group. It also holds a number of characteristics in common with Melittidae and Andrenidae, but these groups seem to have had a somewhat later origin. There is no clear evidence that any of the "higher" families of bees (Apidae, Anthophoridae, or Megachilidae) were derived from a halictid stock, although some of the apids bear some resemblance to halictids and both groups have many species with social behavior.

Since the three halictid subfamilies are all rather homogeneous, tribal associations cannot be made unequivocally and hence are not considered here.

Subfamily: Halictinae

Halictinae is a large but remarkably homogeneous subfamily. It is world-wide in distribution and has many closely related genera. Group characteristics are most evident in the females, and in many genera the males are all but impossible to separate. Numerous attempts have been made to establish a number of genera closely related to *Halictus,* but differentiating characters seem rather inconsequential and apply only to females in most cases.

The most distinctive character of this subfamily is the strongly bent basal vein of the forewing. Another feature, equally as distinctive and nearly as universal, is the linear, longitudinal pseudopygidium on the fifth tergum of the females from which the name "furrow bees" was derived. However, this character is weak or absent on the parasitic genus *Sphecodes* and the Old World pollen-collecting genus *Nomioides.*

Genus *Halictus* Latreille: *Halictus* is a large, world-wide genus—here considered in the inclusive "European" sense. In the United States the generic names *Dialictus, Chloralictus, Paralictus, Evylaeus, Lasioglossum, Hemihalictus, Sphecodogastra, Seladonia, Odontalictus,* and *Halictus* have been used for various species in our genus *Halictus* (Mitchell, 1960). Michener (1944a) recognized two North American genera from the above list, *Halictus* for the last three and *Lasioglossum* for the first seven. However, in our opinion, the differences between *Halictus* and *Lasioglossum sensu* Michener are no greater than those between several of the groups within *Lasioglossum.*

A revision of the North American *Halictus* is needed before a reasonable estimate of the number of species can be made. Muesebeck and others (1951) listed about 260 names as valid, and of these we estimate at least 50 are found in the Northwest. The subgenus *Dialictus* (=*Chloralictus* of authors) is the most numerous in species, followed by the subgenera *Evylaeus, Lasioglossum,* and *Halictus.*

Halictus is readily distinguished from *Sphecodes* by the presence of a strong pseudopygial plate in the female, somewhat finer sculpturing in both sexes, and the shape and vestiture of the face in the male. It can be distinguished from *Augochlora* and *Agapostemon* by the absence of brilliant metallic coloring.

HALICTIDAE

Subfamily: Halictinae	Subfamily: Dufoureinae	Subfamily: Nomiinae
1. ♀ tergum V with elongate median pseudopygidial plate (except *Sphecodes*).	1. ♀ tergum V without pseudopygidial plate but with terminal fimbria.	1. As in Dufoureinae.
2. ♀ tergum VI with pygidial plate broadly rounded or nearly truncate, with sides only slightly diverging, with basal area poorly developed.	2. ♀ tergum VI with pygidial plate narrowly rounded or pointed, triangular, well developed basally.	2. As in Dufoureinae.
3. ♂ tergum VII with pygidial plate broad and well developed or reduced to broad, median apical thickening.	3. ♂ tergum VII with pygidial plate well developed and narrowly triangular, reduced to narrow median thickening, or absent.	3. ♂ pygidial plate absent.
4. Basal vein sharply bent below the middle.	4. Basal vein nearly straight or only slightly, evenly curved.	4. As in Dufoureinae.
5. Marginal cell narrowly rounded or pointed at or near wing margin.	5. As in Halictinae.	5. Marginal cell broadly rounded apically, appearing almost parellel-sided.
6. Three submarginal cells, rarely two.	6. Two submarginal cells in northwestern genera (except *Conanthalictus*).	6. Three submarginal cells.
7. Third submarginal cell much shorter than first.	7. Third submarginal cell, when present, slightly shorter than first.	7. Third submarginal cell about as long as first along posterior margin.
8. Antennal sockets with upper margin at or above middle of face.	8. Antennal sockets with upper margin below middle of face.	8. As in Halictinae.
9. Clypeus longer than labrum.	9. Clypeus short, no longer than labrum.	9. Clypeus much longer than labrum.
10. Clypeus not protruding beyond supraclypeal area when seen in profile.	10. Clypeus protruding conspicuously beyond supraclypeal area when seen in profile.	10. As in Halictinae.
11. Eyes usually convergent below, often sharply incurved above.	11. Eyes parallel or divergent below, inner margins straight or gently, evenly curved.	11. Eyes usually convergent below (not in ♀ *Nomia triangulifera*), sometimes gently incurved above.
12. Pre-episternal suture well developed below scrobal suture.	12. As in Halictinae.	12. Pre-episternal suture poorly developed or absent below scrobal suture.

Genus *Agapostemon* Guérin-Méneville: *Agapostemon* is a small North American genus with about 10 species of which 5 are known to occur in the Northwest. It is a homogeneous and easily recognized group. In the Northwest the only other rather brilliantly green metallic halictid is a single species of *Augochlora*. From this it is readily distinguished by the yellow- and black-banded abdomen of the male, the absence of the basitibial plates, and the truncate and strongly carinate posterior margin of the horizontal surface of the propodeum of the female. *Agapostemon* is apparently allied to the other brilliantly metallic genera, all of which are supposedly of Neotropical origin.

Genus *Augochlora* Smith: *Augochlora* is primarily a Neotropical genus with four species in America north of Mexico. One of these species, *pura*, extends northward through California into southern Oregon. Both sexes are brilliant metallic green and have the propodial enclosure rounded and not carinate behind.

Genus *Sphecodes* Latreille: *Sphecodes* is a large, worldwide genus parasitic on Halictinae. One species, *albilabris*, is parasitic on an andrenid, *Melitturga clavicornis*. A revision is needed before the number of species in North America can be accurately judged, but on the basis of Muesebeck and others (1951) there are about 70 valid species of which perhaps 20 are found in the Northwest. Females of this genus differ markedly from other halictines in lacking all but a trace of a pseudopygial plate on the fifth tergite and in having poorly defined basitibial plates. This genus, like most other parasitic bees, has a coarsely sculptured integument. Females of most species have a dark red, polished abdomen. Many of the males have partly or entirely black abdomens. Besides the coarse sculpturing, males can be distinguished from *Halictus* (*Evylaeus*) by the combination of shorter antennae and face, more uniform facial pubescence, and entirely black clypeus.

Subfamily: Nomiinae

This is a large subfamily of morphologically diverse bees that are world-wide in distribution but represented in North America only by the genus *Nomia*. Nine genera are now recognized in the subfamily, but a world revision is badly needed before the systematic position of the genera can be understood.

It is believed that Nomiinae is most closely allied to Halictinae, and that both subfamilies are of early origin. The remaining subfamily, Dufoureinae, probably arose more recently and represents a second evolutionary line of Halictidae.

The nomiines may be distinguished from other halictids by: basal vein of forewing straight or only slightly curved; three submarginal cells in the forewing, with the third subequal to the first along the posterior margin; males with pygidial plates; and antennal sockets inserted at or above the middle of the face.

Genus *Nomia* Latreille: *Nomia* is the only genus of the subfamily which occurs in both the Old and the New worlds. This large genus of moderate- to large-sized bees is represented in North America by 21 species, 3 of which are found in the Pacific Northwest. One species, *N. melanderi*, is the most important pollinator of alfalfa in the Pacific Northwest. It is distinguishable from all other Northwest bees by the iridescent, yellowish or greenish-yellow, integumental bands present on the abdominal tergites of both sexes. The other two species, *N. nevadensis* and *N. triangulifera*, lack integumental maculations and appear to collect pollen only from composites.

Nomia can readily be distinguished from other North American bees by those characteristics used in the key and in the list of subfamily characteristics.

Subfamily: Dufoureinae

Dufoureinae is a subfamily of moderate diversity and size, containing 12 genera, 6 of them found in North America and 3 in the Northwest. This subfamily is primarily Holarctic, but one genus is found in South America and two reach the Ethiopian and Oriental regions. Dufoureinae appears to be about equally related to Halictinae and Nomiinae on the basis of characteristics described in the subfamily table, but its distribution indicates a somewhat more recent origin.

Dufoureines are readily distinguished from other halictids by the low antennal sockets; short, protuberant clypeus; gently curved basal vein; and complete preepisternal suture.

Genus *Dufourea* Lepeletier: *Dufourea* is by far the largest genus in the subfamily, with about 60 North American and 14 northwestern species. Considerable diversity is found in the genus, and many generic names have been proposed by earlier systematists in recognition of these differences. In Europe, *Dufourea* and *"Halictoides"* are considered distinct, but in this country they blend imperceptibly.

The genus is distinguishable from *Conanthalictus* by the absence of a real pygidium in the male and the relatively well-punctured integument in both sexes. A more obvious characteristic is the presence of two submarginal cells in *Dufourea*, although some specimens of *Conanthalictus* can be found with only two. It differs from *Micralictoides* in the deeper punctures and longer marginal cell. Metasomal sternite VIII of the male is deeply bilobed basally instead of being unilobed, and metasomal sternite VII has relatively straight posterior arms.

Genus *Conanthalictus* Cockerell: *Conanthalictus* is a small, primarily southwestern genus (10 species), and only an undescribed species has been collected in the Northwest. On the basis of the three submarginal cells (two in a few specimens), the genus appears to be more primitive than *Dufourea* and *Micralictoides*. It shows some relationship with *Protodufourea*, another southwestern genus with three submarginal cells. Species of *Conanthalictus* are all small, weakly punctured, feebly metallic blue or blue-green in color, have sparse body pubescence, and lack basal and apical abdominal fasciae.

Genus *Micralictoides* Timberlake: *Micralictoides* is a small genus of about six species found in California, Arizona, and Nevada. Only one species is known to reach the Northwest. The genus resembles small species of *Dufourea* in body form and in its two submarginal cells. However, the peculiar form of the seventh and eighth sternites and genitalia of the male indicate that the relationship is not very close. It was probably derived independently from an ancestor with three submarginal cells. The broad, shallow body punctures of the integument and relatively short marginal cells are distinctive features.

Family: ANDRENIDAE

Andrenidae is the largest bee family in North America in terms of number of species, but from the standpoint of diversity of higher categories it is smaller than either Anthophoridae or Megachilidae. Of the two distinct subfamilies in the Northwest, Andreninae and Panurginae, the former is more numerous in species and the latter more numerous in genera. Andrenidae is best represented in the Holarctic region, but many panurgine genera are found in the Neotropical and Ethiopian regions. On the basis of its distribution and certain specialized characters, such as the absence of a pre-episternal suture, it is considered to have a later origin than either the Colletidae or Halictidae, possibly from an early melittid-like ancestor.

Andrenids are always somewhat dorsoventrally flattened and have an oval rather than parallel-sided abdomen. The metanotum is horizontal and the female pygidium is conspicuous. The face is nearly always rather flat, and the inner orbital margins are not arcuate above and seldom convergent below. The principal northwestern genus of Melittidae, *Hesperapis*, most nearly resembles those *Andrena* with two submarginal cells in the forewing, but *Hesperapis* can be distinguished by the absence of facial foveae and the shining vertex and upper portion of the frons. Andrenids are sometimes confused with certain halictine species, but the straight or only slightly curved basal vein in the former serves to separate them. They also resemble certain dufoureine halictids, but they can be distinguished at once by their antennal insertions which are at the middle of the face.

The two northwestern subfamilies of andrenids differ as shown in the tabulation below.

Subfamily: Andreninae

Andreninae is a very homogeneous subfamily, represented in the Northwest by the genus *Andrena*, and in the Southwest by two other genera, closely related to *Andrena*. The subfamily is almost entirely Holarctic in distribution with only a few species occurring as far south as Central America and the northern plains of India.

Andrenine bees are generally more densely pilose than panurgine bees and this is often most conspicuous on the face. Integumental maculations of Andreninae, if present, are confined to the clypeus and the lower portion of the paraocular area. The many specific characters for distinguishing Andreninae from Panurginae are readily seen.

Genus *Andrena* Fabricius: *Andrena* is primarily a Holarctic genus of moderate- to large-sized bees with approximately 200 species found in the Northwest and 1,000 in the world. About one fourth of the species of bees found in the Northwest are in this genus, and it is probably the largest genus of bees in the world. There are 34 recognized subgenera in North America, but because of the morphological homogeneity of the genus, they are difficult to characterize.

Subfamily: Panurginae

Panurginae includes a number of distinctive but rather closely related genera. In the Palearctic region, the genus *Melitturga* is quite distinct from the others and possibly warrants tribal designation. The North American genera are best considered in the single tribe, Panurgini. Because of the flattened and somewhat elongated palpal segments, Panurginae is usually considered to be more specialized than Andreninae; in fact Michener (1944a) expressed the opinion that the higher groups of bees might have arisen from an ancestral panurgine stock.

Panurginae is best represented in the New World, both in North and South America. Most genera con-

ANDRENIDAE

Subfamily: Andreninae (*Andrena*)	Subfamily: Panurginae (*Panurgini*)
1. Facial foveae of ♀ broad, shallow, usually covered with minute hairs.	1. Facial foveae of ♀ narrow or pit-like, without pubescence.
2. Facial foveae of ♂ broad, shallow, but poorly defined.	2. Facial foveae, when present in ♂, sharply defined.
3. Labial palpi subequal, and subcylindrical.	3. Labial palpi with first segment elongate, or flattened.
4. Marginal cell pointed on or evenly rounded at or near the wing margin.	4. Marginal cell truncate or obliquely bent away from wing margin.
5. Almost always with three submarginal cells.	5. With two submarginal cells. (*Psaenythia* has three.)
6. Scopa present from coxa to basitarsus.	6. Scopa confined to tibia and basitarsus.

tain moderate numbers of species, but the number of *Perdita* species is very large.

Panurgine bees are less pilose than andrenines in general and more extensively maculate, especially the males. The marginal cell, which is truncate or strongly bent away from the wing margin, facilitates identification.

Genus *Perdita* Smith: This is a large genus of small to moderate-sized bees restricted to North America. Most of the species are found in the southwest area of the United States and in Mexico, although 46 species occur in the Northwest. *Perdita,* especially the maculate species, resembles *Nomadopsis* except that it is smaller and has conspicuously white wings with pale veins; dark areas of body submetallic, or body entirely yellow; vertex of head minutely roughened (plicate) between very fine punctures, if any; and the marginal cell bent away from the wing margin at nearly a right angle apically.

Genus *Nomadopsis* Ashmead: *Nomadopsis* is a rather small genus of moderate-sized bees whose distribution is restricted to the New World. Integumental abdominal maculations are almost always present in this genus, which, together with *Perdita,* represents the only panurgines north of Mexico with this feature.

Nomadopsis is represented in the Northwest by 15 species. It most closely resembles *Perdita,* but the species are nearly always larger and they have dark wing veins; dark areas of body nonmetallic; body never completely yellow; vertex of head shiny between moderate-sized punctures; marginal cell bent away from the wing margin at about a 45° angle apically; and metasomal terga without distinct apical fasciae.

Genus *Calliopsis* Smith: *Calliopsis* is a small genus of small to moderate-sized bees found only in the New World and represented in the Northwest by two species. This genus contains pale-haired bees with integumental maculations on the head and thorax like those of *Nomadopsis,* which it closely resembles in body form. It is readily separated from *Nomadopsis* by its nonmaculated abdomen, well-defined abdominal faciae, and shorter, narrower pterostigma.

Genus *Panurginus* Nylander: *Panurginus* is a small Holarctic genus of small-sized, dark-haired, usually jet black bees with a yellow clypeus in some males. It is well represented in the Northwest by seven species that most closely resemble *Pseudopanurgus*. *Panurginus* can, however, be distinguished from *Pseudopanurgus* by the fine punctures and minutely roughed integument, especially around the vertex, and the characters cited in the key. Metasomal sternum VI of the male is thickened apically and shallowly emarginate medially.

Genus *Pseudopanurgus* Cockerell: *Pseudopanurgus* is a moderate-sized genus restricted in distribution to the New World and represented in the Northwest by eight species. *Pseudopanurgus* resembles *Panurginus* but is more heavily armored and coarsely punctured. In addition, the areas between the punctures on the vertex of the head are shiny instead of minutely roughened as in *Panurginus* and *Perdita.*

Family: OXAEIDAE

Oxaeidae is a small Neotropical family reaching as far north as the southwestern United States. It is mentioned here for the sake of completeness at the family level. Michener (1944a) considered it to be a subfamily of Andrenidae; but Rozen (1965a), on the basis of larval and adult characteristics, considered the taxon (*Oxaea* and *Protoxaea*) to form a small but distinctive family. Oxaeids resemble andrenids in general body form and in having two subantennal sutures below each antenna. They differ in having an extremely long marginal cell and almost no stigma. In addition, the females also lack arolia and have a vertical propodeum.

There is an interesting convergence between males of *Apis,* Oxaeidae, *Melitturga* (a Paleartic panurgine), and *Caupolicana* (Neotropical colletid). They all have enlarged compound eyes, ocelli low on the face, elongate first flagellar segment, box-like thorax, short abdomen, and long, thin legs that hang downwards in flight. The similar mating habit, in which the males hover beneath the females and dart upwards after them in flight, apparently has been responsible for this convergence.

Family: MELITTIDAE

Although Melittidae is a small family from the standpoint of number of species, its four subfamilies represent considerable diversity. Three of these subfamilies occur in North America and two are found in the Northwest. In degree of specialization, the family appears to be about equivalent to Andrenidae, but it probably arose separately from a progenitor common to both families. Since anthophorids have more characteristics in common with andrenids than with melittids, it seems likely that the higher bees arose from a primitive andrenid rather than a melittid branch.

Melittidae superficially resembles Andrenidae but differs in lacking facial foveae and subantennal plates and from most andrenids in having the scopa confined to the posterior tibia and basitarsus.

Subfamily: Dasypodinae

Dasypodinae is a Holarctic and Ethiopian subfamily with about six genera of which only *Hesperapis* occurs in North America. Division into tribes does not seem to be warranted. Members of the subfamily resemble Melittinae in general but differ in having two submarginal cells. Judging from genera we have seen, they also have longer hairs on the scopa and a more polished appearance of the vertex.

Genus *Hesperapis* Cockerell: *Hesperapis* has a peculiar distribution, with species known from southern Africa

MELITTIDAE

Subfamily: Macropidinae	Subfamily: Dasypodinae
1. Male with yellow clypeus, paraocular areas.	1. Male without yellow facial markings.
2. Posterior basitarsus less than twice as long as broad.	2. Posterior basitarsus more than three times as long as broad.
3. Second submarginal cell subequal to first.	3. Second submarginal cell much shorter than first.
4. Sting unusually long.	4. Sting moderate in length.
5. Posterior face of propodeum vertical.	5. Posterior face of propodeum strongly slanting.

and western United States. There are about 22 North American species and 2 in the Northwest. The genus is characterized by long, rather sparse pubescence; a flat, usually "sway-backed" abdomen; well-defined abdominal fasciae; and a shining vertex.

Subfamily: Macropidinae

Macropidinae contains only the Holarctic genus *Macropis*. It is a highly specialized genus with an exceptionally long sting and very broad fore tibia and basitarsus.

Genus *Macropis* Klug: There are only six known species of *Macropis* in North America of which only one, *Macropis steironematis opaca*, has been collected in the Northwest. As indicated, the genus is readily recognized by the characters mentioned above. The males with their yellow marked faces have some superficial resemblance to *Pseudopanurgus*, but they are easily distinguished from that genus by pointed marginal cells and broad basitarsus.

Family: Fideliidae

Fideliidae is a small family with two genera in South Africa and one in Chile. Michener (1944a) considered it as a subfamily of Apidae, but Mouré and Michener (1955) decided that it is more primitive than any other family of long-tongued bees and elevated it to family rank. Fideliidae resembles Megachilidae in having an abdominal scopa and a long labrum. Unlike Megachilidae, basitibial plates are present, at least in the female, but they are weakly developed. The presence of tibial scopae (poorly developed in the Chilean genus), narrow mandibular apices, and three submarginal cells differentiate it readily from the Megachilidae. In spite of its long tongue, it has many apparently primitive characteristics, such as a partial pre-episternal suture, horizontal volsellae with cuspis and digitus, and large apical lobes of the seventh sternite of the male (except in the Chilean genus).

Family: Megachilidae

Megachilidae is a large family of specialized, morphologically rather uniform bees found throughout the world. It is well represented in the Northwest both at the generic (20 genera) and specific levels (219 species).

The family appears to have had an earlier origin than that of other long-tongued bee families. Megachilidae is peculiar in several respects: (1) it represents the only family of bees whose members all have two submarginal cells; (2) all members have subantennal sutures directed to the outer edges of the antennal sockets (the outer subantennal sutures of Andrenidae are also directed to the outer edges of the antennal sockets but they appear to be evolved as secondary sutures); (3) the scopa of all nonparasitic females is restricted to the abdominal sterna; and (4) with the exception of *Trachusa, Heteranthidium,* some *Anthidium,* some *Callanthidium,* some *Osmia,* and some *Megachile,* all species nest in existing holes or in the open and construct cells from nonsecreted materials. Like most megachilids, the social Apidae and the genus *Hylaeus,* family Colletidae, construct cells in existing holes, but the cells are formed from secreted materials. Euglossini (Apidae) and some *Centris* (Anthophoridae) construct nests resembling those of megachilids which nest in existing holes, but since neither taxon occurs in the Northwest we feel that point (4), above, is valid within our area.

Megachilidae is divided into two subfamilies, Megachilinae and Lithurginae, but only the former taxon is represented in the Northwest.

Subfamily: Megachilinae

Megachilinae can be distinguished from Lithurginae, a more primitive subfamily containing only the genus *Lithurgus,* by several characteristics: jugal lobe less than one-half as long as vannal lobe; epistomal suture complete; first metasomal tergite large, its posterior edge straight; posterior basitarsus much shorter than tibia; and posterior legs of males not expanded. Both subfamilies are world-wide in distribution, but *Lithurgus* is restricted to Mexico and the southern portion of the United States in North America. Megachilinae is divided into two distinct tribes (Anthidiini and Megachilini) by the characteristics cited in the tabulation at the top of the next page.

Tribe Anthidiini. Anthidiini occurs on all major continents and is richly represented in the Northwest by nine genera. This tribe can easily be distinguished from other Northwest bees by a combination of several obvious characteristics: abdomen with integumental maculations; forewing with two submarginal cells; stigma

Subfamily: MEGACHILINAE

Tribe: Anthidiini	Tribe: Megachilini
1. Tarsal claws of females cleft or at least with inner tooth.	1. Tarsal claws of female simple.
2. Stigma small, its length to the base of the radial vein not much, if any, longer than width of stigma.	2. Stigma larger, its length to the base of the radial vein much longer than width of stigma.
3. Abdominal integumental maculations present, except in *Trachusa,* some *Dioxys,* and some *Stelis.*	3. Abdominal integumental maculations absent.
4. Posterior margin of scutellum vertical or at a distinct angle to the dorsal surface.	4. Posterior margin of scutellum not elevated and without distinct angle to the dorsal surface.

small; jugal lobe greater than one fourth as long as vannal lobes.

Before 1900 all the maculated, nonparasitic forms of this tribe were placed in the genus *Anthidium.* Since then, over 30 generic names have been proposed for various segregates, most of which are readily acceptable as genera or subgenera in that they are morphologically distinct, contain numerous species, and exhibit different nesting habits.

At least one attempt (Mouré, 1947) has been made to divide the Anthidiini into two tribes, Anthidiini *sensu stricto* and Dianthidiini, on the basis of the number of mandibular teeth and the point of insertion of the second recurrent vein. Unfortunately, these characteristics break down in Old World specimens, and there are instances (e.g., *Paranthidiellum*) where a genus has the mandibles of the dianthidiine type and the wing venation of the anthidiine type.

Genus *Heteranthidium* Cockerell: *Heteranthidium* is a small genus of moderate- to large-sized North American bees containing nine species and represented in the Northwest by *H. zebratum.* Its close relationship with the most "primitive" genus in the tribe, *Trachusa,* is indicated by such characters held in common as fine body puncturation; general absence of carinae, sulci, and propodeal pits; and nesting burrows in the soil with cells composed of leaf cuttings and resin. *Heteranthidium* differs from *Trachusa* by the presence of integumental maculations on the abdomen and three- rather than five-segmented maxillary palpi. However, *Heteranthidium ridingsii* has very limited pale maculations on the abdomen and its seventh metasomal tergum resembles that of *Trachusa perdita.* Furthermore, the Palearctic genus *Archianthidium* bridges *Heteranthidium* and *Trachusa* by possessing four-segmented maxillary palpi. It appears, therefore, that *Heteranthidium* could be placed as a subgenus of *Trachusa.*

Genus *Paranthidium* Cockerell and Cockerell: *Paranthidium* is a Nearctic genus of moderate- to large-sized bees whose abdominal terga are usually maculated. Four species occur in this country, one of which occurs in the southeast corner of the Pacific Northwest.

The closest relative of *Paranthidium* is the Old World genus *Paraanthidium.* With the possible exception of *Stelis,* it does not appear to be closely related to other anthidiine genera occurring in the New World, and it can easily be distinguished from other North American anthidiine genera by those characteristics cited in the key.

Genus *Anthidium* Fabricius: *Anthidium* is a large genus of moderate- to large-sized bees distributed in both the New and the Old worlds. Forty species occur in America north of Mexico, of which 15 are found in the Northwest. Members of this genus are rather broad and robust and most closely resemble the genus *Callanthidium.* Together, they can be distinguished from all other North American anthidiines by a combination of several obvious characters: arolia absent; scopa present in females; and, metanotum without a median spine.

Genus *Callanthidium* Cockerell: *Callanthidium* is a small genus of large bees restricted to the western United States. There are two species in the genus; both occur in the Northwest. *Callanthidium* is very closely related to *Anthidium* and may warrant only subgeneric ranking. The two genera can be separated only by those characters found in the key.

Genus *Dianthidium* Cockerell: *Dianthidium* is a medium-sized genus of somewhat small bees represented in both the Old and New worlds, but most species are found in the Americas. Eighteen species are known from North America north of Mexico and eight are found in the Northwest. The Nearctic *Dianthidium* can be distinguished from other anthidiines by the large lamellae of the posterior lobes of the pronotum. All *Dianthidium* can be distinguished by the pronotal lamellae and by the presence of coxal spines on the hind legs, greatly extended in the males.

The Nearctic bees of this genus (*Dianthidium sensu stricto*) are black with yellow or white integumental maculations. Occasionally there is a suffusion of red at the base of the abdomen.

Genus *Anthidiellum* Cockerell: *Anthidiellum* is a small genus of small, robust bees occurring on all continents and represented in America north of Mexico by three species. One species, *A. notatum robertsoni,* occurs in the Northwest. In addition to characteristics used in the key, this genus may be distinguished from other maculated anthidiines by unusually coarse puncturation; subantennal sutures arcuate outwardly; anterior face of mesepisternum separated from lateral face by a carina; females with scopae; and preoccipital ridge carinate above rather than below.

Genus *Dioxys* Lepeletier and Serville: *Dioxys* is a small Holarctic anthidiine genus parasitic on other megachilids. Seven species are found in North America of which three occur in the Northwest. The median spine on the metanotum distinguishes it from all other North American bees. In addition to the characteristics used in the key and structural modifications common to the parasitic habit, the genus possesses a number of distinguishing features: body with coarse puncturations and body without distinct integumental maculations, but sometimes reddish in females; abdominal tergites with apical pubescent fasciae; arolia absent; anterior face of mesepisterna separated from lateral face by a carina; and mandibles bidentate in both sexes.

These distinguishing features of the genus support the tenet of some systematists that the taxon is an aberrant one deserving tribal rank. However, tribal rank should not be proposed before a comprehensive world study of the genus is completed.

Genus *Stelis* Panzer: *Stelis* is a moderately large, world-wide genus parasitic on other Megachilinae, and in two cases on the apid, *Euglossa*. There are about 40 species in North America and 18 in the Northwest. It is a diverse group for which many generic names have been proposed. In the northwestern fauna, *Protostelis* is the most distinct and is considered as a separate genus here. *Heterostelis*, a segregate occurring in North America outside our area, also seems sufficiently distinct to warrant generic status. Other groups sometimes given generic rank, such as *Microstelis*, *Melanostelis*, *Pavostelis*, *Stelidium*, *Stelidina*, and *Chelynia*, are here considered as infrageneric taxa of the genus *Stelis*.

One of the most characteristic features of all species of *Stelis*, as herein constituted, is a black, multi-toothed comb at the apex of metasomal sternum IV in the male. This suggests a relationship with *Paranthidium*, the only other anthidiine we were able to find with such a comb. Michener (1948) and Popov (1945) suggested that a number of the groups sometimes placed with *Stelis* might be independently derived from nonparasitic anthidiine genera. Since *Heterostelis* has only a hair fringe on sternum IV and *Protostelis* has a pair of finger-like processes instead of a comb, their conclusions may apply to these genera.

Stelis females are readily separated from nonparasitic genera by the absence of a scopa. Both sexes can be distinguished from *Dioxys* by the absence of apical fasciae on the terga as well as the absence of the median metanotal spine, and from *Protostelis* and *Heterostelis* by the rounded summit of the mesepisternal declivity. The males are distinct from other anthidiines except *Paranthidium* on the basis of the comb on tergum IV, and from *Paranthidium* they can be distinguished by the absence of long, lateral projections on metasomal tergum VII.

Genus *Protostelis* Friese: *Protostelis* is a small Neotropical and Nearctic genus with four or five North American species, of which *laticincta* is found in the Northwest. The close resemblance of this genus to the South American *Bothranthidium* suggests a common origin for the two genera. *Protostelis* may be distinguished from *Stelis* by the presence of the mesepisternal carinae and the deeply grooved basal area of the propodeum.

Tribe Megachilini. The tribe Megachilini consists of a rather homogeneous subtribe, Megachilini, and a more diverse subtribe, Osmiini. Together they comprise 12 genera in North America, 11 of them northwestern. It is a world-wide tribe with numerous species, best distinguished from Anthidiini by simple tarsal claws in the female and larger stigmata.

TRIBE: MEGACHILINI

Subtribe: Megachilini

1. Arolium absent.
2. Tergum VI of male strongly produced medially and subapically, the projecting area strongly overhanging apical margin.

Subtribe: Osmiini

1. Arolium present.
2. Tergum VI of male not convex medially and subapically or, if generally convex, the convexity uniform to apical margin.

Subtribe Megachilini. The subtribe Megachilini consists of three genera in North America, all of them represented in the Northwest. Apparently at least two other genera are found in the Old World. The subtribe is more homogeneous than Osmiini, even though it possesses a rather widely divergent parasitic genus (*Coelioxys*). Megachilini *s. str.* is specialized in lacking an arolium and in having a strongly projecting subapical area medially on tergum VI of the male.

Genus *Megachile* Latreille: *Megachile* is a large, world-wide genus, well represented in tropical forests, warm deserts, high mountains, and the subarctic as far as trees and shrubs extend. There are about 115 North American species, of which about 40 are found in the Northwest. The genus is diverse with many subgenera occurring throughout its range. As far as we know, all of the New World species merit the designation "leaf cutting bees," although the subgenus *Sayapis* uses more resin and mud in its nest construction than it does leaf pieces. An interesting feature of many males is a "flower-like" development of the front legs. This characteristic occurs in males of many subgenera, but it is usually not present in all species of the subgenus in which it occurs.

Megachile is recognized by the absence of arolia, the presence of beveled intermediate areas on the mandibles of females, and the presence of four exposed, well-sclerotized sterna in the male. Most of the species are about the size of a honey bee, but in other countries some very large species occur. An East Indian species is reported to be the largest of all bees (*M. pluto*).

Genus *Chelostomoides* Robertson: *Chelostomoides* is found in the New World and Eurasia. There are 18 North American species, 2 of which occur in the Northwest. Most authors have treated *Chelostomoides* as a subgenus of *Megachile,* but Michener (1962a) considered it as a subgenus of *Chalicodoma,* a genus based on the Old World group of "mason bees." Although *Chalicodoma* and *Chelostomoides* both use substances other than leaf pieces for cell construction and neither has mandibles specialized for leaf cutting, there are few other similarities. The concealment and modification of sternum IV in the male occurs only in *Chelostomoides,* and this characteristic is accompanied by other differences from both *Megachile* and *Chalicodoma.* Consequently, we are considering *Chelostomoides* as a distinct genus, not particularly closely related to *Chalicodoma.*

Chelostomoides can be distinguished from other New World Megachilini by the absence of beveled areas on the mandibles of the female and the concealment of tergum IV of the male. The species are more slender than most *Megachile* (except *Sayapis*).

Genus *Coelioxys* Latreille: *Coelioxys* is a large, worldwide genus with about 50 North American species, of which about 18 are found in the Northwest. This genus, is parasitic on *Megachile* and, although it has diverged considerably in many characters, it still retains some basic similarities. The erection of a separate subtribe or tribe for *Coelioxys* could probably be justified on the basis of its distinctness, but this would fail to indicate its apparent origin from a *Megachile*-like ancestor.

The elongated, tapered abdomen, sharply pointed in the female and with a number of sharp or blunt, horn-like apical processes in the male, is highly characteristic. The strongly produced scutellum with horn-like axillae is unique within the tribe. In addition, the anterior face of the mesepisternum is separated from the lateral face by a strong carina that extends across the posterior lobes of the pronotum. The genus derives its name from its hairy compound eyes, a character otherwise known to be well developed in few other bees, for example, *Apis* and most *Holcopasites*.

Subtribe Osmiini. Osmiini is a diverse subtribe with nine North American genera, eight of them found in the Northwest. Several of the genera have the metanotum nearly horizontal and the propodeum strongly slanting (a supposedly primitive characteristic in bees), but others have the thorax nearly as box-like as the subtribe Megachilini. There is considerable variation in the number and size of teeth on the apical margins of terga VI and VII of the male, but the subapical portion of tergum VI is not produced as it is in Megachilini.

Genus *Chelostoma* Latreille: *Chelostoma* is a small Holarctic genus, consisting of six North American species (all western), two of which are found in the Northwest. Of the three other northwestern genera with slender body form, it resembles *Hoplitis* in having the anterior face of tergum I rounded but even more slender. It is much like *Heriades* in size, shape, and color, but *Chelostoma* is much less coarsely punctate and lacks a carina at the border of the anterior face of tergum I. It differs from either of the above and from *Chelostomopsis* in having three or four long projections on tergum VII of the male. The basal area of the propodeum is long and horizontal, about as long as the metanotum; the hind coxae are carinate along the inner ventral margins, and the metasomal terga are fasciate.

Genus *Chelostomopsis* Cockerell: *Chelostomopsis* is based upon a single species, *ribifloris,* which is restricted to the far west. However, we have seen one specimen collected in Germany that apparently belongs to this genus. Like *Hoplitis, Chelostomopsis* is moderately slender but it has carinate hind coxae. The male bears some resemblance to *Heriades* but is less coarsely punctate and its metasoma has four visible sterna in repose. The female has several bizarre characteristics, including a spatulate process on the clypeus, a long curved bristle on the labrum (not present on the German specimen), and a head shaped like that of a carpenter ant.

Genus *Heriades* Spinola: *Heriades* is Holarctic and Ethiopian with 10 North American species, 3 of which occur in the Northwest. It is a highly distinctive genus of small, slender bees with coarsely sculptured integument and a sharp carina bordering the anteriodorsal face of tergum I. The metasoma of the male is remarkable in having only two visible sterna in repose. Its relationships with other osmiine genera are obscure. Additional characteristics include a single row of plumose hairs along the apex of the metasomal terga and a carina along the inner ventral margin of each hind coxa.

Genus *Ashmeadiella* Cockerell: *Ashmeadiella* is a Nearctic genus containing about 45 species (most of them in the arid west), nine of which reach the Northwest. The genus is set apart from all other osmiines in having a sharply differentiated anterior mesepisternal face, separated from the rest of the mesepisternum by a weak carina, most pronounced ventrally. The males differ from other osmiines, except some *Chelostoma,* in having four finger-like processes on sternum VI. However, in some species the processes are very short. The metasomal terga are distinctly fasciate apically, and in many species the integument is partially reddish. *Ashmeadiella* is apparently most closely related to *Anthocopa,* but it also resembles *Proteriades*.

Genus *Hoplitis* Klug: *Hoplitis* is a moderately large Holarctic and Ethiopian genus with about 26 North American species. Eleven of these are recorded from the Northwest. The genus is extremely diverse, with 10 North American subgenera currently recognized (*Alcidamea* Cresson, *Andronicus* Cresson, *Chlorosmia* Sladen, *Cyrtosmia* Michener, *Formicapis* Sladen, *Monumetha* Cresson, *Robertsonella* Titus, *Hoplitina* Ckll., *Acrosmia* Michener, and *Dasyosmia* Michener). Until recently *Hoplitis* was divided into six genera (Hurd and Michener, 1955). The species are slender to moderately slender and vary greatly in size. Some are brightly metallic (*Chlorosmia*), some are black with weak white fasciae and some have a red, or red and black, abdomen with weak white fasciae.

Of the four relatively slender northwestern osmiine genera, *Hoplitis* and *Chelostomopsis* are the least slender. From the latter, *Hoplitis* can be told by the less concave anterior face of tergum I and the absence of a carina on the hind coxa. From *Chelostoma* it is distinguished by the absence of a hind coxal carina and by the longer sulcus on tergum I. From *Heriades* it differs in being less coarsely punctate and in lacking a transverse carina on tergum I. Metasomal tergum I of *Hoplitis* has a distinct longitudinal median sulcus on its anterior face, and the sculpturing of the anterior face blends into that of the dorsal face. These two areas are not separated by a carina, although occasionally a very weak carina may be noted at the summit of the sulcus. The males have a tooth at the lateral margin of tergum VI, and the basal area of the propodeum is almost vertical.

Genus *Proteriades* Titus: *Proteriades* is a small genus of robust, small bees whose distribution is restricted to the western United States. The genus contains 22 species, one of which, *P. jacintana*, occurs in the Northwest. All species occur in California and only two have been collected in adjacent states. The genus collects pollen principally from *Cryptantha* for which the stiff, hooked hairs found on the bee's galea and labial palpi are adapted.

With the exception of the peculiar hairs found on the mouth parts, the genus resembles both *Hoplitis* and *Anthocopa*. The carinate ventral margin of each hind coxa is an *Anthocopa*-like characteristic, but the anterior face of metasomal tergum I and the lateral dentations or angulations of tergum VI in males more closely resemble *Hoplitis*. At least a portion of the basal metasomal terga are red in *Proteriades*, a characteristic common to several species of both *Anthocopa* and *Hoplitis*.

Genus *Anthocopa* Lepeletier and Serville: *Anthocopa* is a rather large genus of small- to moderate-sized bees found in Eurasia, Africa, and western North America. Thirty species are known in North America, seven of which have been collected in the Pacific Northwest.

Anthocopa most resembles *Osmia* in America but differs from it by the linear parapsidal lines; the weakly carinate ventral angles of the hind coxae; the nonmetallic coloration of the metasoma; and the broadly concave, scarcely punctate anterior face of metasomal tergum I that is separated from the punctate dorsal surface by a distinct carina. *Anthocopa* demonstrates more diversity in the Old World, and some species are difficult to distinguish from *Hoplitis*. In addition to the anterior face characteristic of metasomal tergum I, *Anthocopa* males differ from those of *Hoplitis* by normally having metasomal tergum VI untoothed laterally and by being more robust.

Genus *Osmia* Panzer: Osmia is a large Holarctic genus with about 130 North American species, of which about 75 are found in the Northwest. Although it is a diverse genus with many subgenera, most of the species have an unmistakable generic stamp. They are robust, mostly moderate in size, and have a uniform dark metallic (or rarely black) color. They lack distinct abdominal fasciae or other hair patterns. The parapsidal lines comprise the most distinctive character; they are markedly reduced, punctiform, pit-like or oval, and represented by small, often slightly elevated areas, at times consisting of only a few large punctures with shiny interspaces. These may be somewhat elongate in the subgenus *Diceratosmia*. Additional characteristics include: arolia present, eyes bare, and scutellum distinctly convex.

Family: ANTHOPHORIDAE

Anthophoridae, as here interpreted, is a very large, morphologically heterogeneous assemblage of bees, including the subfamilies Anthophorinae, Nomadinae, and Xylocopinae. The three taxa have been variously treated by other authors. Linsley and Michener (1939), as well as many European workers, considered the Anthophorinae and Nomadinae as separate families. Xylocopinae has usually been regarded as a subfamily of the Apidae (*sensu stricto*), and Michener (1944a) considered all three taxa plus the Apinae as subfamilies of his inclusive Apidae.

The extreme morphological diversity of the taxa included in the Anthophorinae and Nomadinae is, in large measure, a result of the proliferation of parasitic genera. As Michener (1944a) indicates, "The rate of evolution among the parasitic forms . . . has been very rapid, so that their relationships are often difficult to determine." Yet the number of adult characteristics which are common to these subfamilies lends credence to the probability that both the parasitic and nonparasitic forms were derived from a common pollen-collecting ancestor. Certainly, the subfamilies share more common characteristics with each other than they do with other higher taxa here recognized. In most characteristics, as shown in the family tabulation, Anthophoridae appears to be an "advanced" family, ranking with the Apidae and Megachilidae in this regard.

The monophyletic nature of the family as we interpret it is still open to question and awaits more detailed, critical study.

ANTHOPHORIDAE

Subfamily: Nomadinae	Subfamily: Anthophorinae	Subfamily: Xylocopinae
1. Tibial scopa absent.	1. Tibial scopa present (except in parasites).	1. Tibial scopa present.
2. Basitibial plate absent in females (in northwestern genera).	2. Basitibial plate present in females, rounded, evenly raised, not more than twice as long as broad.	2. Basitibial plate present in females, toothed apically, poorly developed basally, elongate.
3. Second abscissa of M + Cu of hind wing (if present) two or more times as long as vein m-cu.	3. Second abscissa of hind wing present and variable (much shorter than m-cu in Melectini).	3. Second abscissa of hind wing present and one and one-half to two times as long as m-cu.
4. Tergum VII of ♂ with apical half as viewed from above composed principally of well defined, usually rather narrow pygidial plate.	4. Tergum VII of ♂ with apical half as viewed from above composed principally of broadly triangular, sometimes poorly defined, pygidial pate.	4. Tergum VII of ♂ with apical half as viewed from above not distinctly narrowed and without pygidial plate.
5. Tergum VI of ♀ with apical half normally retracted (except *Neolarra*), nearly hidden, dominated by broadly triangular raised pygidial plate (pygidial plate absent in *Neopasites* and poorly defined in *Oreopasites*).	5. Tergum VI of ♀ with apical half normally exposed in some genera, dominated by triangular, raised pygidial plate.	5. Tergum VI of ♀ with apical half as viewed from above normally exposed, not distinctly narrowed, and with pygidial plate absent or scarcely elevated except on lateral margins.
6. Tergum V of ♀ (except *Neolarra* and *Oreopasites*) with apical portion bearing specialized reflective patch or marginal fringe of hairs or bristles (pseudopygidium). Pseudopygidial area usually deflexed.	6. Tergum V of ♀ (except Melectini) with apical hair band somewhat better developed (especially medially) than on preceding terga and often with a different color (prepygidial fimbria). Area of prepygidial fimbria not deflexed.	6. Tergum V of ♀ without pseudopygidium or prepygidial fimbria.

Subfamily: Anthophorinae

Anthophorinae is the largest subfamily of Anthophoridae in number of genera and species, although it shows little, if any, more diversity than Nomadinae. Melectini, which is the only parasitic tribe in the Northwest, exhibits a superficial resemblance to some nomadines, but it appears to be separately derived, probably from a rather specialized anthophorine. Anthophorinae seems to be more closely related to Nomadinae than it is to Xylocopinae. Because of the diversity in both Nomadinae and Anthophorinae and the presence of parasitic forms in both, the problem of characterizing them as separate subfamilies is difficult. The monophyletic nature of Anthophorinae is commonly accepted, but that of Nomadinae, as indicated in the discussion of that subfamily, is often questioned.

Tribe Exomalopsini. This primarily Neotropical tribe contains 10 genera and is represented in America north of Mexico by *Ancyloscelis* and *Exomolopsis*. Both genera are found in southwestern United States, but only one species of *Exomalopsis* has been collected in the Northwest.

The tribe is considered the most primitive extant anthophorine taxon because the scopae contain strongly plumose hairs, the stigmata are large and broad, a scrobal suture is present below the pre-episternal suture in some genera, the pygidium and basitarsal plates are present, and the majority of species are robust and hairy.

Genus *Exomolopsis* Spinola: The tribe (especially the genus *Exomolopsis*) is unusual among bees in that the wing venation is highly variable interspecifically. Some species have two submarginal cells, while others possess three; the jugal lobe varies from one third to over one half the length of the vannal lobe; and the second abscissa of vein M+Cu varies from less than twice to over three times as long as the cu-v vein. Consequently, our generic key will only distinguish the one species found in the Northwest and a few additional species of *Exomolopsis*.

Exomolopsis may best be characterized among northwest bees by the presence of facial foveae in the paraocular areas of the head; the absence of subantennal areas; and a narrow, hairless, and shiny band between the compound eyes, across the vertex, and down to supra-antennal area. The northwest species is moderate in size (6 mm.) and has large, very plumose scopae.

Tribe Emphorini. This American tribe contains large-sized, pollen-collecting bees that are represented in the Northwest only by *Diadasia*. The center of distribution of the tribe, however, lies in South America where four additional genera are represented.

Subfamily: ANTHOPHORINAE

Tribe: Exomalopsini	Tribe: Emphorini
1. Marginal cell longer than first two submarginal cells.	1. Marginal cell longer than first two submarginal cells.
2. Second abscissa of vein M+Cu over three times as long as cu-v vein in northwest forms.	2. Second abscissa of vein M+Cu not over one and one-half times as long as cu-v vein.
3. Pubescence normal, not flattened and appressed against sclerites.	3. As in Exomalopsini.
4. Jugal lobe three fourths as long as jugal and vannal lobes in northwest forms.	4. Jugal lobe half as long as jugal and vannal lobes.
5. Same as Eucerini, except fimbrial pubescence longer than surrounding pubescence.	5. As in Eucerini.
6. Basitibial plates present in female.	6. As in Exomalopsini.

Tribe: Eucerini	Tribe: Anthophorini
1. Marginal cell longer than first two submarginal cells.	1. Marginal cell longer than first two submarginal cells.
2. Second abscissa of vein M+Cu twice as long as cu-v vein.	2. Second abscissa of vein M+Cu not more than one and one-half times as long as cu-v vein.
3. As in Exomalopsini.	3. As in Exomalopsini.
4. Jugal lobe over one third and less than one half as long as jugal and vannal lobes.	4. Jugal lobe one third as long as jugal and vannal lobes.
5. Female with prepygidial fimbria present on metasomal tergum V as a transverse section of pubescence whose color differs from surrounding pubescence.	5. Female with prepygidial fimbria present on metasomal tergum V as a submarginal, triangular-shaped tuft or long pubescence.
6. As in Exomalopsini.	6. As in Exomalopsini.

Tribe: Centridini	Tribe: Melectini
1. Marginal cell longer than first two submarginal cells.	1. Marginal cell shorter than first two submarginal cells.
2. Second abscissa of vein M+Cu subequal to or slightly shorter than cu-v vein.	2. Second abscissa of vein M+Cu extremely short, virtually absent in northwest forms.
3. Pubescence normal, not flattened and appressed against sclerites.	3. Pubescence mostly short, flattened, appressed against sclerite, at least on abdomen.
4. Jugal lobe about half as long as jugal and vannal lobes.	4. Jugal lobe less than one third as long as jugal and vannal lobes.
5. Female with prepygidial fimbria present on metasomal tergum V as a submarginal, variously shaped tuft or long pubescence.	5. Prepygidial fimbria absent.
6. Basitibial plates present in female.	6. Basitibial plates absent.

Emphorines can generally be differentiated from other anthophorine bees, with the possible exception of Exomalopsini, by the general convexity of the vertex. The vertex of most other bees is raised around the ocelli but dips below the dorsal level of the compound eyes and genal areas towards its lateral margins. The undulatory vertex thus gives other bees the impression of being macroptic, whereas the convex vertex in emphorines does not accentuate compound eye size and allows the front view of the head to be more spherical in shape. The emphorines can be easily distinguished from exomalopsines by their larger size, reduced scopal plumosity, absence of facial foveae, and their produced clypeus.

Genus *Diadasia* Patton: *Diadasia* is represented in the Northwest by at least 6 species and in America north of Mexico by approximately 30 species. The genus is diverse in general appearance, ranging from large to moderately small bees and from very light-colored to black species. The diagnostic vertex and spherically shaped head, in addition to the key characters, readily distinguish this genus from some eucerine genera having a similar general appearance.

Tribe Eucerini. This widely distributed tribe also contains large pollen-collecting bees, represented in the Northwest by six closely related genera (*Melissodes, Svastra, Anthedonia, Xenoglossodes, Peponapsis, Tetralonia*). Eucerini is a very large tribe in the sense that it contains more genera than any other apoid tribe but all the genera are closely related and difficult to separate.

In general the eucerines most closely resemble the emphorines, but they are easily separated from them by characters used in the generic key as well as by the following characteristics: antennae of male long, extending beyond the thorax when in repose; pygidial and basitibial plates present in male; and paraglossa long, about as long as the first two segments of the labial palpus.

Genus *Melissodes* Latreille: This New World genus is the most common eucerine in the Northwest in both numbers and species, while *Tetralonia* is the second most common. Because the majority of eucerines collected in this area will be shared between these two genera, the following characteristics are provided to differentiate between them.

Characteristics (2) and (6) will distinguish male *Melissodes* from other northwestern eucerines, but only characteristic (3) will distinguish *Melissodes* from all other eucerines.

Genus *Tetralonia* Spinola: The distribution of this genus is Holarctic and Ethiopian. Except for *Melissodes,* male *Tetralonia* can be distinguished from other northwestern eucerines by the long antennae which reach well beyond the thorax in repose. The females, however, can be distinguished from other eucerines only by a combination of characters used in the key plus the complimentary characters provided above.

Genus *Svastra* Holmberg: *Svastra* is a New World genus, represented in the Northwest by one abundant species, *obliqua expurgata.* This genus closely resembles *Melissodes,* but the antennae in the male are somewhat shorter. Its best differentiating character, spatulate hairs on the first two metasomal terga, allies the genus to *Anthedonia.* In addition to key characters, *Svastra* can be differentiated from *Anthedonia* in the field by plant-host data. *Svastra* is polylectic, but it is rarely, if ever, found on Onagraceae, the plant family to which *Anthedonia* is seemingly restricted.

Genus *Anthedonia* Michener: *Anthedonia* is represented in the Northwest by one species, *A. compta,* which is relatively rare in collections. It is closely allied to *Svastra* on the basis of spatulate hairs present on the abdominal terga, and it can be distinguished from *Svastra* and other eucerines by the differentiating characters used in the key and those mentioned in the above discussion of *Svastra.*

Apparently, *A. compta* is distributed throughout the eastern United States and has its western limits in northern Utah. A second species is found in the Southwest and California.

Genus *Xenoglossodes* Ashmead: *Xenoglossodes* is represented in the Northwest by one or two species that are rare in collections. The female characteristics of this genus strongly overlap those of *Tetralonia,* while some species resemble certain subgenera of *Melissodes.* It is, therefore, difficult to find consistent distinguishing characteristics of this genus other than those used in the generic key. *Xenoglossodes* occurs in both the New and Old worlds.

Genus *Peponapis* Robertson: This genus is restricted to the New World south of Canada and includes 30 species. Only one species, *P. pruinosa,* is found in the Northwest and it is transcontinental. *Peponapis* collects pollen only from the plant genus *Curcurbita.* Since *Curcurbita* pollen is available only during the early morning, adult flight is usually restricted to this period. Oligolecty on *Curcurbita* and the daily matinal flight pattern is shared with the closely related genus *Xenoglossa* that does not occur in the Northwest. Distinguishing characteristics of *Peponapis* in the northwestern eucerine fauna include relatively short antennae in the male, protuberant clypeus, and abundant, close-cropped, pale brown pubescence basally on the terminal three terga.

Tribe Anthophorini. This is a cosmopolitan tribe of moderate- to large-sized, pollen-collecting bees. It is represented in the Northwest by two closely related genera (*Anthophora* and *Emphoropsis*). It is easily separated from Eucerini, Melectini, and the northwestern Exoma-

Melissodes	Tetralonia
1. Fly from midsummer to fall.	1. Fly in spring.
2. Tooth on lateral margin of tergum VII of ♂.	2. Without such a tooth on ♂.
3. Tegula narrowed anteriorly, with concave lateral margin anteriorly.	3. Tegula not narrowed anteriorly, uniformly rounded laterally.
4. Clypeus usually only moderately protuberant.	4. Clypeus strongly protuberant.
5. Antennae of ♂ usually light colored.	5. Antennae of ♂ dark.
6. Maxillary palpi four- (occasionally three-) segmented.	6. Maxillary palpi six-segmented.

lopsini by comparing the lengths of the cu-v vein and second abscissa of the M+Cu vein of the hind wing. In Anthophorini the two veins are subequal in length, whereas the second abscissa of vein M+Cu is at least almost twice as long as the cu-v vein in the other three tribes. Anthophorini can also be distinguished from Emphorini on the basis of jugal lobe size (1/3 that of the vannal lobe in Anthophorini and 1/2 in Emphorini) and the head shape (spherical in outline in Emphorini, not spherical in Anthophorini).

Genus *Anthophora* Latreille: *Anthophora* is a large genus of fast-flying bees found on all continents except Australia. It is best distinguished from *Emphoropsis,* the only other northwestern Anthophorini, by the submarginal cell characteristic used in the generic key, the apex of the labrum broadly subtruncate with the margin thickened or deflexed, and the relatively short terminal three segments of the maxillary palpi, whose combined length is often scarcely if any longer than the second. There is, however, doubt in our minds whether *Emphoropsis* should be considered a valid genus; for, on the basis of male genitalia, comparative morphological studies of larvae, and comparative biological studies, it appears that it could be a primitive subgenus of *Anthophora.*

The *Anthophora* in North America can be divided into four distinctive subgenera, all of which occur in the Northwest. (1) *Clisodon,* represented by a single Holarctic species, *A. furcata,* has tridentate mandibles and the basitibial plates are pointed apically in females. Other *Anthophora* have bidentate mandibles and apically rounded basitibial plates. *Clisodon* is the only *Anthophora* nesting in wood; all others nest in soil. (2) *Micranthophora* is distinguishable from other *Anthophora* by the presence of more integumental maculation on the female clypeus and less on the male clypeus, by extensive areas of appressed hairs on abdominal terga, and by generally smaller size (approximately 11 mm or less). (3) *Amegilla* is a subgenus of moderate-sized bees with apical integumental bands across the abdominal terga. (4) *Anthophora sensu stricto* includes the large robust species lacking the distinguishing characteristics of the other subgenera.

Genus *Emphoropsis* Ashmead: *Emphoropsis* is closely related to *Anthophora sensu stricto.* Approximately 19 species occur in North America north of Mexico, of which 9 species are found in the Pacific Northwest. This genus is separated from *Anthophora* on the basis of the shape of the last submarginal cell, but there is some question of whether or not it should be a separate genus (see discussion of *Anthophora*). Among northwestern forms, the apex of the labrum is rounded and not thickened and the last three segments of the maxillary palpus together are much longer than the second.

Tribe Centridini. This tribe contains numerous species of moderate- to large-sized, robust, pollen-collecting bees which are restricted to the Western Hemisphere. Most species are found in the moist tropics, but some occur in more arid areas to the south and north. Members of this tribe resemble those of Anthophorini, but they are easily separated by comparisons of jugal lobe lengths. The lobe is one half as long as the jugal and vannal lobes in Centridini and about one third as long in Anthophorini. In addition, the arolia are absent in Centridini and present in American forms of Anthophorini. The tribe is represented in America north of Mexico by the genus *Centris.*

Genus *Centris* Fabricius: The geographical distribution of the tribe Centridini is based upon that of the type genus. However, only one species, *Centris* (*Paracentris*) *californica,* reaches northwestern America. In addition to the characteristics cited in the key and a description of the tribe, this moderately large-sized species can easily be distinguished from other northwestern bees by the first flagellar segment which is longer than the scape and by the large, coarsely plumose scopae.

Tribe Melectini. This tribe contains robust parasitic bees of moderate to large size distributed throughout the world. The melectines are parasitic on Anthophorini and can easily be distinguished from them and other Anthophorini by the absence of scopae in females, absence of basitibial plates, and the absence or reduction of other structures associated with the pollen-collecting habit. Three genera (*Melecta, Xeromelecta,* and *Zacosmia*) are represented in the Northwest.

Genus *Zacosmia* Ashmead: *Zacosmia* is a small genus of bees containing two species, both restricted to western North America. The genus parasitizes *Micranthophora* and is represented in the Northwest by one species, *Z. m. maculata.* This highly specialized taxon differs from other genera in many ways. In addition to characteristics used in the key, it can be distinguished from other northwestern melectines by the presence of a pygidial plate in both sexes; male with flagellar segments of antennae swollen; and maxillary palpi reduced to a single segment.

Genus *Xeromelecta* Linsley: *Xeromelecta* is a small genus of large robust bees, parasitic on *Anthophora.* The genus is represented by three species in western North America, only one of which, *X. californica,* is found in the Pacific Northwest. In addition to key characteristics, *Xeromelecta* may be distinguished from other northwestern melectines by wide, subapical bands of appressed pubescence on metasomal terga I-IV, broadly interrupted on the medial portion of each tergum; four-segmented maxillary palpi; and blackish wings.

Genus *Melecta* Latreille: *Melecta* is also a small genus of large robust bees parasitic on *Anthophora* and *Emphoropsis*. It is the most generalized taxon in the subfamily and is restricted to North America west of the Mississippi River. This genus, unlike *Zacosmia* and *Xeromelecta,* is primarily restricted to montane habitats, although one species is found on coastal sand dunes. The genus contains six species, three of which are found in the Northwest. In addition to the generic key characteristics, the maxillary palpi are five- or six-segmented, the male lacks a pygidial plate, and mid-flagellar segments of the male are about as long as broad and are not greatly expanded.

Subfamily: Nomadinae

Nomadinae comprises a diverse assemblage of parasitic anthophorids. Linsley and Michener (1939) considered it as a family, but Michener (1944a) considered the various tribes to be independently derived from different tribes of anthophorids and, therefore, gave the group no separate status. Since independent origins are not clearly indicated, we feel that the nomadines should be retained as a subfamily for the present.

Because of its diversity, it is difficult to find characters common to all genera that distinguish it from all other anthophorids. The subfamily tabulation indicates the difficulty we encountered. The presence of a parasitic tribe (Melectini) in the Anthophorinae complicates the problem by reducing the diagnostic value of several morphological characters reflecting the parasitic habit.

Besides their usual wasp-like color pattern and sparse pubescence, most Nomadinae carry the abdomen in a high and arched position, hold the wings low, and tip the face upwards. This is the usual position assumed in the killing jar, but it is not always demonstrated by pinned specimens.

Tribe Ammobatini. Ammobatini has only one genus, *Oreopasites,* in North America. Other genera are found in Eurasia and Africa. *Ammobatini* is characterized in all genera by the long labrum, lack of pseudopygidium, and presence of a sharply deflexed, densely pubescent pygidium in the female, and by the sharply truncate marginal cell.

Genus *Oreopasites* Cockerell: *Oreopasites* is parasitic on *Nomadopsis* and other panurgines. There are 2 or 3 northwestern species and perhaps 10 or 12 in North

Subfamily: NOMADINAE

Tribe: Nomadini (*Nomada*)	Tribe: Epeolini (*Epeolus* and *Triepeolus*)
1. Marginal cell pointed or narrowly rounded at or close to wing margin, longer than distance from its apex to wing tip.	1. Marginal cell almost symmetrically rounded apically, as long as or longer than distance from its apex to wing tip.
2. Three submarginal cells, I nearly as long as II and III together.	2. Usually three (rarely two) submarginal cells, I slightly shorter than II and III.
3. Area between antennal sockets sharply carinate, carina usually low.	3. Area between antennal sockets sharply carinate, carina higher.
4. Thirteen antennal segments in male, pedicel less than one half the length of flagellar I.	4. Male antennae as in Nomadini, pedicel sometimes nearly one half the length of flagellar I.
5. Maxillary palpi long, five-segmented.	5. Maxillary palpi very short, with one or two poorly differentiated segments.
6. Maxillae long, slender.	6. Maxillae broad, usually rather short.
7. Labial palpal segments III and IV shorter than II, the three together shorter than I.	7. Labial palpal segments as in Nomadini.
8. Second abscissa of hind wing about three times as long as cu-v.	8. Second abscissa of hind wing two and one-half to three times as long as cu-v.
9. Labrum shorter than broad.	9. Labrum shorter than broad.
10. Pygidium of ♂ well differentiated, longer than broad, tapered and rounded, nearly bare to pubescent.	10. Pygidium of ♂ well differentiated, broad and convex laterally (*Epeolus*) or longer and incurved laterally (*Triepeolus*).
11. Pygidium of ♀ broad, rounded apically, pubescent to nearly bare, well differentiated.	11. Pygidium of ♀ as in Nomadini but always densely pubescent.
12. Tergum V of ♀ strongly arched medially or in profile, pseudopygidium well defined, with flattened, truncate apical shelf.	12. Tergum V of ♀ with semi-lunar pseudopygidium of minute silvery pubescence (*Epeolus*) or with longer, dark bristled one (*Triepeolus*).
13. Sternum VI of ♀ with long, parallel basal arms, truncate or rounded apically, with stout hooklets on corners.	13. Sternum VI of ♀ with short basal arms, long apical arms with small serrations (*Epeolus*) or hooklets (*Triepeolus*).

Tribe: Neolarrini (*Neolarra*)	Tribe: Biastini (*Neopasites*)
1. Marginal cell truncate or nearly so, extremely short and separated from wing margin by elongated stigma.	1. Marginal cell almost symmetrically tapered to a point below wing margin, longer than distance from its apex to wing tip.
2. One or two submarginal cells, I over twice as long as II.	2. Two submarginal cells, I a little longer than II.
3. Area between antennal sockets convex but with convexity medially flattened.	3. Convex, sometimes feebly carinate between antennal sockets.
4. Thirteen antennal segments in male, pedicel longer than flagellar I.	4. Twelve antennal segments in male, pedicel about as long as flagellar I.
5. Maxillary palpi moderately long, five-segmented.	5. Maxillary palpi four-segmented, I as long as II and III.
6. Maxillae long, slender.	6. Maxillae long, slender.
7. Labial palpal segments III and IV longer than II; the three together longer than I.	7. Labial palpal segments as in Nomadini.
8. Second abscissa of hind wing nearly absent.	8. Second abscissa of hind wing slightly over twice as long as cu-v.
9. Labrum shorter than broad.	9. Labrum shorter than broad.
10. Pygidium of ♂ projecting as narrow spine-like process, nearly bare.	10. Pygidium of ♂ as in Nomadini, nearly bare.
11. Pygidium of ♀ poorly differentiated basally, projecting but slightly apically as emarginate process.	11. Pygidium of ♀ essentially absent, tergum VI broadly emarginate.
12. Tergum V of ♀ not strongly arched medially, without pseudopygidium.	12. Tergum V of ♀ arched in profile near apex, with narrowly transverse pseudopygidium and apical transparent shelf.
13. Sternum VI of ♀ with short, V-shaped basal arms, narrowly emarginate apically, without hooklets.	13. Sternum VI of ♀ with long, widely separated basal arms, deeply emarginate apically, with hooklets on corners.

Tribe: Holcopasitini (*Holcopasites*)	Tribe: Ammobatini (*Oreopasites*)
1. Marginal cell as in Biastini.	1. Marginal cell obliquely truncate at apex, usually appendiculate, shorter than distance from its apex to wing tip.
2. Two submarginal cells, I nearly twice as long as II.	2. Two submarginal cells, I no longer than II.
3. Area between antennal sockets convex and carinate, carina low, often dull.	3. Area between antennal sockets convex but not carinate.
4. Twelve antennal segments in male, pedicel about half as long as flagellar I.	4. Thirteen antennal segments in male, pedicel about two thirds as long as flagellar I.
5. Maxillary palpi as in Neolarrini.	5. Maxillary palpi five-segmented, moderately short.
6. Maxillae long, slender.	6. Maxillae long, slender.
7. Labial palpal segments as in Nomadini.	7. Labial palpal segments as in Nomadini.
8. Second abscissa of hind wing one and a fourth to one and a half as long as cu-v.	8. Second abscissa of hind wing over three times as long as cu-v.
9. Labrum longer than broad.	9. Labrum longer than broad.
10. Pygidium of ♂ well differentiated, protruding as long, parallel-sided, apically rounded process.	10. Pygidium of ♂ well differentiated, tapered and broadly rounded, sparsely pubescent.
11. Pygidium of ♀ very broad, nearly truncate.	11. Pygidium of ♀ poorly defined, strongly deflexed, marked by dense pubescence.
12. Tergum V of ♀ emarginate apically, ridged medially, with poorly defined narrowly transverse pseudopygidium.	12. Tergum V of ♀ strongly arched medially, without pseudopygidium.
13. Sternum VI of ♀ with moderately long basal arms, U-shaped emargination apically, hooklets on corners.	13. Sternum VI of ♀ with long V-shaped basal arms, narrow, emarginate apical projection, without hooklets or bristles.

America, to which continent the genus is confined. The species are all small with a black thorax and red, or partly red, abdomen. The noncarinate interantennal area separates this genus from its Old World relatives.

Tribe Biastini. Biastini has only one North American genus, *Neopasites.* It shows some affinities with Holcopasitini, especially in the unusual characteristic of the 12 antennal segments in the male.

Genus *Neopasites* Ashmead: *Neopasites* is a small Nearctic genus parasitic on *Dufourea.* There are only one or two northwestern species and perhaps five or six in other parts of the west. The species resemble small, dark *Nomada,* but they have two submarginal cells. *Neopasites* also bears some resemblance to *Oreopasites* and *Holcopasites,* but it is readily distinguished from them by its short labrum.

Tribe Epeolini. The Epeolini are generally moderate- to rather large-sized, robust bees with white or yellow appressed hair patches on a black or dark red integument. The propodeum is exceptionally vertical, and the greatly reduced maxillary palpi are characteristic. As usually considered, North American Epeolini consists only of *Epeolus, Odyneropsis,* and *Triepeolus.* However, in areas outside the Northwest, several rather divergent forms show some affinities to the above genera. These include *Epeoloides* on the eastern seaboard and *Protepeolus* in the Southwest.

Genus *Epeolus* Latreille: *Epeolus* is a moderate-sized, worldwide genus parasitic on *Colletes.* There are about seven northwestern species, all of them black with white or creamy body markings composed of minute, closely appressed hairs. Of the approximately 25 North American species, a number of eastern representatives have black and red integument. The genus is closely related to *Triepeolus* and can be distinguished in the male by the evenly convex lateral margins of the pygidium, and in the female by the apical arms of the sixth sternite which are widely spaced and have serrations but no hooklets apically. In addition, the female has a transverse, silvery pseudopygidium that is basally arched in profile.

Genus *Triepeolus* Robertson: *Triepeolus* is a rather large Holarctic and Neotropical genus parasitic on Eucerini and Anthophorini. The estimated 20 northwestern and 90 North American species have markings similar to those of *Epeolus.* The male pygidium is slightly incurved on its lateral margins near the base, and the female pseudopygidium is flattened and covered with short, dark bristles. Sternum VI of the female also has long, parallel apical arms with strong apical hooklets.

Tribe Holcopasitini. Holcopasitini is composed of a single genus (*Holcopasites*). Its nearest relative is probably Biastini, although the box-like thorax resembles that of Epeolini and the long labrum that of Ammobatini.

Genus *Holcopasites* Ashmead: *Holcopasites* is a small Nearctic genus parasitic on *Calliopsis* and *Pseudopanurgus.* There are about 10 species, most of which are eastern or southwestern, but at least one reaches the Northwest. The species are small and have a nearly vertical propodeum, an emarginate apex to the abdomen in the female, and a striking pattern of small white patches of scale-like hairs. The characteristic of 12 antennal segments in the male is shared with *Neopasites.*

Tribe Neolarrini. Neolarrini is composed of the single genus, *Neolarra.* It shows no obvious affinities with other tribes in the subfamily, although it bears at least a superficial resemblance to the southwestern tribe Townsendiellini. As shown in the table, it differs from the other tribes in most of the characteristics given.

Genus *Neolarra* Ashmead: *Neolarra* is a rather small Nearctic genus parasitic on *Perdita.* Two of the 13 or more species have been collected in the Northwest. The species are all very small, somewhat flattened dorsoventrally, and have abundant, strongly appressed pubescence. The reduced venation and much shortened cells in the wings are highly characteristic.

Tribe Nomadini. This tribe is composed of several divergent genera, but only *Nomada* is found in the Northwest. In general appearance it resembles the Biastini, but its affinities are probably closer to the Epeolini. The southwestern genus *Hexepeolus,* in particular, has some features in common with Epeolini.

Genus *Nomada* Scopoli: *Nomada* is a large, diverse, primarily Holarctic genus. There are about 270 North American species, of which about 90 are found in the Northwest. Most of them are parasitic on *Andrena,* but a few are known as parasites of halictids and panurgines. The species are black with extensive cream-colored, yellow, or red maculations in various combinations. Three submarginal cells separate northwestern representatives of this genus from other northwestern nomadines except Epeolini. The integumental markings and absence of white hair patch markings distinguish it readily from the latter tribe.

Subfamily: Xylocopinae

Xylocopinae is a small subfamily composed of only two tribes, Xylocopini and Ceratinini. Since these tribes are very divergent, characters differentiating them are more abundant and often more obvious than those characterizing the whole subfamily. A rather close relationship with Anthophorinae is shown by the Old World genus *Proxylocopa,* which nests in the soil and has well-developed pygidium and basitibial plates as in anthophorine genera.

Tribe Ceratinini. Ceratinini is represented by the genus *Ceratina* in the New World. Several rather closely

Subfamily: XYLOCOPINAE

Tribe: Xylocopini	Tribe: Ceratinini
1. Maxillae short, broad, stiff.	1. Maxillae long, slender, flexible.
2. Stigma of forewing very short, poorly defined.	2. Stigma of forewing long and broad, well developed.
3. Marginal cell of forewing at least six times as long as broad.	3. Marginal cell of forewing not over four times as long as broad.
4. Second submarginal cell much longer than first along posterior margin.	4. Second submarginal cell shorter than first along posterior margin.
5. Labrum very short, mostly in same plane as clypeus.	5. Labrum about two thirds as long as broad, held at right angles to clypeus in repose.
6. Mandibles tapering gently from base, roughly quadrate.	6. Mandibles with basal half broad, apical half narrow.
7. Male with tergum VII only slightly more deflexed than base of VI.	7. Male with tergum VII strongly undercurled.
8. Hind basitarsus longer than hind tibia.	8. Hind basitarsus shorter than hind tibia.

related genera forming the subtribe Allodapini are found in the Old World. These are renowned for their social and semisocial behavior, based on the communal development of their brood in a single chamber.

Aside from the distinguishing characteristics given in the tribal tabulation, Certinini differ from Xylocopini by their much smaller size, sparser scopa, and shorter, more slender basitarsus.

Genus *Ceratina* Latreille: *Ceratina* is a widespread but homogeneous genus of small, usually submetallic bees that nest in wood, sometimes taking existing cavities, but most commonly boring in pithy stems. There are probably about 15 northwestern species and 30 or 40 in North America. They present a distinctive appearance with their rather slender, dorsoventrally flattened form, somewhat pear-shaped abdomen, weak pubescence, and upturned head and abdomen. Other obvious characteristics include the sharp point at the end of tergum VI in the female, a similar point on the undercurled tergum VII in the male, a horizontal metanotum, and frequent possession of yellow maculations on the clypeus, pronotal lobes, and legs.

Tribe Xylocopini. Xylocopini is composed of three genera, of which *Xylocopa* (the only genus found in the Northwest) is by far the largest. The tribe is primarily Pantropical in distribution, with relatively few species found in temperate regions. All members of the tribe are large and robust in form, with powerful, sharp mandibles and broad, stiff maxillae. Except for members of the small genus *Proxylocopa* that nest in soil, the species nearly always nests in wood.

Genus *Xylocopa* Latreille: This large, mainly Pantropical genus is represented in the southern fringes of the Northwest by two species. Like other species in the genus, they are robust and round-headed, with flattened clypeus and densely haired scopa. The very long hind basitarsus, the long slender marginal cell in the forewing, and the vertical metanotum are other readily observable characteristics of the genus.

Family: APIDAE

The family Apidae, as here considered, includes only those taxa whose nonparasitic members have polished corbiculae on the hind legs for transporting pollen. Other diagnostic characters are indicated in the family table.

Apidae appears to be more closely related to Anthophoridae than to other bee families, and it probably diverged at an early date from a primitive anthophorid stock. Although most of the genera have a well-developed social organization, the Euglossini are solitary.

The family is divided into two subfamilies, which are primarily tropical and best represented in the New World. In north temperate regions, only the endemic genus *Bombus* is represented by a large number of species.

Subfamily: Apinae

Apinae has two tribes, Meliponini and Apini, with only the latter represented in the Northwest. Meliponini includes the subtribes Meliponini and Trigonini, the former Neotropical and the latter Pantropical. Although the two tribes are not closely related and have many divergent characteristics, their similarities are sufficient to warrant placing them in the same subfamily. In addition to the characters listed above, Apinae differs from Bombinae in the smaller size of the individuals, weaker integument, and absence of hair on the apophyseal depression of the prosternal ventral plate.

Tribe Apini. Apini is represented by the single genus *Apis,* which was introduced to the New World from Europe about 200 years ago. It is readily distinguished from the tribe Meliponini by its well-developed sting, complete wing venation, hairy eyes, presence of an inner ramus on the claws, and holoptic males.

Family: APIDAE

Subfamily: Apinae	Subfamily: Bombinae
1. Mid tibia with one hind tibia with no apical spurs.	1. Mid tibia with one hind tibia with two apical spurs.
2. Jugal lobe of hind wing over half as long as vannal lobe.	2. Jugal lobe of hind wing absent or present as a minute scale.
3. Marginal cell open-ended, or at least twice as long as distance from its apex to wing tip.	3. Marginal cell closed apically and much less than twice as long as distance from its apex to wing tip.
4. Five larval instars.	4. Four larval instars.
5. Prosternum without ventral flaps on the ventral plate.	5. Prosternum with ventral flaps on the ventral plate.

Genus *Apis* Linnaeus: *Apis* is represented in the New World by the single introduced species, *mellifera* Linnaeus. Three or more other species occur in southeast Asia, the number depending upon which authority is followed. *Apis,* as represented by *mellifera,* is probably the most widespread and abundant genus of bees both in the Northwest and in the world.

Subfamily: Bombinae

Bombinae has two tribes, Bombini and Euglossini. Only the former is represented in the Northwest; the latter has six small genera restricted to the New World tropics. The two tribes are not closely related and have many divergent characteristics, but the subfamily table indicates that they can be logically grouped together. Members of this subfamily vie in size with Xylocopini and some of the larger *Megachile.* All Bombinae have at least moderately long tongues, and those of Euglossini in particular are the longest found among bees.

Tribe Bombini. Bombini is composed of two closely related genera, *Bombus* and *Psithyrus,* the latter parasitic on the former. Both are represented in the Northwest. The tribe is distributed generally through the temperate parts of the northern hemisphere and even reaches arctic and arctic alpine areas. To the south, several species extend into South America and southeast Asia; but there are no species in Australia or in Africa south of the Sahara. Bees in this tribe are characterized by their large size and long, dense pubescence. Bombini can be readily distinguished from the Euglossini by the shorter proboscis, longer pubescence, narrower hind tibiae, and less parallel-sided second submarginal cell.

Genus *Bombus* Latreille: *Bombus* is a large, diverse genus with numerous subgenera throughout the range indicated above for Bombini. Twenty-nine species are found in the Northwest and 45 in North America north of Mexico. In the female, the polished corbiculum and relatively blunt, densely haired apical terga facilitates separation from *Psithyrus.* In the male, the hind tibia is broader, more polished, and has a longer posterior fringe than in *Psithyrus,* but the contrast is not nearly as great as in the female.

Genus *Psithyrus* Lepeletier: *Psithyrus* is a small, homogeneous group parasitic on certain species of *Bombus.* There are about four species in the Northwest and seven in America north of Mexico.

Although some authors have recommended establishment of a separate tribe for *Psithyrus,* in our view it is closely related to *Bombus.* In addition to the characters for separation from *Bombus* mentioned in the paragraph above, the male genitalia differ in having the gonocoxites less massive and considerably shorter than the gonostyli.

Distribution and Estimated Number of Species Of Northwestern Bee Genera

Genus	Northwest	America North of Mexico	Distribution
Agapostemon	5	9	North America
Andrena	200	1,000	Holarctic (primarily)
Anthedonia	1	2	North America
Anthidiellum	1	3	World
Anthidium	15	40	Old World, North and South America
Anthocopa	7	30	Western United States, Eurasia, and Africa
Anthophora	15	60	World, except Australia
Apis	1	1	World
Ashmeadiella	9	45	North America
Augochlora	1	4	New World
Bombus	27	45	Holarctic and South America
Callanthidium	2	2	Western United States
Calliopsis	2	20	North America
Centris	1	12	New World
Ceratina	5	20	World
Chelostoma	2	6	Palaearctic and western United States
Chelostomoides	2	18	New World and Eurasia
Chelostomopsis	1	1	Western United States
Coelioxys	18	50	World
Colletes	21	115	World, except Australia
Conanthalictus	1	10	Western United States
Diadasia	6	23	Western United States and South America
Dianthidium	8	18	New and Old worlds
Dioxys	3	7	Holarctic
Dufourea	14	60	Holarctic
Emphoropsis	4	19	Holarctic
Epeolus	7	25	World, except Australia
Exomalopsis	1	28	Neotropical and western United States
Halictus	50	260	World
Heriades	3	10	Holarctic and Ethiopian
Hesperapis	2	25	Western United States and South Africa
Heteranthidium	1	9	North America
Holcopasites	1	10	United States and Mexico
Hoplitis	11	26	Holarctic and Ethiopian
Hylaeus	20	50	World, except South America
Macropis	1	6	Holarctic
Megachile	40	118	World
Melecta	3	6	Holarctic
Melissodes	40	97	New World
Micralictoides	1	8	Western United States
Neolarra	2	13	North America
Neopasites	1	6	Western United States
Nomada	90	272	Primarily Holarctic
Nomadopsis	15	39	New World
Nomia	3	21	World
Odyneropsis	0	1	Neotropical
Oreopasites	2	10	Western United States
Osmia	75	130	Holarctic
Panurginus	7	17	Holarctic
Paranthidium	1	4	North and Central America
Peponapis	1	3	New World
Perdita	46	329	North America
Proteriades	1	22	Western United States
Protostelis	1	5	New World
Pseudopanurgus	8	55	New World
Psithyrus	4	7	Holarctic and South America
Sphecodes	20	70	Almost world-wide
Stelis	18	40	World
Svastra	1	11	New World
Tetralonia	10	40	Holarctic and Ethiopian
Triepeolus	15	90	Holarctic and Neotropical
Xenoglossodes	1	15	North America and Europe
Xeromelecta	1	3	Western North America, West Indies
Xylocopa	2	7	World-wide, tropical, and warm temperate
Zacosmia	1	2	Western North America
TOTALS	879	3,510	

The Biology and Behavior of Bees

Geographical and Ecological Distribution

Friese (1923) and Michener (1955a) estimate that between 19 and 20 thousand species of bees in the world will be recognized when descriptive work has been completed. Muesbeck and others (1951) list 104 genera containing approximately 3,300 species and subspecies of bees in America north of Mexico.

Of these, 63 genera are recognized as occurring in northwestern America, but the precise number of species in this area is not known. Among the several hundred northwestern species of bees, it is estimated that 10 percent are either social or semi-social, 10 percent parasitic, and the remaining 80 percent solitary. Solitary bees are found throughout most of the world wherever flowering plants grow and suitable conditions are found for nesting. Social bees of the genus *Bombus* predominate in the higher altitudes and latitudes. A limited number of species of *Megachile, Hoplitis, Osmia, Andrena, Halictus, Hylaeus,* and *Colletes* share the subarctic alpine areas. Malyshev (1935) states that only bumble bees are found in many of the Arctic Ocean islands, as well as on the extreme peninsulas of Alaska, Labrador, and Murmansk, but he indicates that on Spitzbergen even bumble bees are absent. In the southern hemisphere as well, certain species of *Bombus* (*dahlbomi*) and *Halictus* penetrate the farthest southward.

The number of species of solitary bees is greatest in the warmer, more arid sections of the world, particularly in the semidesert areas as typified by those of western North America, North Africa, South Africa, Australia, northwestern Argentina, and South-central Eurasia. An abundant and diverse solitary bee fauna is also common adjacent to mountainous areas where moderate rainfall conditions exist. The rich bee fauna found in mountains adjacent to arid or semiarid areas is only partially explained by the stratification into altidudinal zones. The varied soil types and exposures, rock niches, beetle holes in wood, and pithy-stemmed plants offer many diverse nesting niches. Diversity in the bee fauna from one range to another is assured through isolation provided by surrounding tracts of desert unsuitable for the mountain-adapted species. In many regions where desert conditions are of relatively recent origin, isolation has existed only long enough for subspeciation or "incipient" speciation to take place. Finally, the broken terrain in the mountains, especially where precipitation is not great, assures breaks in the forest canopy, thus allowing for extensive flowering and bee activity. Even at timberline, the presence of south-facing slopes and pockets protected from the wind sometimes allow for a surprisingly good bee fauna in otherwise bleak and inhospitable territories.

The world-wide distribution of bees and the remarkable proliferation of species attests to their high degree of adaptability. The diversification of bee species has to a large extent proceeded hand in hand with a diversification of plant species. Thus, in the northern and higher climes, characterized by short growing seasons, diversity of both plants and animals is small, whereas the geographical areas occupied by each species is usually extensive. Approaching the extremely cold polar regions, species numbers rapidly decrease until areas are reached that are all but biologically denuded.

Malyshev (1935) points out that humidity also exerts a limiting influence on the distribution of bees. This is particularly evident in the rain forests common to the tropical regions of the New and Old worlds, where the excessive moisture and humidity affect the vegetative growth patterns. Profuse arboreal vegetation reduces sunlight, thus curtailing flowering and limiting the pollen supply on which bees depend. Malyshev also indicates that since honey is hygroscopic, the stores of most bees would rapidly liquify under humid conditions unless the cells were enclosed in a sufficiently watertight material to protect them from the external environment. An examination of the habits of bees found in tropical rain forests indicates that most of the nests are found in above-ground situations. The nests are usually constructed in woody materials, and the cells are lined with resins, leaves, or other nonhygroscopic materials.

The high rainfall and humidity of the extreme coastal strip of northwestern America have probably made nesting difficult for all except a few highly adapted or adaptable species of bees. The low maximum temperatures of the area have also restricted the number of species. Finally, the dense forest canopy with its effect on light, temperature, and humidity is generally unfavorable for most kinds of bees.

Contrasted with the cold and humid regions are the semiarid and arid areas of the world, particularly those of western America, where both plant and bee species are abundant and often stratified into sharp ecological or seasonal niches. In these zones the duration of bloom and flight periods of associated insects is short. As the bloom of one group of plant species disappears, that of another emerges to take its place. Each new "flush" of bloom in the semiarid regions ushers in a new plant-bee association.

Most of northwestern America occupies a transitional zone between the subarctic and arctic-alpine areas to the north and the desert zones to the south. This allows for the presence of many species with northern origin and many with southern origin. Austral genera (*Exomalopsis, Heteranthidium, Augochlora, Xylocopa, Peponapis,* and others) barely reach the Northwest, and they are represented by at most a few species in the northern parts of the Great Basin. Existing with these genera and sympatric with them are many representatives of Holarctic or Cosmopolitan genera (*Halictus, Megachile, Andrena, Dufourea, Ashmeadiella,* and so forth). It is apparent that most of these genera are in the process of range extension and subsequent adaptation to the new niches available to them. Because bees depend upon pollen and nectar for survival, we would expect to find the greatest degree of species proliferation in those ecological zones having the richest entomophilus vegetation and the longest season for potential bee activity. In northwestern America this is the Great Basin region, where bees achieve their varietal maximum.

Solitary and Social Behavior

To the majority of laymen, bees are social insects living in colonies. Actually, the vast majority of genera and species of the world are solitary, that is, each female builds and provisions her own nest without assistance from other bees and has no contact with the offspring after the eggs are laid. The word "contact" here is used in the sense that no adult-larval contact is made for the purposes of feeding and tending. Physical contact between mother and adult offspring occurs in forms that have multiple generations which nest side by side, or when, as in the case of some xylocopids, the offspring emerge while their mothers are still in the nests.

The honey bee represents the ultimate in social organization among bees. In this species the colony is the basic reproductive unit, containing a single long-lived reproductive (queen), a large number of nonreproductives (workers), and a few males (drones). The workers tend the brood from the time the egg is laid until it is a mature larva, feeding it small quantities of food at intervals during each day (progressive provisioning). Even more significant in terms of social development is the complex division of labor made possible through the development of communication and the constant food inter-exchange and the stimulation they provide through bodily contact.

Numerous definitions have been proposed to distinguish between social and solitary bees, but recent information has shown that hard and fast distinctions cannot always be made. Few bee species can be considered to be either social or solitary, for all intergradations between these two extremes have been described, representing intermediate stages in the evolution of social behavior.

Michener and Lange (1958a) define three terms applied to the behavior pattern of nonsolitary insects: *social insects* occur in groups or colonies in which one or both parents survive to cooperate with their young when the latter are mature, and in which there is a division of labor; *semisocial insects* occur in groups or colonies consisting of individuals of the same generation (no parent-offspring relationship), and in which there is a weak or temporal division of labor or cooperative activity; *subsocial insects* occur in groups or colonies in which one or both parents survive to protect and feed the young, but they die or leave the young before the latter reach maturity.

Recent papers reporting on the habits of bees of the subfamily Halictinae (*Halictus, Corynura,* and others) reveal that species in this group display all stages of social behavior from solitary to highly social (Sakagami and Michener, 1962). Even a cursory examination of the observations recorded for species in this group reveals the inadequacy of the definitions proposed above, yet they serve as standards of reference from which deviations can be described.

There has been general acceptance of the historical premise that social behavior in bees developed in much the same manner as that described for ants, termites, and social wasps, that is, through a subsocial stage (Ribbands, 1953; Wheeler, 1923). The premise traces the evolution of the organism through several steps; an increase in the longevity of the parent, permitting it to coexist with its young; a transition from mass to progressive provisioning of the young; and the development of trophallaxis among the aggregation of reproductives from which there results a division of labor and ultimately a caste system.

This concept was favored by students of social behavior of bees because of the well-documented ethological studies on the xylocopid genera, *Allodape* and *Exoneura* (Brauns, 1926; Skaife, 1953). Comparative studies in the biology of this group reveal that eggs are laid in a large communal chamber lacking enclosures or partitions. Some of the primitive species of this group prepare "loaves" of pollen, each of which is provided with an egg. Other species lay a series of eggs in close proximity to each other and provide a common pollen mass from which all larvae feed. In several more highly evolved species, the adults feed each larva individually. In all species the adults and the larvae are in constant contact.

New females of some *Allodape* may establish their own nests or may remain in the parental chamber with their mother, where they tend their own as well as their sisters' young, remove refuse, and exhibit varying degrees of cooperation. Thus, this species group displays subsocial and semisocial behavior patterns; the latter apparently arose through a subsocial stage.

Yet, in all of the social Halictinae and many of the social Apidae (Meliponinae), cells are mass provisioned so that there is no contact between larva and adults. Michener (1953b) and Michener and Lange (1958a) feel that the development of social behavior in these groups did not proceed through a subsocial stage. Rather, they propose that social behavior in most bees developed through the following series of steps: 1) nesting aggregations; 2) use of a common nest by several females, each of which constructs and provisions her own cells; 3) initiation of division of labor and cooperation among such females; 4) differentiation of females into queens and workers and the establishment of numerical preponderance of females over males. Steps 1, 2, and 4 are known for a number of species of bees, but until 1958 the third step was conjectural. The description of the bionomics of *Augochloropsis sparsalis* by Michener and Lange provides a convincing example of the occurrence of the semisocial third step. In this species a number of morphologically similar, mated females occupy a single nest and a division of labor has been established among them. Some become reproductives, some collect pollen, and oftentimes several females provision a single cell. The authors noted a few unmated females in some of the nests examined, and reported that they worked more diligently than the mated females. They suggest that this characteristic would have a positive selective value from which we would expect the establishment of a regular nonreproductive caste.

It is thus likely that social behavior in most bees has and is evolving through semisocial intermediaries (except for the Allodapini mentioned above) and that this feature has arisen independently in several different groups.

Bionomics

The biology and behavior of the solitary bees has attracted the attention of an increasing number of research workers during the past 15 years: those exploring the value of solitary bees for pollination purposes (Bohart, 1953, 1957, 1967; Hobbs, 1956, 1957; Hobbs and Lilly, 1958; Linsley, 1946; Popov, 1956; Stephen, 1959, 1960, 1962); and those attempting to evaluate the significance of biological patterns as a supplementary tool for the determination of phylogenetic relationships among bees (Linsley, 1958; Linsley and MacSwain, 1957; Linsley, MacSwain, and Smith, 1952, 1955, 1956; Michener, 1953c; Michener and Lange, 1957, 1958b; Sakagami and Michener, 1962; Stephen and Torchio, 1961).

The biology of only a few species of solitary bees is thoroughly known. More biological information is available on the alkali bee, *Nomia melanderi,* than any other species of solitary bee, and for this reason it is used here as a standard of comparison. In addition, comparisons are made with the biology of other solitary and social bee genera where they are known to deviate significantly.

This summary of bee behavior is intended to indicate the variety of biological patterns found among bees and to introduce a more exhaustive treatment presented in the later sections dealing with each taxon. It has proved impossible to restrict the comparisons to species that occur only in the Northwest, for the ethology of relatively few species is known. We have drawn extensively on world literature and unpublished data to make our comparisons as complete as possible.

Life cycles[5]

In temperate regions most species of bees have only one generation a year and spend the winter (and much of the rest of the year) as prepupae in their natal cells. For example, the alkali bee usually emerges as an adult in early July and lives for about one month, during which time it lays up to 20 or 25 eggs. The eggs develop into prepupae (completely defecated larvae) in about 15 days, some time in late July or August, and enter a period of dormancy until June of the following year. The pupal period is relatively short (10 to 15 days at normal temperatures), and adults spend a few days in their cells in a teneral condition. When temperature conditions are suitable, the alkali bee experiences multiple (up to four) generations (Stephen, 1965a). Under such conditions, diapause of prepupae is never initiated and each generation is expressed over a 30-day period.

Other prominent bee groups with a similar life cycle to that of single-generation alkali bees (although the period of adult and larval activity may be different) include *Colletes,* most panurgines, *Dufourea,* most *Megachile,* eucerines, nomadines, a few *Andrena,* and some *Anthophora.*

In the Northwest about half of the *Megachile rotundata* larvae of the first generation pupate and emerge as adults in the late summer. In some seasons a small percentage of the progeny of the second generation emerge as a third generation, although they usually have little time for nesting before being killed by cold temperatures. Apparently, some *Megachile* and *Hylaeus* and some *Anthophora* have more than one complete generation and overwinter as prepupae.

Some single-generation species overwinter as adults in their natal cells. For example, *Osmia lignaria* usually emerges as an adult in April and flies for about three weeks. The larval feeding period is longer than that of the alkali bee (from 25 to 45 days, depending on the temperature) and the prepupal period lasts for about one month. It is probable that this is not a deep diapause with extremely low metabolism as in the case of the overwintering alkali bee prepupa. The pupal period lasts for about 20 days, and the adult emerges within the cocoon during the summer. There it remains in a dormant condition until the following spring. When the temperature reaches its threshold of activity in the spring, the adult takes only a day or two to chew out of its cocoon and take flight.

The type of life cycle described above is apparently an adaptation for early spring emergence, although some species exhibiting it (for example, *Osmia texana*) do not emerge until late spring. It is interesting to note that another species with relatively late emergence, *Osmia californica,* usually has some individuals overwintering as prepupae. Other bees overwintering as unemerged

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[5] For a summary, see the chart on page 72.

adults include most *Osmia* and *Andrena* and some *Anthophora, Megachile,* and *Emphoropsis*.

Apparently only a few species overwintering as unemerged adults have more than one generation per year. *Andrena candida* and *A. prunorum* seem to have more than one generation, although the possibility that there are two emergence periods has not been eliminated.

In a number of species which have two or more complete generations, adult females of the last generation mate and overwinter in special hibernacula. The males die with the onset of cold weather. For example, fertilized females of *Halictus farinosus* emerge from hibernation quarters in April and return (most of them) to the old nesting site and dig in to remain nearly inactive for up to two weeks waiting for ovarian development. They then lay a small number of eggs which develop within a month to adult females, most of which stay with the parental nest and serve as workers. Their progeny and those of the original female emerge in mid or late summer as both sexes and mate. The females leave the nesting site to hibernate and the males eventually die. With some halictines there are more than two generations, the percentage of males increasing with each generation.

Bumble bees undergo a life history similar to that of halictines. The overwintered female is the sole egg layer for several generations, which overlap broadly because egg laying is continuous. The overwintering females (queens), which are distinctly larger than the earlier generations of workers, are usually produced after the worker:brood ratio is favorable for intensive feeding of queen brood.

Some of the species hibernating as emerged, fertilized females make hibernacula in the nests in which they were reared (*Halictus viridatus*). Others remain at the nesting site but do not necessarily confine themselves to the parental nests. These include species like *Agapostemon virescens* that hibernate in large numbers in a single nest. Sometimes they construct special burrows for hibernacula below one of the old nests. In some cases the gregariously overwintered females cooperate in enlarging the parental nest each subsequent year. Finally, a number of species of halictines leave the nesting site entirely; some return to the site in the spring to found new nests (*Halictus farinosus*) and some establish new sites each spring (*Bombus, Halictus rohweri*).

Bombus and halictines are the only bees known to have the life-history pattern described above. With the exception of a few supposedly solitary halictines, these are all social or subsocial forms.

The life cycle of *Apis* is similar to that of *Bombus* and halictines in that females (queens) overwinter and males are produced in the summer to mate with the females and then perish. It differs in that unfertilized females (workers) overwinter in the brood nest with the fertilized female (queen). Furthermore, they overwinter in an active state and commence rearing brood in the late winter after the colony has been only a month or two without immature forms. Thus, the honey bee and its close relative, *Apis cerana* in Asia, are the only temperate species without any period of dormancy and with only a short cessation in egg laying. *Apis* is also peculiar in that the fertilized female is perennial, sometimes living as long as five years, and in that the colony reproduces by swarming. The stingless bees of the tropics have a similar life history except that the newly produced queen, rather than the original queen, leaves the colony with the swarm. Thus, the original colony dies with its queen unless it is taken over by members of another colony.

The Xylocopinae overwinter as emerged adults, as do halictines and many apids. However, both sexes of Xylocopines overwinter in a dormant condition and mate in the spring (some mating is reported to take place also in the fall). The females usually overwinter in the natal nest with males from other nests often joining them.

All forms of dormancy described above occur either in the adult or the prepupal stage. Other stages of *Apis* and various tropical bees may be alive during the winter months but not in a dormant condition. The only bees known to have dormancy in other stages are the colletid, *Chilicola albida,* and certain temperate and subtropical allodapines, such as *Exoneurella* and *Allodapula*. The overwintering nests of the allodapines are reported to contain immature larvae, prepupae, pupae, and adults, the development or activities of which are interrupted by the onset of cooler weather (Michener, 1962b, 1964a). Herbst (1922) reports that *Chilicola albida* overwinters as a pupa in Chile, a situation that is unique among the bees.

Mating behavior

Mating is usually the first activity of adult bees once they have emerged from the nest. In the alkali bee, as in most bee species, the first bees to emerge are males, and they, like the females, reach their peak emergence during the late morning hours of each day. The alkali bee is gregarious in that numbers of individuals nest in close proximity to each other, and the newly emergent males return to patrol the nesting site each morning. During this period, the males mate with newly emergent females whose wings have not completely hardened. In this rather helpless condition, females may be mated several times before they can take flight. Patrolling males often attempt to mate with nesting females as they leave or return to their tunnels. In fact, according to Nielsen (personal communication) females are intermittently attractive and unattractive to males throughout their adult lives.

In *Anthopora urbana urbana* multiple mating occurs for 10 to 15 minutes after emergence, but the female is never approached after that time. Although mating of the alkali bee usually occurs at the nesting site, large populations of males have been seen on occasion patrolling adjacent alfalfa fields, attempting to mate with the few foraging females visiting the field. Most of the foraging females from these sites were flying to more distant fields where males were less abundant. Male alkali bees return to the nesting site each morning for a period of approximately two to three weeks. Later in the season more males can be observed on alfalfa and sweet clover in proximity to the nesting site than patrolling the site itself.

The most common mating site among species of solitary bees is at or near the nesting site. A few species of *Andrena, Halictus,* and *Osmia* mate in the burrow, either before emergence or soon after re-entry. Some bees have mating stations at a distance from the nests. Males of *Colletes* and *Anthophora pacifica* gregariously patrol distant areas of soil well removed from the nesting site, where they also spend the night. Many species of *Andrena,* as well as *Ancylandrena,* swarm around certain bushes or branch tips. In such cases the females are presumably attracted to the mating sites. According to Rozen (1958), males of many species of *Nomadopsis* patrol the pollen sources, apparently awaiting the arrival of females. *Anthidium* males patrol the pollen sources in a regular pattern and rigorously defend their territory from other males.

The males of several subgenera of *Bombus* establish special mating stations or mating pathways by biting leaves, grassblades, and so forth and liberating a mandibular gland secretion with pheromone activity. Virgin females are attracted to the sites by the pheromone (believed to be farnesol in *B. terrestris,* Stein, 1963), where they are mated by the lurking males. *Apis,* certain bumble bee species (section Boopobombus), and *Melitturga clavicornis* (a European panurgine bee) mate in the air. All of the males of this group are similar in body conformation and all possess greatly enlarged compound eyes which approximate on the vertex.

Males of most bees can copulate numerous times. Until recently *Apis* was thought to be the only genus of bees in which the male lost its genitalia (and its life) during copulation. However, Kerr and Krause (1950) observed a queen of *Melipona quadrifasciata* returning from her nuptial flight with male genitalia in her vagina. Sakagami and Zucchi (in Sakagami and Laroca, 1963) made a similar observation on *Trigona (Nannotrigona) postica.* Apparently, females of all species are capable of multiple mating, but it is not known to what extent each copulation contributes to the acquisition of spermatozoa. In *Apis* it is known that several successful matings take place, often on successive days, but invariably they occur prior to the time of egg laying.

The duration of copulation is short in most species, but in some *Nomadopsis* and several other panurgine genera it is prolonged, and males have been observed attached to the females moving from the food source to the nesting site (Rozen, 1958). In *Nomia* copulation may last from a few seconds to as long as a half minute, but prolonged copula is rare.

Sex determination

Nearly all bees exhibit male haploidy (arrhenotokous parthenogenesis, haplodiploidy); that is, males develop from unfertilized eggs and are consequently haploid, and females develop from fertilized eggs and are consequently diploid. Cytological studies made on 11 bee species in 7 genera show a range in chromosome number in the meiotic stage from 6 in *Bombus fervidus* males to 16 in *Osmia cornuta* and *Apis mellifera* males (Kerr and Laidlaw, 1956). White (1954) states that all Hymenoptera, except for a few that are secondarily thelytokous (parthenogenetic production of females), exhibit male haploidy, and that the characteristic is one of great antiquity.

The sperm (usually from several matings) is stored by the female in her spermatheca, and individual or small groups of spermatozoa are released from the spermaduct into the vagina when the egg reaches that point. Apparently the female can control the operation of the spermaduct and thus control the sex of each egg. Polyspermy appears to be the rule in the case of honey bees, at least, and this sometimes results in peculiar types of intersexes in which one of the sperm cells, unsuccessful in uniting with the egg nucleus, divides and produces a patch of male tissue persisting into the adult organism.

Parthenogenetic production of females has long been known to occur in honey bees. On rare occasions a queenless colony without brood is able to requeen itself. In such cases, a laying worker (worker honey bees cannot mate) produces a diploid egg. According to Ruttner (1965), one of the three polar bodies during egg maturation acts as a sperm cell and effects "self fertilization" with the egg nucleus instead of disintegrating. Although this type of queen production is rare in most *mellifera* varieties, it is common in the South African race, *A. m. capensis.*

The same mechanism that occurs in honey bees seems to be more common in the alkali bee. Nielsen (unpublished) has examined the progeny of several unmated individuals and found variable but sometimes high percentages of females. Daly (1966) reports that in California *Ceratina dallatorreana,* a recently introduced species from Europe, is entirely parthenogenetic.

When normal fertilization occurs in honey bees (and supposedly in all other bees), the resultant offspring are female. However, according to Woyke (1965), when honey bees are closely inbred, a high percentage of the diploid offspring are males. Apparently, male offspring result when the sex chromosomes do not pair (X^1) or when the pairs are alike ($X^1 + X^1$). Somehow, the nurse bees recognize the eggs of diploid males and destroy them before they hatch. Presumably, this accounts for the low egg viability that results from inbreeding.

Mating and nest construction

It is often assumed that mating is a necessary prelude to nesting; however, the authors have experienced no difficulty in inducing *Osmia lignaria* and *cornifrons* to nest in a greenhouse without males. Alkali bees (Nielsen, unpublished) and the leaf-cutter *M. rotundata* (Osgood, unpublished) nested as well in the open without males as with them. Obviously, the supposition that mating must precede nesting requires verification for many species.

Sex ratio

Social species of bees normally produce female broods early in the nesting season. This mechanism allows the worker population to increase until, during a period of maximum forage, large numbers of sexuals (queens and drones) can be produced. The seemingly excessive numbers of male *Bombus* and halictines produced late in the season are often the progeny of laying workers.

There is little information on the sex ratios of most species of solitary bees. An approximate 1:1 ratio is usually assumed, but there is little objective evidence to substantiate this. In *Nomia melanderi* the overall ratio is usually close to 1:1, but unexplained differences in different areas of a nesting site are sometimes observed. Furthermore, eggs deposited early in a nesting season have a higher percentage of resultant females than those deposited later (Nielsen, unpublished).

In many megachilids, males appear more numerous but the exact ratio varies. Exact causes leading to the variance are not well understood. In *Megachile rotundata* the ratio of males to females in large samples taken from different nesting populations has been seen to vary from 1:1 to 10:1. The difference in ratios is directly correlated with the diameter of the tunnel in which they are nesting (Stephen and Osgood, 1965). Single-celled nests usually contained males, but no relationship between length of cell series and sex ratios was evident for series of two or more cells. Medler (1958) reported a 3:1 preponderance of males over females in *Megachile inermis*.

Position of sexes in nests

In honey bee colonies the slightly enlarged drone cells may be constructed anywhere to replace damaged comb or to fill irregular spaces. They are usually most abundant near the periphery of each comb. There is little information concerning position of the sexes in the nests of burrowing bees. Sakagami and Michener (1962) report that in nests of *Pseudagapostemon divaricatus* each lateral has a series of cells with only one sex, but in *Paragapostemon mutabilis* nests the sexes alternate in the cells of each series.

Information is more complete on the sequence of sexes in nests of lodger bees, which normally position their cells in linear series. There is a tendency among these bees for the first-formed or innermost cells of each series to contain females, and the upper, males. This varies from a poorly developed but statistically significant tendency for *Osmia lignaria* (Levin, 1966) to an almost invariable rule for *Megachile rotundata*. However, even with species such as *rotundata*, it is not uncommon for all cells in one series to contain males or females, or for the sexes to be intermixed. As indicated in the following paragraphs, the sequence of sexes in the nests of lodger bees is related to their sequence of emergence.

Emergence of the sexes

Emergence of males in advance of females is evident in the alkali bee and in *Megachile rotundata*, as well as in most other species of bees that have been studied. This phenomenon, referred to as *proterandry*, is a general rule among solitary bees and is interpreted as an evolutionary adaptation, assuring the presence of males for mating with emerging females. However, most of the information on which this rule is based has been gathered from collection data rather than empirical observation. Michener and Rettenmeyer (1956) report that the emergence of the *Andrena erythronii* is not sharply proterandrous, but males do precede females in nectar gathering at the pollen source. In several species of *Anthidium*, at least, males appear later than females (protogyny).

If proterandry is common in bees, a special problem exists for species whose cells are arranged in a linear series. Males located in inner cells must escape without damaging later emerging females in the outer cells.

Four solutions to this problem have evolved in different groups of bees: (1) Males emerge from inner cells several days ahead of females but remain inactive for up to five days before leaving the nest. After this period they work their way through the blocked passageway, destroying any immature bees in their path (*Megachile rotundata*). (2) The innermost bee emerges first and carefully works its way to the front of the burrow by gently pushing undeveloped bees and sawdust materials towards the bottom of the burrow. Subsequent emergents follow the same pattern until all adult bees are resting end to end immediately behind the entrance plug. They overwinter in this condition and issue from the nest together in the spring (*Ceratina*, Rau 1922). (3) The outermost cells contain males and the innermost cells contain females (most megachilids). This method takes full advantage of proterandry since it alone assures that males will leave the nest first. (4) The entire cell series is of one sex.

Sleeping habits

After emerging, and intermittently until they die, bees undergo periods of torpor. Since females usually return to their nests at night and during inclement weather, their activities under these conditions are not readily observed. Many species burrow actively throughout the first night after emerging, and for varying periods during subsequent nights. Females of nonparasitic species rarely sleep gregariously in the open, although females of both *Anthophora montana* and *A. urbana* were observed sleeping gregariously in company with males (Linsley, 1962). Both sexes of parasitic bees normally sleep in the same manner as males of the nonparasitic species.

The sleeping habits of male bees are more distinctive and more readily observed than those of the females. Many sleep gregariously, even though females of the same species exhibit no gregarious tendencies. Recorded observations are largely limited to gregariously sleeping species located in above-ground or exposed situations (Evans and Linsley, 1960; Linsley, 1962). Apparently, the males of many species habitually sleep in underground situations, sometimes in the nest burrows made by the females (*Andrena viburnella*). *Hesperapis regularis* males dig short separate burrows, seal the entrance from the inside, and spend the night (Burdick and Torchio, 1959).

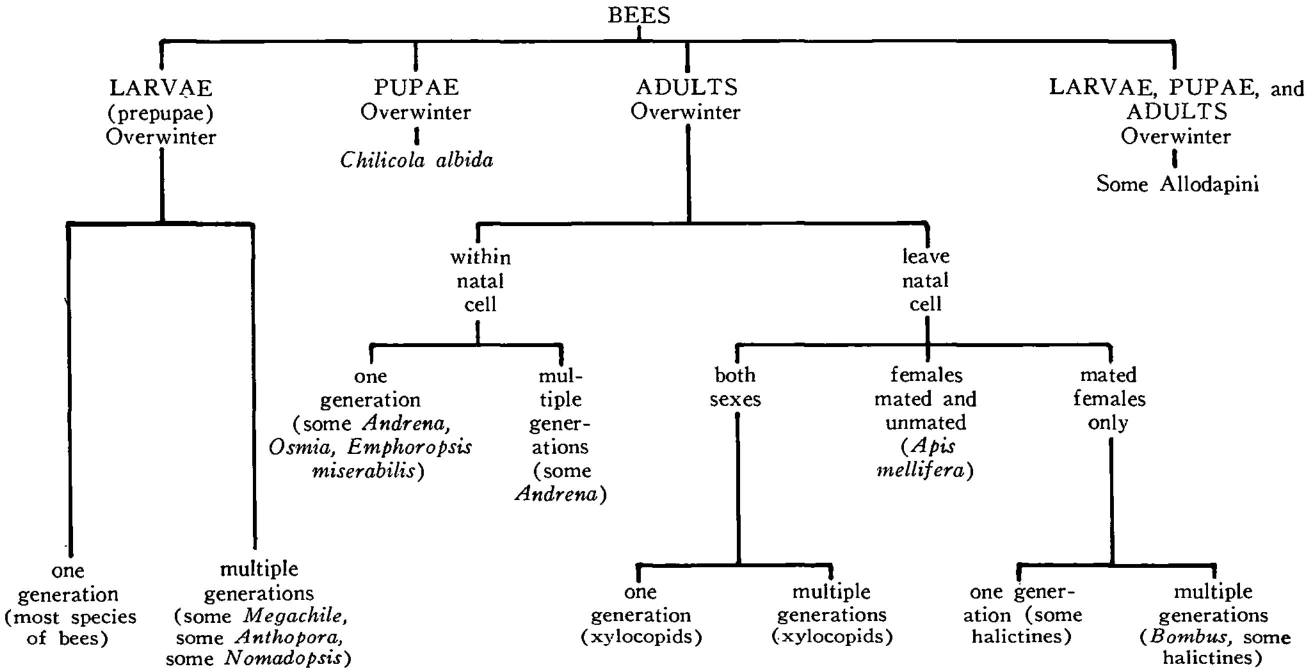
Gregarious underground sleeping has been observed in males of *Nomia melanderi*, although this species also often sleeps above ground. As many as several hundred males were observed in a single cavity between large clods in a ploughed field. They were also observed congregating in smaller numbers in soil cracks and distributed uniformly through small mounds of gravel. An interesting example of cooperative excavation was observed in which approximately 100 males enlarged a small space into commodious sleeping quarters, ejecting over a cupful of sand from the entrance. Schremmer (1955) reports a large aggregation of males of *Halictus pygmaeus* and *H. morio* located in a small hole in the ground.

Above-ground sleeping by bees usually occurs on stems that protrude above the general vegetation level. Clusters of *Nomia melanderi* as large as footballs have been reported, but usually this species clusters in smaller groups composed of from only a few to several hundred individuals. Males, when marked according to the stem on which they were clustering, were found to return night after night to the same cluster (unpublished). Similar fidelity on the part of males of *Megachile rotundala* to a sleeping location was observed in eastern Oregon. Males returned to a cavity under the siding of a building continuously for a period of several weeks, their numbers gradually diminishing, presumably as a result of death (Osgood, unpublished).

Often a large number of aculeates belonging to several superfamilies choose the same clump of vegetation, but they tend to stratify into groups along family or generic lines. It is possible to distinguish an overall gregarious tendency in such associations with tighter associations exhibited among the lower included taxa (Evans and Linsley, 1960). Two species of *Centris* were observed to form a single cluster during a light rain in Puerto Rico. Adjacent stems harbored small, discreet groups of several other families and genera of aculeates. Several other instances of interspecific clusters are reported by Schremmer (1955) and Linsley (1962).

Various distinctive sleeping positions are assumed by male nonparasitic bees and by both sexes of parasitic bees. These positions may be specifically distinct (*Melissodes*) or generically distinct (*Coelioxys*). Several

Generations and Overwintering Stages in Bees



species of *Anthophora* (*urbana* and *montana*) sleep with their heads downward and with only the mandibles grasping the stem. The legs are held tightly against the body with the abdomen above the head and curved to one side of the stem. *Coelioxys* also sleeps with its head directed downward, grasping the stem with its mandibles and the first two pairs of legs. The hind pair of legs is folded up against the abdomen, the antennae pointed forward, and wings held rigidly straight on top of the abdomen. The whole body closely resembles a thorn. *Anthidiellum* sleeps at the very end of the stem with its head down and its abdomen curled in a C-shaped manner over the stem apex. The bee grasps the stem tightly with its mandibles, its legs under its body, and extends the wings laterally (Linsley, 1962). *Melissodes tristis* also sleeps with its head down, grasping the stem with its mandibles and all three pairs of legs. Additional descriptions of sleeping positions could be provided, but the foregoing serves to indicate some of the variation encountered.

Nesting Activities

After mating, most species of bees begin searching for suitable niches in which to nest. However, there is sometimes an unexplained delay during which time the bee remains at the entrance of the natal nest for a day or more. During certain years, *Nomia* females will not begin tunneling until 10 to 16 days following emergence, while in other years, burrowing begins almost immediately. There is an obvious delay in nest-searching activities among those species that overwinter as fertilized adults. Even after nest building has made significant progress, there may be a long delay before cells are readied for provisions. For example, *Halictus farinosus* Smith and *rubicundus* dig the main burrow to somewhat below the eventual cell level and remain there for a number of days without further activity. Foraging and cell construction then proceed normally.

Many species, including the alkali bee, may make a number of attempts at starting tunnels, only to abandon them and begin the process again at another location. Malyshev (1935) notes that certain *Osmia* even construct a portion of a cell and then abandon it to begin the process elsewhere. He interprets this as a sign of "awakening of the maternal instincts" since the same phenomenon has also been reported in social wasps and birds.

Site selection[6]

The availability of suitable substrates for nesting is one of the most common factors limiting the population and distribution of bee species. The principal types of nesting microenvironments include soil, wood, small and large cavities, and even fully exposed surfaces.

Species nesting in soil may select horizontal to gently sloping surfaces or vertical banks. The vertical surface may be bare or overhung with vegetation, or rarely with a grassy cover, and its exposure may provide maximum or minimum shade. Vertical banks are usually dry, but they may be moist in shaded gullies or drain ditches. The soil surface may be wet or dry, but appreciable moisture is usually available where and when the cells are constructed. At least one observation has been made of *Anthophora* species tunneling in moderately hard sandstone. The size and density of roots is often a restrictive feature of nesting soils, associated with the type and density of the vegetative cover.

Many ground-nesting species are extremely exacting in the selection of a nesting site, while others, even in the same genus, tolerate considerable diversity. The alkali bee nests only in flat to gently sloping terrain in which the soil is moist at the surface, of a specific texture, and relatively free of vegetative cover. In the genus *Anthophora, occidentalis* nests only in clay banks, whereas *urbana* and *edwardsii* nest both in clay banks and flat ground and tolerate a wide variety of soil textures.

Most of the eucerines and many of the anthophorines exhibit a distinct preference for hard packed clay soil, whereas other eucerines prefer loose sandy soil. The presence of available water often influences the selection of the site by those species nesting in hard dry soils (turret-forming *Anthophora*). These species transport quantities of water which are applied to the hard dry surface in order to moisten and soften it enough to be able to proceed with the excavation of the tunnel and construction of the turret. Most ground-nesting species construct their nests in areas having a sparse cover of vegetation or refuse, so that the entrance to their nesting tunnel is partially obscured, presumably from parasites and predators.

Aside from soil, wood is the most common substratum in which bees nest. The wood may be hard, soft, or punky, and dry or damp. Nesting may take place in logs, tree trunks, and timbers, or in twigs and stems. The majority of bees that nest in wood utilize existing insect burrows or hollow stems. These same species of bees frequently accept man-made tubular spaces or abandoned mud dauber or paper wasp nests.

Ceratina, some *Megachile,* some *Xylocopa,* and several genera of small sphecid wasps burrow in the soft pithy plant stems of plants such as raspberry, blackberry, and sunflower in constructing nesting tunnels. Species of many other genera, such as *Hylaeus,* most osmiines, some anthidiines, and other *Megachile,* use these burrows for their own nests in subsequent years. Other species construct nests in decaying wood, crevices between pieces of wood, cracks in plaster, abandoned beetle holes, or utilize any aperture that may provide some protection for the nest. Certain species of *Xylocopa* and *Lithurgus* bore holes into sound timber. One species of *Anthophora* (*A.* (*Clisodon*) *furcata*) bores holes in

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[6] This selection excludes parasitic bees since they do not construct nests.

wood somewhat softened by decay. Greenhouse studies in Utah and field observations in Oregon indicate that many species, under stress, will utilize entrance holes excavated by their own or other species to gain access to their nesting substrate. Supersedure of nests under such conditions is not uncommon.

A wide variety of nesting materials is utilized by megachilids. Their nests may be found in snail shells (Old World *Osmia*), pockets or cracks in rocks (many osmiines), attached to twigs or rock surfaces (some *Dianthidium*), or in narrow crevices in almost any material (*Megachile rotundata*).

Most apidae utilize large cavities, such as rodent burrows, hollow tree trunks, caves, boxes, and spaces between walls. *Bombus,* depending on the species, accepts underground, ground surface, or above-ground spaces, but it requires the availability of fibrous nesting materials. Consequently, rodent nests are frequently chosen. *Apis* usually locates its colonies in large cavities above ground, but *A. dorsata* normally hangs its combs from the branches of trees.

Some bees seek a nesting place in which their entrance burrows will have natural concealment. Many species of *Andrena* crawl under a leaf or a fallen branch before starting to dig. *Melissodes agilis* when nesting in areas without vegetation, nearly always conceals its nest entrances under large objects on the ground, such as dried cow dung. *Melissodes minuscula* crawls down between soil cracks for 3 to 5 inches before initiating nest burrows.

Families, subfamilies, and genera of bees are often, but by no means exclusively, restricted to a single type of nesting microenvironment. Colletids nest in the soil, in pithy stalks, or in tubular spaces in a variety of materials. Anthophorids and halictids usually burrow in soil, but a few genera use punky or hard wood. The Xylocopinae nest in wood, except for the primitive genus, *Proxylocopa,* which burrows in the soil (Hurd and Mouré, 1963). Megachilids utilize firm or punky wood, soil, vacant cavities above or below ground, or may construct nests in the open.

Differences in nesting microenvironments are found not only among and between the various genera and tribes of bees, but also among different species within the same genus. For example, *Megachile rotundata* may construct a series of cells almost any place that provides some protection from the external environment. Nests of *rotundata* have been found in nail holes, copper and rubber tubings, cracks between shingles on roofs or on walls of buildings, abandoned cells of mud wasps and paper wasps, abandoned tunnels of beetles in vertical soil banks, and between a wall and a coat suspended on a nail against that wall. This species has never been observed to prepare its own nesting tunnel and always seems to adopt existing cavities for its cells. Another species, *Megachile inermis,* nests almost exclusively in partially decayed aspen or poplar logs. It rarely if ever utilizes other decaying timber and rarely, if ever, will it accept a prepared tunnel for occupancy (Stephen, 1956). A third species of this same genus, *latimanus,* constructs its tunnels only in soil; it prefers to excavate its own burrow but occasionally utilizes other tunnels of adequate size for its nest.

There are additional and equally important factors which influence site selection by nesting females. Both solitary and social bees nest in proximity to nectar and pollen sources when a series of alternative nesting areas is available to them. The initial site may be maintained by the female for the duration of its life (i.e., *Bombus*). However, a decline in the food supply often causes the nesting population to move considerable distances in search of a new area providing both nesting sites and food. *Megachile rotundata* has been observed to abandon its nesting site within a few days of the time when surrounding alfalfa fields were mowed.

Gregarious nesting and aggregations

The term gregarious has a variety of meanings and, in its broadest sense, may include aggregations of adults within a limited area or the coexistence of more than one adult within a single nest.

Our concept of gregarious nesting refers to those forms of nest concentrations in which bees are attracted to the vicinity of the nest from which they emerged or to active nests or groups of nests of the same species. Nest concentrations resulting simply from filling limited suitable nesting environments are not considered as aggregations, although, admittedly, it is not always possible to determine the responsible factors. Although social or semisocial habits of some bees may have evolved from nesting aggregations, it is awkward to consider them as illustrating gregarious nesting.

Gregariousness is first manifested when the female bees emerge, mate, and start seeking for a place to nest. In most gregarious species, a high percentage of females search the immediate vicinity of the nest from which they emerged. Usually, the natal nest itself is used again by one of the emergent bees.

Malyshev (1935) states that the tendency of bees to renest in close proximity to their parent's nest is one of the main causes of gregariousness, and that selection of a peculiar soil condition has a minor effect. There is evidence to indicate that both factors result in the gregarious responses of certain species of bees. However, Fabre's statement that the first impression young bees receive when they leave the nest plays the most important role in their selection of a nesting site better fits observations the authors have made on *Megachile rotundata.*

In the latter species, emergent bees prefer to renest in the type of material from which they emerged, whether it is plastic or paper straws, holes in wood, or corrugated cardboard, if they do not have to search far to find it. A report of *Osmia* reacting in a similar manner indicates that lodger bees may be more responsive to this type of conditioning than other bee taxa.

Michener's (1960b) postulate that odors liberated either by searching bees or the previously nesting populations may serve as the initial attractant in the gregarious habitat agrees with observations made on new alkali bee sites, although the evidence is only circumstantial. Emergent females of *Nomia melanderi* tend to construct their new tunnels in close proximity to those from which they emerged if soil conditions remain acceptable for bee occupancy.

It is during this period between the time of emergence and site selection that most dispersal occurs. Females may fly a few yards or a few miles in search of suitable nesting sites. Often, in a matter of days, a site that had but a dozen bees in it may have nesting populations in excess of several thousand. Searching females exhibit a definite preference for sites that contain nesting alkali bee females to those that are unoccupied. At entirely new sites, some individuals search over the ground for a day or more—scratching and making small pits before the first bee digs in. Almost at once, many more females begin excavating nearby. If the first nest is excavated near the corner of a suitable piece of ground, many nests are started in unsuitable ground near at hand before suitable areas several yards distant are occupied. This demonstrates that gregariousness sometimes outweighs the instinct to select the most suitable soil.

Sequence of nesting activities

Each bee species follows a rather consistent sequence of activities in nest construction. Differences between species in the sequence followed are usually dictated by different types of nests. Consequently, the following discussion of nesting activities borrows to a limited extent from the subsequent descriptions of the nests as finished products.

The nonburrowing species are highly variable in their nest-building sequence. Activities are taken up in the order in which they usually occur but, as indicated, many are deleted by certain species when the type of nest does not call for them.

Among nonburrowing bees, the first activity normally involves cleaning debris from the enclosure in which the nest is to be built. For example, leafcutting bees commonly clean out tunnels formerly occupied by the same or other species of bees. Old cells arranged in linear series of nests are removed in order to facilitate the entire nest enclosure for renesting, or cells in a nonlinear arrangement are sometimes cleaned and re-used. *Hoplitis biscutellae* also practices this habit by re-using cells of *Sceliphron caementarium* as many as eight times, each bee provisioning the cocoon of its predecessor. The honey bee also cleans and reuses the old cells without removing the delicate cocoons. On the other hand, *Bombus,* which also has a nonlinear cell arrangement, does not re-use cocoons for later broods. *Trigona* completely breaks down old brood cells, but utilizes these raw materials for construction of new cells.

Once cleaned, the enclosure is usually lined. *Osmia lignaria* carries mud into the enclosue to reduce the diameter of the nest, if necessary, or to smooth out irregularities. *Chelostoma minutum* customarily lines its burrows with a clear salivary secretion. However, most nonburrowing bees do not line nest enclosures preceding cell construction.

Cell construction follows the preparation of the nesting cavity. Some species bring in foreign materials for this purpose (most megachilids), some use materials taken from the walls of the enclosure (some *Xylocopa*), and some use secreted materials (*Hylaeus*).

The simplest cells are composed of transverse partitions that separate tubular nest enclosures into a series of compartments. Species that construct complete cells form a basal section (cup) in or on which the subsequent provisions are placed, and then a top (cap). After cell construction, species that nest in tubular cavities fashion one or more plugs between the last cell and the entrance.

Burrowing bees do not normally practice preliminary cleaning of the nest. However, those individuals which re-use natal nests, clean the entrance burrows but usually fill in the old cells and laterals.

Bees that nest in hard clay banks usually bring water in their crops to soften the substrate before and during excavation (*Anthophora* spp.). In all burrowing bees, the first part of the nest to be excavated is the entrance or main burrow. Soil brought to the surface during the construction of the main burrow is disposed of about the nest entrance in various ways. These mounds, or *tumuli,* often assume definite forms during nest construction. Some bees dispose of excavated material by using it for the construction of a masonry entrance tube (turret, chimney).

The main burrow is often lined with fine particles of soil, probably tamped into place with the pygidium. Some species line the burrow with a secreted material (*Colletes*) and others with materials brought from the field (*Megachile*).

Most burrowing bees construct laterals from the main burrow with one or more cells arising from each lateral. Exceptions occur among species that construct a main burrow with one or more cells attached to the end, along the sides, or arranged within the main burrow in linear series.

After the cells are provisioned and capped, the nest, or a portion of it, is plugged. Some species only plug the area immediately exterior to each cell, others completely backfill the laterals, and still others plug the entrance when the nest is completed. A few species plug the entrance each time they leave or re-enter. Few, if any, species construct a final nest plug and entomb themselves from within, although many species make temporary plugs from within before spending the night or the winter.

General Nest Architecture

The basic unit of a bee's nest is the brood cell. With the exception of some tropical xylocopids and some *Bombus*, only one larva develops in each cell. In *Allodape* and related genera, eggs are laid in small cavities—such as hollow thorns. The larvae cling to the chamber walls where they are fed progressively. Most *Bombus* also lay their eggs in a communal chamber, but the larvae later wall themselves into separate cells by spinning cocoons. Parasitic bees sometimes lay more than one egg per host cell, but usually only one larva hatches or develops past the first instar. Furthermore, since parasitic bees do not construct nests, they will not be treated in the discussion of nest architecture.

Nests of bees can be divided into two general categories: (1) those which construct one or more cells in the open or in preformed cavities of various sizes and shapes; and (2) those in which cells are connected to a burrow or system of branching burrows constructed by the adult bee. Based on these two nest types, bees can be divided into nonburrowers and burrowers, respectively. Some species of burrowing bees occasionally utilize preexisting burrows, but they use only the entrance shaft and excavate their own side tunnels and cell cavities. A few nonburrowing species excavate to a limited extent but only to adapt existing cavities to their needs. The following tabulation shows how the major groups of bees can be divided on the basis of the burrowing or nonburrowing habit.

Burrowers	Nonburrowers
Colletidae	Colletidae
Colletes, etc.	*Hylaeus*, etc.
Andrenidae	Megachilidae (all others)
Oxaeidae	Anthophoridae (some Xylocopini and all Allodapini)
Halictidae	Apidae
Melittidae	
Anthophoridae (except some Xylocopini and all Allodapini)	
Fideliidae	
Megachilidae	
Heteranthidium (probably)	
Trachusa	
Osmia (some)	
Megachile (some)	
Chelostomopsis	
Anthidium (some)	

Xylocopa, as shown in the above list, seems to belong to both categories. It readily accepts the nests of previous *Xylocopa* generations but also excavates complete nests when ready-made ones are not available. *Ceratina* seems to be a burrower by preference, but it is not known to what extent it may accept existing holes. The family Megachilidae is characterized by heavy mandibles and powerful head muscles, seemingly adapted for extensive burrowing in wood and other resistant materials. Nevertheless, most species nest in preformed cavities, although they sometimes extend or modify the hole, which may account in part for their physical equipment. All species use their mandibles to cut, gather, or masticate nesting materials. Perhaps more species than we realize dig their own burrows when ready-made holes cannot be found.

Although it might seem unlikely that one could determine whether a completed nest had been constructed by a burrower or nonburrower, there are clues which usually make differentiation possible. In the following tabular comparison of the two types of nests, only those nonburrowing bees that nest in narrow, tubular cavities are considered.

If as many as possible of the above criteria are used, few nests can not be properly placed. Borderline cases occur most often in megachilid nests. Some species of *Megachile* (for example, *inermis*) burrow in wood only when they cannot find suitable beetle burrows. They may also make use of a beetle burrow as an entrance and then extend a gallery into sound wood to accommodate the brood cells. *Osmia unca* burrows in soil but in a gregarious nesting site may adopt old burrows of the same species with little modification other than cleaning.

Xylocopa burrows through the side walls of bamboo stems to reach the hollow interior. However, subsequent generations sometimes make use of the same entrance hole. Apparently, in most cases, they avoid the brood cell galleries of their predecessor, but it seems reasonable to suppose that some re-use occurs.

In clay banks, original burrows are often made by such burrowing bees as *Anthophora*. When these burrows and cells are abandoned by their originators, they may be taken over by many nonburrowing bees and wasps (*Megachile rotundata, Osmia texana, Dianthidium* sp., and *Ancistrocerus tuberculocephalus*). In such cases, the generic identity of the original burrower can usually be determined by the presence of entrance turret remnants, characteristic cells, or remains of parasites. Often the original burrower re-uses abandoned main burrows but not old cells. These are broken down and filled in with soil and then treated in the same manner as the surrounding substrate.

Nests of nonburrowing bees

Since most nonburrowing bees construct their cells in small cavities, the form of the nest and of individual cells usually conforms to some extent to the shape of the cavity. When nesting takes place in the open or in large cavities, the nest shape is apt to be variable. Those composed of only a few cells are usually indefinite in organization and shape; those with many cells usually have a rather well-defined inner structure and a variable but often dome-shaped or roughly spherical outer form.

The nest classification on page 89 was devised by using the cavity, if any, and the arrangement of cells as the principal criteria. It would also be possible to construct a classification based primarily on nesting materials, but the two schemes would have little in common. The discussion that follows the classification table is or-

NESTS OF NONBURROWING BEES	NESTS OF BURROWING BEES
1. Many in wood, pithy stems, man-made products, vertical banks.	1. Few in these situations; more often in flat or gently sloping soil.
2. Most have entrance plug composed of materials other than substrate.	2. Most have entrance plug, if any, composed of substrate material.
3. Without tumulus, or only a small amount, composed primarily of nonsubstrate materials.	3. Tumulus usually well developed unless destroyed by wind, water, gravity, or compression.
4. In wood or pith, entrance-exit zone usually darker than area around entrance.	4. In wood or pith, entrance-exit zone as light or lighter than surrounding area.
5. Nest cavity sometimes much wider than diameter of occupant.	5. Nest cavity never much wider than diameter of occupant.
6. In wood; burrows often oval or flattened in cross section (beetle burrows).	6. Burrows never oval or flattened in cross section.
7. Cells arranged in linear series (when occupying tubular cavity).	7. Cells usually in other than linear arrangement.
8. Cells in linear series sometimes not extending to terminus of cavity.	8. Cells in linear series always extending to terminus of cavity.
9. Nest cavity usually unbranched.	9. Nest cavity (burrow) usually branched.
10. Coleoptera or Lepidoptera frass often plug burrow beyond terminal cell.	10. Normally without burrow beyond terminal cell.
11. Cells sometimes highly variable in shape and size.	11. Cells never highly variable in shape and size.
12. Cells (or surrounding structures) often composed of materials brought from outside the nest.	12. Cells and surrounding structures seldom composed of materials from outside the nest.
13. When cell clusters are in chambers, they are covered with materials other than substrate.	13. When cell clusters are in chambers, all structures are composed of substrate materials.
14. Sometimes with more than one cell occupying a borrowed cell.	14. Cells are not borrowed but may impinge on old, filled-in cells.

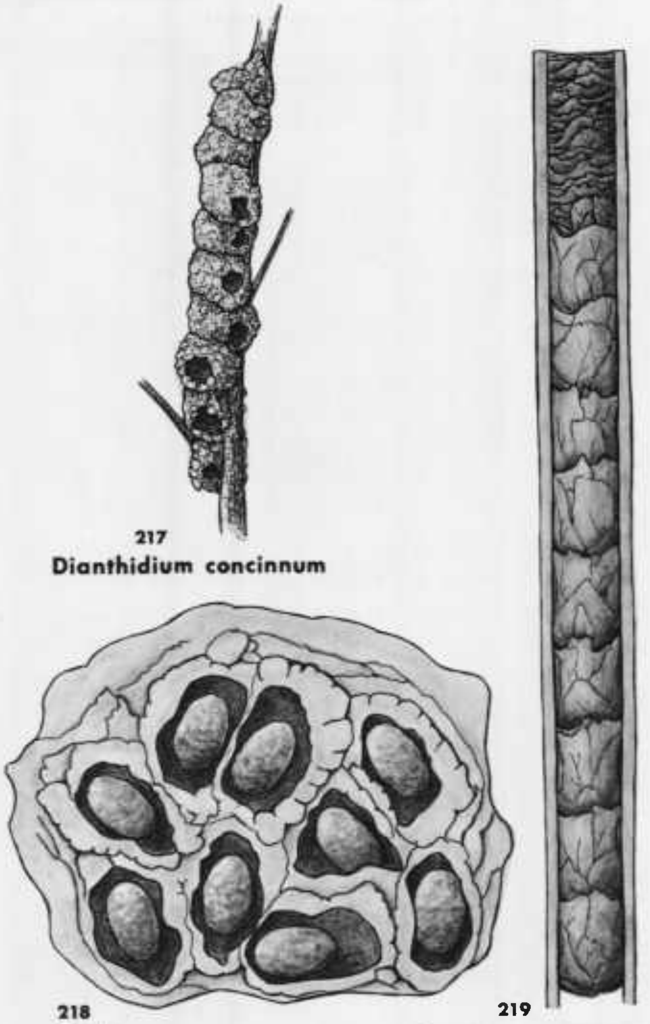
ganized according to groups of bees rather than nest types. By referring to the table, the reader can readily categorize the information either way.

The simplest nonburrowing bee nest is composed of a single cell constructed in the open. Probably no species of bee habitually makes such a nest, but some species of *Dianthidium* construct a small cluster of cells in crotches between tree branches or in shallow rock depressions, while some *Chalicodoma* attach their mud cells to lateral and upper faces of exposed rocks. Occasionally only one such cell is made, and this could be considered as a complete, if somewhat abnormal, nest. In *Dianthidium* nests in shallow depressions, cells are oriented at right angles to the substrate, forming a single layer of adjacent cells. On a highly irregular substrate, such as the crotch between two small limbs, the cell orientation is irregular. In either case, all of the space between the cells is filled with cell-building material (pitch and gravel) and the whole unit of cells is covered and surrounded with this material (Fig. 217).

More commonly, the *Osmia* and *Ashmeadiella* species that nest in small rock pockets make single-celled nests, but, if the pocket is large enough, several cells are grouped together. Moreover, even if there is only enough space for a single cell, additional nesting material is used to seal off the pocket opening, thus adding somewhat to the nest architecture.

Some species of *Osmia* nest in cracks (flat spaces). Several such nests seen in split rocks at Logan, Utah, had cells oriented at right angles to the opposing rock faces (Fig. 218). The rock faces formed the end walls of the cells, and the bees had constructed mud walls to separate the cells laterally. An interesting feature was the roughly hexagonal outline of the closely packed cells, which thus formed a crude comb. Since the space between the rock faces was limited, the cells were constructed wider than long and the cocoons, when formed, were parallel to the rock faces. This orientation allowed the adults to chew through the mud walls as they emerged.

In general, bees nesting habitually in preformed tubular cavities construct little more than a linear series of cells terminated by a plug at the cavity entrance (Fig. 219). When the walls of the tube are suitable as side walls for the cell, some species of megachilids and *Ceratina* construct only partitions instead of complete cells. Megachilid partitions are generally composed of two layers tightly bound to each other. The upper layer serves as the base of one cell and the lower layer serves as the cell cap of the other. Such nests are also provided



FIGURES 217-219. **Nest structures of three bee species.**

with one or more plugs at or near the entrance to the cavity. Some individuals of the same species will modify the cell walls to the proper shape and size with substrate material, particularly if the nesting tube is too large for the growing larva.

Most species that arrange their cells in linear series construct complete cells, i.e., provide walls as well as top and bottom for each cell (most *Megachile, Anthidium*). In *Megachile,* the rounded base of each cell is inserted into the concave apex of the cell below, resulting in a nearly intact, weakly differentiated column of cells (Fig. 219).

Megachile rotundata normally nests in tubular enclosures, but it will accept flat spaces, such as between boards or in the folds of a blanket, when holes are not available. In such places, cells are placed end-to-end in linear series, with each bee making her own series alongside that of another. Occasionally, in places where the space widens, a second layer of cell series may be found. In this case, the cells in the second layer are probably constructed in the small space remaining after the first layer is completed. These layers and masses of cell series are not to be thought of as examples of complex architecture but merely as expressions of the gregariousness of the species and the sequential utilization of available nesting space under stress.

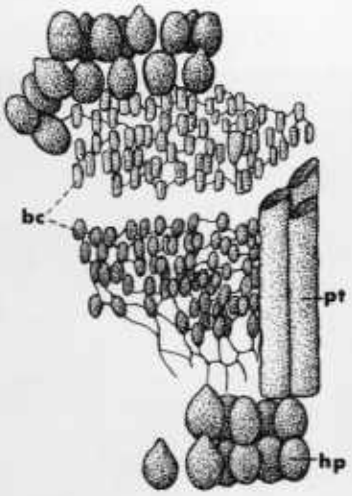
Under stress of limited nesting sites, the nonburrowing bees will utilize a wide variety of peculiar substrates. However, some species apparently select very precise situations for nest construction. For example, *Osmia rufohirta* nests only in the shells of land snails (Ferton, 1897). Preparation of the nesting site by this particular species will often include the transportation of the snail shell from one area to another before constructing the nest therein.

All of the nonburrowing bees thus far treated, construct their cells of gathered materials and build each cell consecutively, i.e., form, provision, and seal one cell before beginning the next. The following nonburrowers construct their cells, entirely or largely, of materials (wax) secreted from specialized body glands, and build their cells serially, i.e., form, provision, and seal a number of cells simultaneously. This group, in which the most elaborate social development occurs, includes the social members of the Apidae (honey bees, bumble bees, stingless bees).

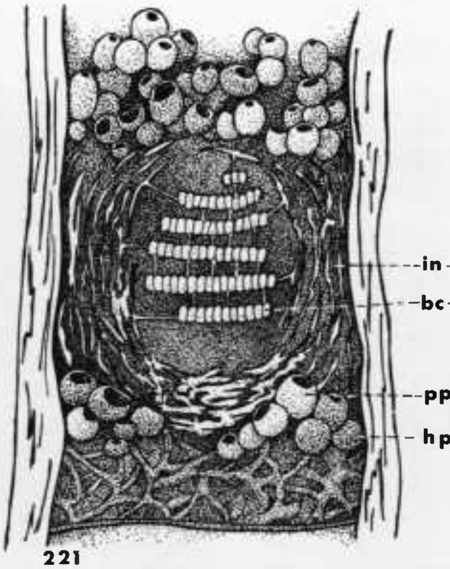
The social groups, *Apis, Bombus,* and Meliponinae, arrange their wax cells on layers (combs) which may be vertical with nearly horizontal cells (*Apis* and *Dactylurina,* Fig. 222) or horizontal with vertical cells (*Bombus,* most Meliponinae, *Eulaema*). *Trigona s.s.* builds clusters or irregular masses of cells instead of definite cell layers (Figs. 220, 221). *Apis* conserves space and material and achieves greater architectural strength by having two layers of tightly fitted hexagonal cells back-to-back against a vertical central comb partition (foundation). *Dactylurina staudingeri* (Fig. 222) is the only meliponine known to have a similar comb arrangement (Smith, 1954). Other social apids construct cells on only one side of the base or foundation. These forms either add layer after layer of cells as their nest grows (*Bombus*) or form several layers (combs) at once (most Meliponinae).

Apis dorsata constructs only a single, large, roughly circular comb. The largest apid nests are usually those made by perennial colonies, but *Apis dorsata* colonies, although perennial, initiate a new nest each year.

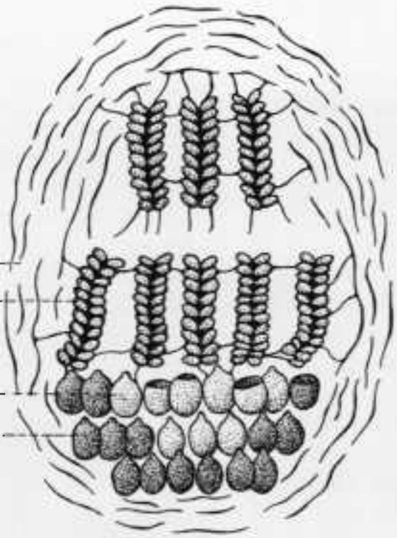
A distinctive feature of the social Apidae involves their use of cells for food storage. *Apis* uses both new and old cells for brood or storage interchangeably. Either honey or pollen, or pollen topped with honey, are placed in the cells, depending on the season and the proximity to the central brood area. *Bombus* stores honey either in special "pots" at the nest periphery (usually early in the season) or in empty cocoons. Some species of *Bombus* feed pollen to their larvae as rapidly as it is brought in (pocket-makers, Fig. 223), but others store pollen sur-



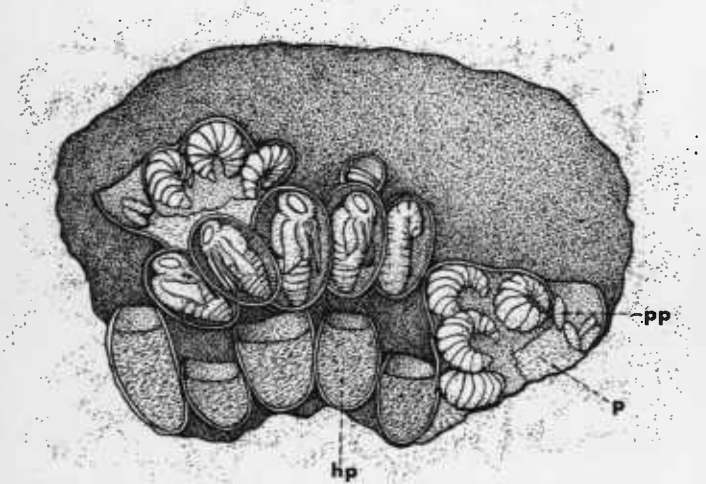
220
Trigona sp.



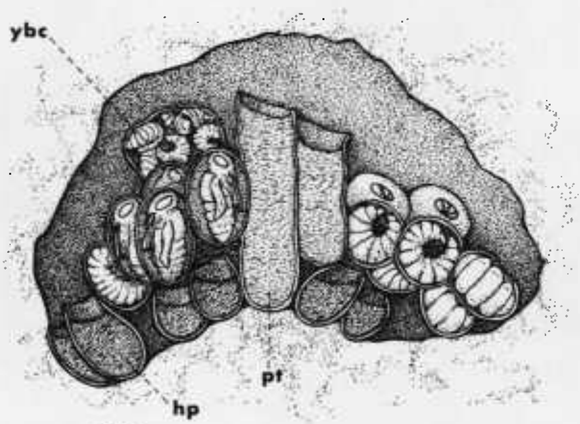
221
Trigona carbonaria



222
Dactylurina staudingeri



223
Bombus sp.



224
Bombus sp.

Figures 220-224. Colony structures of five species of social bees (bc = brood cells; hp = honey pot; in = involucrum; p = pollen; pp = pollen pot; pt = pollen tube; and ybc = young brood cell).

plus in large pots distributed between clusters of brood (pollen storers, Fig. 224). The meliponines usually construct separate pots for honey and pollen storage, which are often quite large and somewhat isolated from the brood cells.

The nest architecture of *Bombus*, the only social apid native to the Northwest, is characterized by brood clusters. In the early spring, the overwintering queens may construct a small cluster of brood cells, each containing a single egg (subgenus *Bombias*) or a large wax-pollen cell containing all of the eggs of the first brood (*Bombus* (*Alpinobombus*) *balteatus;* Hobbs, 1964, 1965). Succeeding brood cells of all species, except *Bombias* (Hobbs, 1965), construct brood cells in which they deposit up to a dozen or more eggs. The characteristic of provisioning the later brood cells with a thin pollen-nectar layer on which the eggs are laid appears to have value as a species, species-group, or possibly even a subgeneric trait, as does the laying of eggs in a vertical rather than a horizontal position. The eggs hatch and the larvae mature in a communal chamber, eventually isolating themselves from each other by the formation of separate cocoons. As the larvae mature, a continual rebuilding and shifting of the chamber is necessary to accommodate the growing brood. Eventually, as the clusters increase in number and size, they become partially contiguous and form rough layers of combs. However, the original clusters never completely lose their original identity and various gaps and irregularities in comb elevation and cell size are always present.

Economy of wax is another feature of *Bombus* nests. The wax is stripped from the cells and re-used as soon as the larvae spin cocoons. Another feature of the nests (shared by most meliponines) is the roughly circular, rather than hexagonal, outline of the cells. In those species of *Bombus* that isolate the eggs of the first brood in separate cells, these cells are roughly hexagonal, but, perhaps due to the need for continually refashioning and shifting the cells, the hexagonal shape is soon lost and never again attempted.

Some bumble bee species construct a wax canopy or *involucrum* over the entire nest. Meliponines also conceal or envelop their nests with one or many layers of wax or with wax intermixed with resin and other materials. In some cases these layers form a complex, irregular system of air spaces such as one finds in a sponge (Figs. 221-222). *Apis* does not envelop its combs, but, when occupying a more or less enclosed space (such as a narrow-mouthed cavity or man-made hive), it seals unused openings with resins gathered from plants (propolis). Many meliponines narrow their nest openings with resinous materials, sometimes drawing a single nest entrance into a long tube guarded by bees armed with soft pitch for daubing invaders. They usually locate their nests where such materials are readily available.

At least two nonsocial apids, *Euglossa* (*Glossura*) *imperialis* and *E.* (*G.*) *ignita chlorosoma,* construct nests that resemble those of other apids, especially *Bombus,* but the cells and cavity linings are fashioned from resinous, nonsecreted materials (Roberts and Dodson, 1967).

The list below compares the *Apis,* meliponine, and *Bombus* nest types in a summary fashion.

The nests of the Paleotropical and Australian allodapines all but lack architectural form. They occupy hollow plant stems and may delimit the upper and lower ends of the nest by a fabricated interior collar (*Allodapula*) to restrict entrance into the nest and aid in its defense (Fig. 225). Aside from this, little or no other construction is undertaken. The eggs are laid individually at the bottom of the communal chamber or attached to the side walls, and as the larvae mature, they are moved progressively nearer the entrance by adults. There is no evidence of cell formation or any other architectural design which typifies bee nests. The only other group using a communal chamber for brood rearing is *Bombus* (see above), and here it is not universal.

Nests of burrowing bees

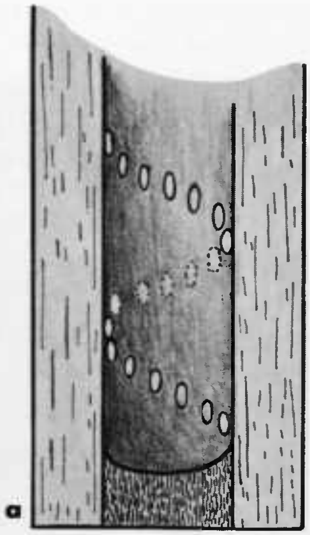
The architectural plans of nests made by burrowing bees are almost endless in their variety. Although nest architecture is a direct expression of behavior which, in turn, is under genetic control, it is probably impossible at this time to construct a phylogenetically significant outline of architectural types. Apparently, various groups of bees have evolved structural patterns along parallel lines and "progress" has not always proceeded toward complexity. The difficulty in organizing a nest classification along phylogenetic lines is demonstrated by the single subfamily Halictinae, in which most of the known types of nest burrows are found. Furthermore, species and genera in different families sometimes build

Summary of *Apis*, Meliponine, and *Bombus* Nest Types

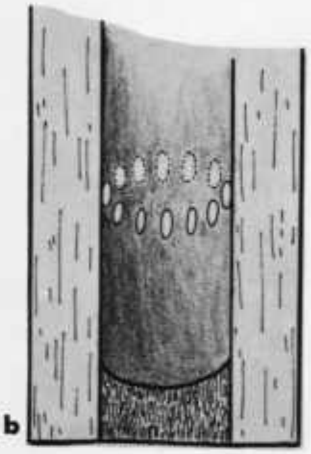
Apis type	Meliponine type*	*Bombus* type
Vertical combs.	Usually horizontal combs.**	Horizontal combs.
Cells on both sides of cell base.	Cells on one side of cell base.**	Cells on one side of cell base.
Brood cells used for pollen and honey storage.	Separate cells used for both honey and pollen.	Separate cells and brood cells (cocoons) used for honey; separate cells used for pollen.
If with several combs, brood develops in more than one at the same time.	Brood develops in several cell layers at once.	Brood develops in uppermost layers only.
Cells open until brood full grown.	Cells closed after eggs laid.	Cells opened intermittently for provisioning.
Occasional pillars and "struts" between combs.	Numerous pillars and other supports between combs.	No support pillars between combs.
No involucrum around nest.	Usually complex involucrum of several layers around nest.	Usually a single involucral layer over nest in some species.
Nest open or, if enclosed, not surrounded by fibrous materials.	Nest open or, if enclosed, not surrounded by fibrous materials.	Nest enclosed and surrounded by fibrous materials.

* Some meliponine nests tend toward the *Apis* type.
** Except *Dactylurina staudingeri.*

225
Allodapula unicolor



Allodape pringlei



226
Allodape halictoides

FIGURES 225-226. Communal chamber of *Allodapula unicolor* containing eggs, larvae, and pupae (225); and egg deposition patterns of the two species of *Allodape* (226).

the same type of nest. Nevertheless, nest types are often characteristic for some taxa.

Malyshev (1935) divided nest burrows into two sections: the *main tunnel,* usually at right angles to the surface and providing the cells with isolation from the fluctuating moisture and temperature of the open air; and the *lateral tunnels* which are branches leading to the areas in which the cells are actually constructed. Sakagami and Michener (1962) make a further distinction among laterals as made by halictine bees. They reserve the term "lateral" for those burrows narrower than the main burrow and connecting each cell or cell series with the main burrow, and they use the term "lateroid" for the comb- and cluster-bearing laterals having the same diameter as the main burrow and arising from it (Fig. 245).

Malyshev also classified nest burrows on the basis of the sequence of cell building in relation to position along the main burrow; species of *Systropha, Colletes,* many *Halictus,* and representatives of many other genera deepen the tunnel as additional cells are added (Fig. 227). The cells may be arranged along one side of the tunnel, in radiating clusters, or in a spiral fashion down the main tunnel, but in each case the lowermost cell of each tunnel is the last to be constructed (progressive). *Exomalopsis caerulea* proceeds in the same manner except that each lateral contains a series of cells (linear progressive). Nests of *Paragapostemon mutabilis* are occupied by more than one female and each usually constructs at least one lateral containing cells in linear series. The nests deepen as each lateral is added and, although the activities of each female cannot be followed, the nest is also considered linear progressive (Fig. 229).

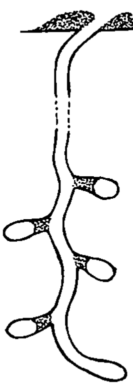
Other bees excavate each tunnel to its full depth before constructing the first cell. This first cell is then provisioned and sealed lowermost in the tunnel, with subsequent cells constructed sequentially nearer the entrance (regressive). *Andrena viburnella,* among others, usually backfills the tunnel with soil excavated from the cells immediately above, and the general tunnel pattern is obscured as one tries to trace it (Fig. 228).

In other species, the female excavates a main tunnel from the end of which she constructs a series of elongate laterals which usually penetrate deeper into the substratum. Each lateral may accommodate a single cell (some *Andrena,* Fig. 230) (stationary), or a series of cells (*Colletes,* Fig. 231) (linear stationary). In *C. michenerianus* the main tunnel of one year's brood is re-used the following year by one of the progeny; however, the female prefers to construct her own new laterals.

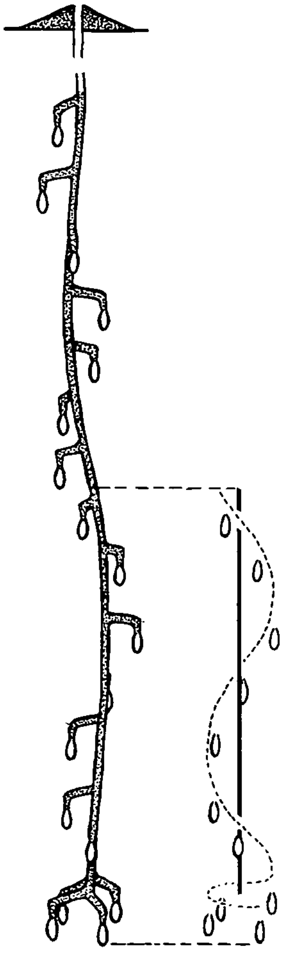
This classification breaks down in those species that construct cells progressively for a time and then excavate one or more cells in a regressive fashion. Another major problem is the practical necessity of excavating several nests while larvae are developing in order to determine the sequence of cell construction.

Several species in several different families of bees construct a burrow with but a single cell at its base. This very simple plan of nest construction is found among many wasps including the scoliids, pomlilids, and sphecids, and its occurrence among the bees should not be construed as a retention of this primitive characteristic by these species. Rather its appearance in a number of different phyletic lines would attest to its independent origin in the bees.

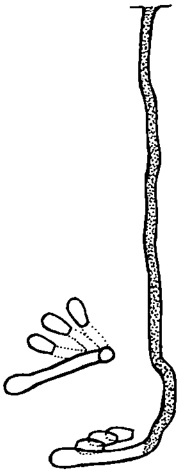
The single-cell pattern of nest construction is uncommon among the bees, but it is recorded in several widely separated genera (*Colletes* sp., *Perdita maculigera* (Fig. 232), *Emphoropsis miserabilis*). Michener (1963) states that bees nesting in sand are more likely to make



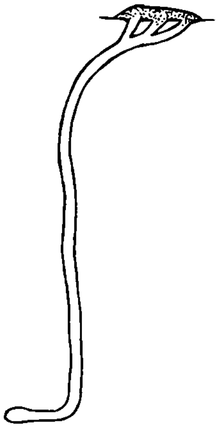
227
Systropha planidens



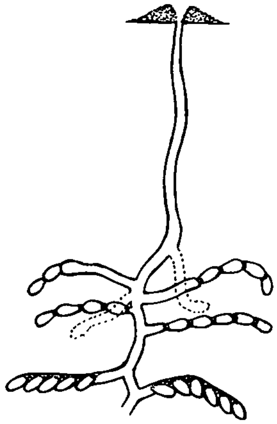
228
Andrena viburnella



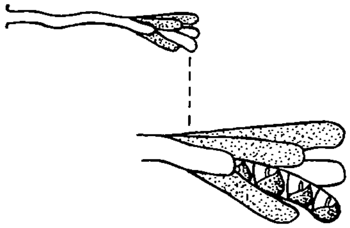
230
Andrena erythronii



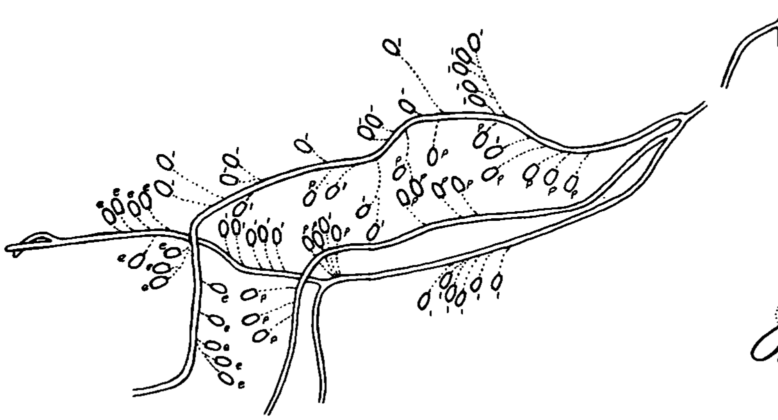
232
Perdita maculigera



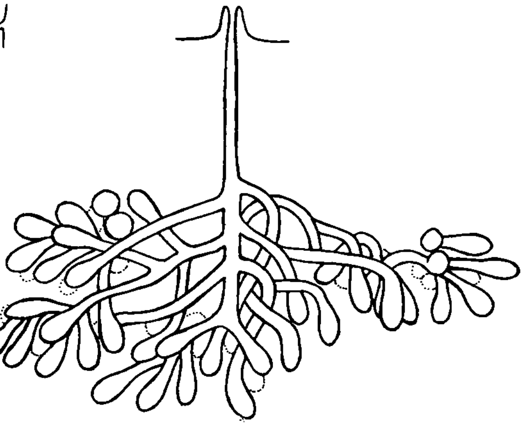
229
Paragapostemon mutabilis



231
Colletes michenerianus



233
Perdita lingualis



234
H. (Lasioglossum) dimorphus

FIGURES 227-234. Nest construction patterns of bees: *Systropha planidens* — progressive (227); *Andrena viburnella* — regressive (228); *Paragapostemon mutabilis*—linear progressive (229); *Andrena erythronii*—stationary (230); *Colletes michenerianus*—linear stationary (231); *Perdita maculigera*—single-celled (232); *Perdita lingualis*—branching root type with cells along main burrows (233); *Halictus* (*Lasioglossum*) *dimorphus*—branching root type with cells near the terminal end of each branch burrow (234).

one-celled nests than those nesting in harder soil because in such easily penetrated material, the economy of excavation represented by multiple-celled nests is relatively unimportant. It is also possible that collapse of the nest, always a danger in sand, would be less critical with one-celled nests. One-celled nests may be quite long in sandy soils (20 to 70 inches in *Emphoropsis miserabilis*) or relatively short in border soils (4 to 6 inches in *Colletes* sp.).

Branched burrows with only primary branches and with one cell at the end of each branch represent the most common general type of burrow. In essence this type of nest is only one step removed from a single-celled burrow. Instead of initiating new nest burrows at the soil suface, the bee economizes its energies by starting other burrows along the main burrow already prepared. The most obvious variation in this type of nest concerns the length of the laterals. Most bees make their laterals several to many times as long as their brood cells, sometimes over a foot in length (*Tetralonia speciosa*) (unpublished). Branches may arise from the main burrow terminus (many *Andrena*) or they may be dispersed along the main tunnel (most Eucerinae and many others).

Nests with extremely short laterals are very common among the Halictinae. Most halictine burrows have short laterals (sometimes cells are nearly sessile) arranged in a somewhat spiral fashion along the main burrow, giving the nest the appearance of a "coat-tree." This resemblance is enhanced by the habit of many halictines of excavating a vertical extension of the main burrow past the zone of laterals. In some subsocial forms, later generations working in the same nest excavate deeper laterals, usually initiated near the main burrow terminus.

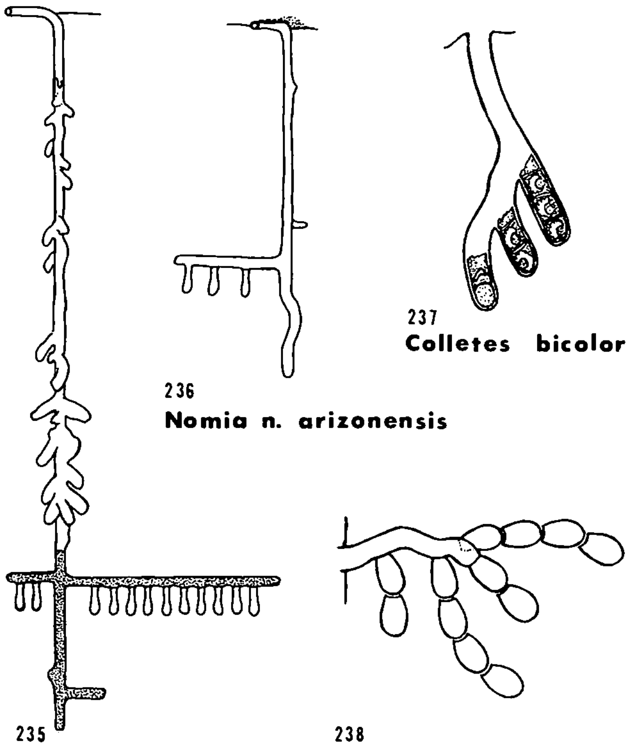
Increasing complexity of the branching nest is represented by nests which have main branches giving rise to secondary branches, both of which terminate at a cell. This type of burrow ramification results in further economy in tunneling operations. Secondary branching is often difficult to detect. When the branches are long and the spaces between their origins short, it is difficult to determine whether some of the terminal burrows are end sections of the main burrow that has changed its course and still gives rise to laterals or whether they are laterals giving rise to sublaterals. The problem is made even more difficult by the habit of many burrowing bees of plugging laterals after cell provisioning is completed. In such nests there is usually a scattering of cells and the burrows may be practically impossible to trace.

The most generalized nest with secondary branching resembles a diagonally oriented branching root system. Nests of this type are often made by one individual (*Melissodes robustior*) (Custer, 1928, 1929) but they reach greater complexity when several individuals work in the same nest (*Perdita lingualis*, Fig. 233). The latter species was shown by Michener (1963) to make as many as 65 cells in a single nest. The density of cells in such a nest may result in one or more irregular clusters, but there are no layers or "combs" of cells.

The branching root type of nest can have the primary branches disposed generally along the main burrow as in *Perdita lingualis*, condensed along the terminal portion of it (*Halictus* (*Lasioglossum*) *dimorphus*, Fig. 234) (Sakagami and Michener, 1962), or at its terminus (*Corynura lepida*) (Sakagami and Michener, 1962).

Nomiine bees often construct from one to three moderately long horizontal laterals from a vertical main burrow. From the lower side of these laterals, they excavate a number of short, vertical sublaterals each ending in cells (*Nomia triangulifera* and *N. nevadensis arizonensis*, Figs. 235, 236). This type of nest seems to be characteristic of the subgenus *Epinomia* (Cross and Bohart, 1960).

Like their nonburrowing relatives, the burrowing lodger bees usually arrange their cells in linear series. Some species construct individual cells at the terminus of separate branches, but more commonly the cells are linearly arranged, presumably reflecting a further economy of energy.



235 **Nomia triangulifera**

236 **Nomia n. arizonensis**

237 **Colletes bicolor**

238 **Melitoma euglossoides**

Figures 235-238. Nest construction patterns of four bee species: two species of *Nomia*—horizontal laterals and vertical cells (235, 236); *Colletes bicolor* (237); and *Melitoma euglossoides* (238)—cells in linear series.

Species that construct linear cell series usually do so consistently, but in some a branch may occasionally have only a single cell. This is a frequent occurrence in some *Anthophora,* whereas in *A.* (*Micranthophora*) *flexipes* and *Hesperapis carinata* one-celled branches are the rule and two-celled branches are only occasionally encountered.

The simplest linear series nests are unbranched. Often these are made by facultative burrowers (many *Megachile,* some *Xylocopa*) as well as a few apparently obligatory burrowers (*Colletes* and some *Megachile*). However, since utilizing ready-made burrows is so convenient for bees with this type of nest, it is difficult to believe the burrowing habit is ever completely obligatory. Bees with linear series of cells may insert each cell into the preceding one, thus making a cell column that holds together (*Colletes,* Fig. 237, and most *Megachile,* Fig. 219) or the cells may be divided by transverse partitions or plugs (*Xylocopa, Ceratina, Ptilothrix plumatus*). *Xylocopa* construct partitions composed of wood fiber, whereas *Ceratina* and *Ptilothrix plumatus* separate cells with short or long plugs.

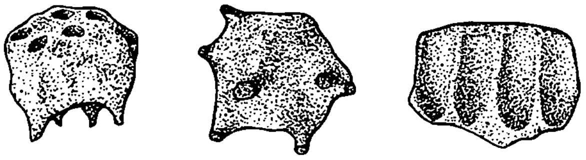
Several bee genera have branching burrows with cells in linear series arising in dispersed fashion along the main burrow. *Melitoma euglossoides* arranges its cells thusly and inserts them into each other (Fig. 238), but other bees with the same cell arrangement separate the cells with partitions or plugs (many *Anthophora*).

Linear cell series in burrows branching from the terminus of the main burrow are constructed by *Diadasia,* some *Anthophora,* and some *Colletes.* The branches may diverge, thus separating each cell series (some *Anthophora*), or they may be closely parallel, thus causing the cells to appear clustered (*Diadasia enavata, Colletes michenerianus,* Fig. 231).

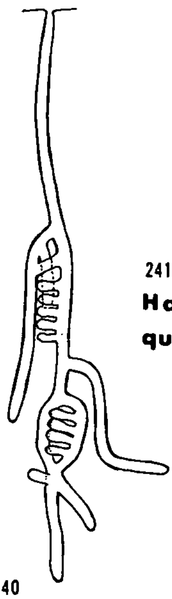
In some halictine bees, a dome-shaped cavity or *chamber* is fashioned over the cell cluster, whereas in others the chamber extends around it, leaving it supported on a broad soil pedestal. Often the pedestal itself is mined away until the cluster is supported by a number of small soil pillars. In most cases the cells are excavated, resulting in a soil block with closely spaced cells. The end point in this direction of specialization occurs in some forms that excavate a cavity and subsequently construct cell clusters from its base. The comb-like clusters of halictines may be rough and irregular or carefully smoothed but not showing the cell outlines (Fig. 239), or they may have the outer cells with their walls so thin that the cell shapes are clearly visible.

Chamber excavation and lining of cells of the cluster usually proceed simultaneously; consequently, the chamber eventually determines the size of the cluster. Thus, in many species the nests are characterized by having several small clusters in close proximity to each other.

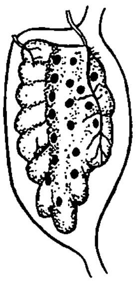
The complexity of the chamber is highly variable among the halictines. In its simplest form it may consist of an expanded section of a lateral which passes close to



239
Megammation insigne

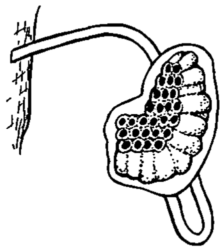


240
Augochlora semiramis

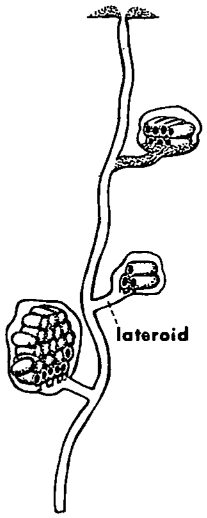


241
Halictus quadricinctus

243
Paroxystoglossa iocasta



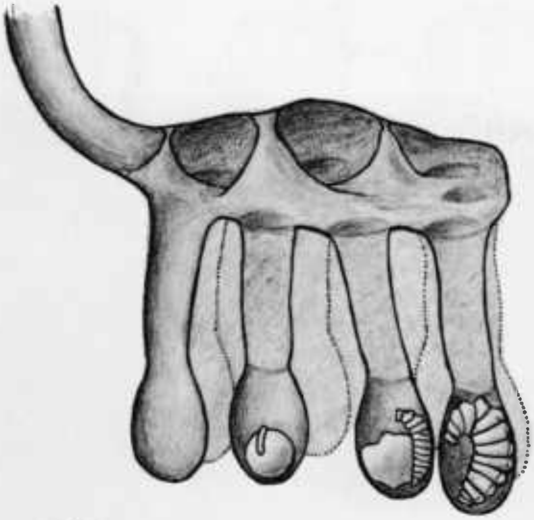
244
Corynura chilensis



245
H. (Lasioglossum) dupiex

246
Corynura apicata

247
Neocorynura polybioides



242
Nomia melanderi

FIGURE 242. Incomplete chamber of *Nomia melanderi* located above cell cluster; soil pillars remain as chamber "support" and cells are dug from the chamber base.

the cell cluster, as in *Augochlora semiramis* (Fig. 240), to the complete chamber of *Halictus quadricinctus* in which the pillars of soil originally present to support the cluster have been removed and the cluster is maintained in the chamber solely by fine rootlets (Fig. 241).

Considerable variation in the extent and elaboration of the chamber is known to occur in nests of *Nomia melanderi*. In some nests the terminus of the burrow is curved horizontally or a horizontal lateral may arise subterminally from the burrow. Short, closely spaced sublaterals are constructed from the lower surface of the lateral, resulting in the formation of a dense cell cluster. A chamber above the cell cluster is absent or difficult to distinguish in such nests. Yet, in the same nesting sites, many or most nests have large chambers over the brood cluster, and the chamber is often provided with a series of pillars between its top and floor (Fig. 242). Chamber construction in this species is influenced by the type of soil in which the nest is constructed (absent in loose sandy soils) as well as by population densities. In heavily populated sites the size of the chamber as well as that of the cluster is limited by the proximity of cells and chambers of an adjacent nesting female. Clusters of four to eight cells and inconspicuous chambers then become the rule, with the female moving to the deeper subsoil to form a second or even a third cluster. With extreme crowding (200 nesting burrows per square foot), there is no evidence of cluster formation or associated chambers. Instead, cells are placed singly wherever space exists and may be arranged continuously from 4 to 22 inches below the soil surface (Stephen, 1960).

◀ **FIGURES 239-241 and 243-247. Nests of cluster and chamber-making halictid bees: *Megommation insigne*—isolated cell cluster with parallel cells (239); *Augochlora semiramis*—cell cluster with chamber as expanded lateral (240); *Halictus quadricinctus*—chamber complete around cluster (241); *Paroxystoglossa jocasta*—chamber in expanded section of main burrow (243); *Corynura chilensis*—chamber and cluster at terminus of main burrow (244); *Halictus (Lasioglossum) duplex*—chamber and cluster at end of lateroid (245); *Corynura apicata*—chamber at end of main burrow, cells irregularly oriented (246); and *Neocorynura polybioides*—incomplete chamber at end of main burrow (247).**

Michener and Lange (1958c) indicate that in the Brazilian *Paroxystoglossa jocasta* a chamber is constructed along the main burrow simply by enlarging a given section of it (Fig. 243). As the size of the cavity increases, cell particles are believed to be removed from the walls and added to an earthen column at its center. The earth is, in fact, molded in such a fashion as to leave space for the cells, which it will ultimately enclose; that is, the cells are built rather than excavated.

Chamber excavations are very often incomplete and difficult to diagnose, or, as in the case of several species, the individuals may or may not form such a cavity (i.e., the species is facultative for chamber formation). There is, in essence, a complete gradation in the extent of chamber formation among the halictine bees, ranging from the undifferentiated cluster to the all but isolated cluster mentioned above. The significance of the chamber is not understood. Sakagami and Michener (1962) suggest that it may facilitate ventilation and drainage, while Verhoeff (1897) states that *Halictus quadricinctus* incubates the immature stages by resting on the back of the cluster, conveying its body heat through the thin cell walls.

Usually cell-cluster formation and the cavity are intimately associated among the halictine bees, but there are numerous examples of cluster makers that do not construct cavities, as well as records of at least two neotropical species in which a cavity is formed without a cluster. These latter species dig their cells into the semi-isolated soil block or else scatter them through it. Sakagami and Michener (1962) present a detailed review of the nest architecture of halictine bees to which the reader is referred.

Classification of Nest Patterns

The classification of the various nest patterns which follows is of descriptive rather than phyletic value. It considers only restricted aspects in the ethology of a species of bee, those of cell construction and the position of the cells in relation to each other and to the access tunnels, if any.

Malyshev (1921, 1935) proposed the most complete classification of nest types among bees, using as his chief criterion "the relation of the shape of the cell to that of the space it occupies." His system is as useful as any classification available, but it involves the usual problems posed by species displaying characteristics intermediate between proposed group limits. The most useful part of his system is included, but with major modifications to make it compatible with contemporary knowledge. Malyshev's terms are included in parentheses as sources of reference if the source of the term is not apparent.

The following classification is based on typical, completed nests of bees, constructed under optimal conditions. There are two main groups of nests: (1) The nests of burrowing bees (odalous) which have an excavated gallery leading from the surface of the substratum to the cell(s); and (2) the nests of nonburrowing bees (anodalous) which lack an excavated tunnel or burrow leading to the cell(s) (tunnels excavated by other insects are frequently used).

Burrowing bees (odalous)

I. One-celled unbranched nests (autodalous). The nests consist of an isolated burrow, terminating in a single cell. Malyshev proposed this category to include only "primitively" one-celled nests. Since there is no reliable method of determining primitiveness as it applies to burrow patterns, we are expanding the group to include any structurally single-celled nest burrow regardless of its origin. *Emphoropsis miserabilis* is the only known northwestern species that belongs here, but the nests of *Perdita maculigera maculipennis, Hesperapis regularis, Halictus (Lasioglossum) victoriellus*, the European *Anthocopa papaveris*, and *Ancyloscelis panamensis* are also single-celled.

II. Branched nests with one cell per branch (heterodalous). The nest consists of a main burrow from which laterals arise, each terminating in a single cell. This pattern, with a wide array of flexibility, is common to most digger bees.

We propose to subdivide this nest pattern on the basis of the length of the branches: A. Branches more than twice as long as the cell; and B. Branches less than twice as long as the cell. Malyshev further subdivides each nest type as follows:

1. Progressive: Cells are added as the main burrow is progressively deepened.
2. Regressive: The first cell is constructed at the maximum depth of the nest after excavation of the main burrow is completed, and each subsequent cell is constructed nearer the nest entrance.
3. Stationary: A series of laterals arise from the bottom of the main burrow, each terminating at a single cell.
4. Dispersed: Laterals terminating at single cells arising from the main burrow, but in no definite sequence.

III. Cells in linear series. Several cells are constructed consecutively in linear fashion along the main burrow and/or its laterals. This pattern is subdivided into:

A. Linear series in unbranched nests (allodalous). The nest lacks lateral galleries and consists only of a main burrow containing all of the cells; the burrow leads directly to the last cell constructed. Malyshev further subdivided "linear" nests into two groups on the basis of the material used to construct the cells: endostechal, in which material from within the nest is used to construct the cells (*Ceratina* spp.); and ectostechal, in which material from outside the nest is used for cell construction (*Osmia, Megachile*).

B. Linear series in branched nests (parodalous). The nest has a main burrow leading to one or more laterals, each containing cells in linear series. The branched series may be subdivided on the basis of the sequence in which each of the laterals is constructed (i.e., progressive, regressive, stationary, and dispersed).

Some species of *Ceratina* and *Megachile* may excavate their own tunnels in firm or punky wood. Under conditions where the substratum does not impede nest expansion, species of *Megachile* may form one or more branches, each with its own linear cell series. Nests of *Megachile inermis* may be either unbranched or branched, depending on the condition of the wood in which it bores (Stephen, 1956) and thus may be included in both categories. In branched nests of *Megachile*, the cells occupy the main burrow as well as its branches. When nests of other bees have branched linear series, the main burrow is not known to be occupied by cells.

IV. Cells in clusters. Cells are formed in clusters along, or at the end of, the main or lateral burrows.

At this point our classification of nest types deviates from Malyshev's. He proposed a division based on the orientation of the cells within the chamber, i.e., cells horizontal and cells vertical. Such a distinction is impossible since the cells of many cluster-forming species are oriented somewhere between the two positions proposed. Indeed, in *Corynura chilensis* (Fig. 244) the cells of the cluster are arranged in an arc-like attitude with some vertical and others horizontal, whereas in *Corynura apicata* the cells are irregularly oriented in an earthen block surrounded by a cavity (Fig. 246).

Nests with cells in clusters can be subdivided into two types, based on the presence or absence of a chamber associated with the cluster. Intergradations sometimes occur between chambered and nonchambered clusters. For example, *Augochlora semiramis* forms a lateral cluster arising directly from the main burrow, but at times may form only an incomplete chamber. In *Nomia melanderi,* isolated, complete nests possess a large chamber above each cluster. Nests in an early stage of construction may have only a trace of a chamber, whereas those in densely populated sites may lack not only a chamber but even the typical cluster. It is not unusual for individual nests of this species to have two or even three smaller sized clusters, again as a result of high populations or suboptimal soil conditions. Nevertheless, since the nest is typically chambered when constructed under optimal conditions, it is best classified under the chambered cluster category.

Chambered nests reach their maximum elaboration among the halictines, and the known structural types have been thoroughly documented by Sakagami and Michener (1962). Their attention was focused on the Halictinae, but we have taken some of their categories and included them in a system which should have wide applicability among bees. For chamber makers, we include the following subtypes:

1. Cluster located in the wall of the main burrow; cluster with the chamber complete or incomplete (*H.* (*Halictus*) *quadrincintus,* Fig. 241).
2. Cluster with chamber complete or incomplete, connected to the main burrow by a lateroid, (*Halictus* (*Lasioglossum*) *duplex,* Fig. 245).
3. Cluster with chamber complete or incomplete, constructed in an enlargement along the main burrow (*Paroxystoglossa jocasta,* Fig. 243), subterminally or terminally (*Nomia melanderi,* Fig. 242; *Neocorynura polybioides,* Fig. 247).

Nonburrowing bees (anodalous)

I. Nests with communal egg chamber. Includes nests of two unrelated taxa, the xylocopine subtribe Allodapini, and certain species and/or certain stages of the nests of *Bombus.*

   A. The nest of the Allodapini consists of a hollow stem or thorn which is often accepted without modification by the nesting female. Eggs are laid in the bottom of the cavity, or are attached to its wall. The nest is devoid of cells; eggs, larvae, and pupae remain in a common communal chamber throughout their entire developmental period.

   B. Most species of *Bombus,* on the other hand, construct a single egg chamber (cell) to accommodate several eggs. The larvae are not isolated from each other until they spin their cocoons.

II. Nests with eggs laid in separate cells. Includes nests built in exposed situations or concealed in preexisting cavities. This category is subdivided according to the manner in which the cells are constructed and the source of the nesting materials employed.

   A. Cells constructed consecutively: Each cell is completed before the next cell is started. The materials from which the cells are constructed are collected, rather than secreted, and consist of materials such as mud, resin, stones, and fibers. Nests of this group can be divided into (1) those that occur in an exposed situation (attached to branches of trees, rocks, walls, etc.); and (2) those that occur in pre-existing crevices or tubular cavities.

   Nests of those in group (1) usually occur as irregular clusters of cells covered by a common ceiling (some *Dianthidium, Chalicodoma*). Those of group (2) most often possess cells in linear series, but they may assume comb-like groups in narrow crevices or be composed of a single cell when in small pockets. The nests of Hylaeinae, most megachilids, and many Xylocopini belong to this group.

   B. Cells constructed serially as a comb. In this group a number of cells are constructed simultaneously. Included are those bees in which social behavior is highly evolved and division of labor well established. The group is further characterized by constructing its cells principally, or exclusively, from materials secreted by the body, and is biologically unique in that many of the cells are not used for brood rearing (Apinae).

Alternative classification of nests

An alternative classification adopted by one of us (Stephen) combines features of Malyshev (1935), Sakagami and Michener (1962), and Iwata (1942). The symbolic designations used by Iwata and by Sakagami and Michener are here associated with descriptive designations as used above.

The following is a translation of the symbols used in the classification:

O — Main burrow

L — Lateral arising from and narrower than main burrow (OpL, laterals with terminal cell (s) constructed progressively down the main burrow; OrL, regressively; OsL, stationary; OdL, dispersed).

L^1 — Lateroid arising from and of same diameter as main burrow.

H — Chamber above, around, or below cell cluster (Hp if partial or incomplete).

C — Cell, (Ch, horizontal cell; Cv, vertical cell; Ci, cell inclined or with irregular orientation; Cb, cell built rather than excavated. Chb indicates a horizontal, built cell, etc.).

C° — Cells wanting or developed after larvae approach maturity.

C′ — Cells clustered, radiating in various directions (the prime mark has the same meaning following Ch, Cv, Ci, and Cb).

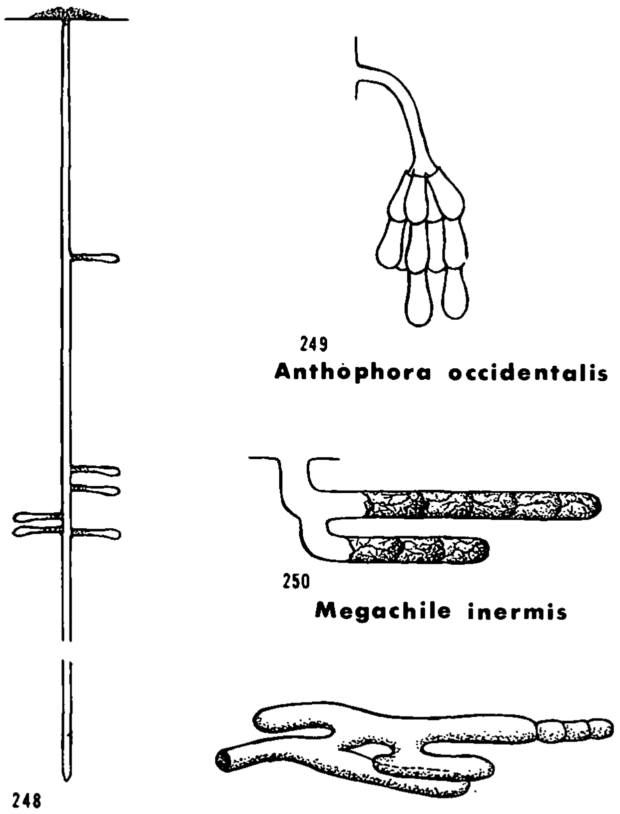
C″ — Cells clustered with axes more or less parallel, often forming a comb (the double prime mark has a similar meaning when used following Ch, Cv, Cb, and Ci).

Cs — Linear series of more than one cell (Csb indicates linear cell series that are built).

B — Lower blind burrow.

n, m — Replication marks.

The following table provides an abbreviated consideration of the descriptive classification, along with the symbolic Iwata formulae which indicate identical nest patterns. In order to include examples of each type of pattern, it has been necessary to draw extensively on ethological data of species outside of the Northwest and, sometimes, outside of North America.



248
H.(Sphecodogastra) texanus

249
Anthophora occidentalis

250
Megachile inermis

251
Xylocopa frontalis

FIGURES 248-251. *Halictus* (*Sphecodogastra*) *texanus* with one-celled branches arising from main burrow (248); *Anthophora occidentalis* with terminal cell cluster (249); *Megachile inermis* branched nest with cells in series (250); and *Xylocopa frontalis* branched nest with cells in series (251).

Classification of Nest Patterns Among the Bees

DESCRIPTIVE	SYMBOLIC (Modified Iwata)	EXAMPLES
Burrowing bees:		
I. One cell in simple unbranched nest	OCv	*Perdita maculigera maculipennis* (Graen.) (Fig. 232)
II. One cell in each branch of branched nest	$\mathrm{O(LC)^n}$	
A. Branches more than twice as long as cell		
1. Branches arising from terminal end of burrow	$\mathrm{Os(LCh)^n}$	*Andrena erythronii* Robt. (Fig. 230)
2. Branches constructed progressively, regressively, or dispersed along burrow	$\mathrm{Op(LCh)^n}$	*Halictus* (*Sphecodogastra*) *texanus* (Cresson) (Fig. 248)
B. Branches short, less than twice as long as cell		
1. Cells constructed progressively or regressively along main burrow	$\mathrm{Or(LCv)^n}$ $\mathrm{Op(LCh)^nB}$	*Andrena viburnella* Graen. (Fig. 228) *Halictus sexcinctus* (Fabr.) (Fig. 226)
2. Cells constructed from one side of a horizontal segment of main burrow	$\mathrm{Or(L'Cv^n)^mB}$	*Nomia triangulifera* Vach. (Fig. 235)
III. Cells in linear series		
A. Simple unbranched nests	OrCsb	*Megachile rotundata* (Fabr.) (Fig. 219)
B. Branched nests (not arranged in a cluster)	$\mathrm{O(LGs)^n}$	
1. Branches arising from terminal end of burrow	$\mathrm{Os(LCs)^n}$	*Colletes michenerianus* Mouré (Fig. 231)
2. Branches constructed progressively, regressively, or dispersed along main burrow	$\mathrm{Or(LCsb)^n}$ $\mathrm{Op(LCs)^nB}$ $\mathrm{Od(LCs)^n}$	*Megachile inermis* (Prov.) (Fig. 250) *Paragapostemon mutabilis* (Spinola) (Fig. 229) *Xylocopa frontalis* (Olivier) (Fig. 251)
IV. Cells formed in clusters		
A. Cluster lacking chamber		
1. Cluster at end of unbranched burrow	$\mathrm{Os(LCl')^n}$	*Anthophora occidentalis* Cresson (Fig. 249)
2. Cluster located in wall of main burrow; not terminal	$\mathrm{Op(CH''^n)^mB}$	*Augochlora semiramis* (Schrottky) (Fig. 240)
B. Cluster with at least a partial chamber		
1. Cluster located in wall of main burrow; not terminal	$\mathrm{OHCh''^nB}$	*Halictus quadricinctus* (Fabr.) (Fig. 241)
2. Clusters and chambers separated from main burrow by a lateroid	$\mathrm{OL'HCh''^nB}$	*Halictus* (L.) *duplex* (D. T.) (Fig. 245)
3. Cluster and chamber in terminal enlargement of main burrow, lateral, or lateroid; cells built or excavated	$\mathrm{OHCv''B}$ $\mathrm{OHCvb''B}$ $\mathrm{OpHCv''^n}$ *or* $\mathrm{Op(HCv''^n)^m}$	*Paroxystoglossa jocasta* (Schrottky) (Fig. 243) *Neocorynura polybioides* (Ducke) (Fig. 247) *Nomia melanderi* Ckll. (Fig. 242) (m = more than one cluster)
Nonburrowing bees:		
I. Eggs laid in communal chamber		
A. Brood never divided by cells	$\mathrm{OC^\circ}$ *or* $\mathrm{C^\circ}$	Allodapini (Figs. 225, 226)
B. Brood eventually walled into separate cells	$\mathrm{(C^\circ)^n}$	Most *Bombus* (Figs. 223, 224)
II. Eggs laid in separate cells		
A. Cells constructed consecutively; cavity (if present) small, tightly enclosing cells; materials mostly gathered	$\mathrm{Cib^n\text{–}(Cib^n)^m}$ *or* $\mathrm{Cib\text{–}(Cib)^m}$ *or* $\mathrm{Chb''^n\text{–}(Chb''^n)^m}$	
1. Cells in exposed situations, usually constructed in clusters		Some *Dianthidium, Chalicodoma* (Fig. 217)
2. Cells concealed in (and tightly enclosed by) tubular or crevice-like cavity		Hylaeinae, most Megachilidae, many Xylocopinae (Figs. 218, 219)
B. Cells constructed serially as a comb; cavity (if present) large; materials mostly secreted	$\mathrm{Chb''^n}$ *or* $\mathrm{(Chb''^n)^m}$	Apinae, some *Bombus* (Figs. 222, 287)

General Nest Features

Nest entrance features

Burrow construction in soil-nesting species involves the excavation of a considerable amount of soil which is usually deposited at or near the entrance. Where they appear, the nest entrance characteristics are nearly as diagnostic as burrow design and cell arrangement and are more readily seen. However, unless a definite turret is formed by those species nesting in vertical banks, steep slopes, or in blown sand, all evidence of how the excavated material was handled is destroyed. Both turrets and the freshly excavated soil at the burrow entrance (*tumulus*) may be disarranged or destroyed by winds and rain, or they may be assimilated into the general profile of a moist soil. Thus in many species the nest entrance structures are present for only a brief period during the active adult life.

The simplest type of entrance structure is a conical (symmetrical) mound with an entrance-exit tunnel at its center. This is the usual type of tumulus for bees that construct a vertical entrance tunnel. It is formed as the excavated material is brought to the surface and pushed over the lip of the hole with the pygidium (*Halictus rubicundus, Nomia melanderi,* Fig. 252). Another type of symmetrical tumulus covers the entrance to the burrow. The bee kicks loose soil into the entrance as it leaves and, upon returning, literally dives into the loose soil filling the crater at the center of the tumulus (*Nomadopsis, Calliopsis, Perdita,* Fig. 253). An eccentric tumulus is constructed by the Old World *Halictus succinctus* (Fig. 254), while *H. farinosus* in western America constructs a tumulus such as that of *Nomia triangulifera,* which conceals a horizontal access to the main burrow (Fig. 255). The melittid, *Hesperapis regularis,* flings the excavated soil away from the entrance in the same manner as a sand wasp, leaving a loose heap of soil or peripheral tumulus to one side of the burrow (Fig. 256). Another group of bees with diagonal burrows near the entrance back out of their holes, holding soil with their forelegs and making rowing motions with their hind legs. This eventually leaves a trail or series of trails with lateral and terminal "moraines." In some cases, as with *Emphoropsis miserabilis,* excavated material is swept so far away from the nest and scattered so gradually that it becomes almost indistinguishable from the surrounding surface.

Turrets

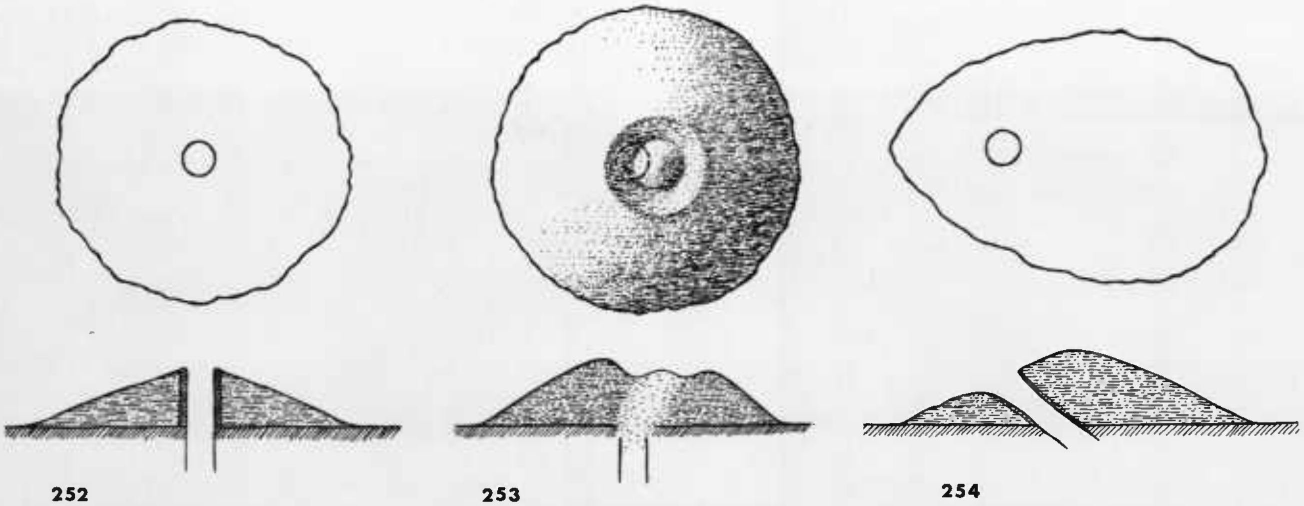
Many bees add moisture to the walls of the burrow that rises through the tumulus, but it is not known whether a secreted material is also added. When the tumulus is blown or washed away, the walls of the burrow remain as a turret. Another type of hidden turret is constructed as a horizontal tunnel after the symmetrical tumulus has been completed. This tunnel opens at the edge of the tumulus, and the original central opening is closed.

Exposed turrets are built by several species of bees by applying small strips of mud to the lip of the burrow, much as a brick-layer would build up the walls of a chimney. The mud is placed on the rim with the mandibles and tamped into position with the pygidium. The turret may be from a few millimeters to an inch or more long and it may be straight or curved; the longer turrets are usually curved. On horizontal ground the excess excavated material is usually piled to form a small ring of loose earth close to the turret. *Ptilothrix,* however, balls up the excess excavated material into small clods which are then scattered around the turret to form a dispersed but distinct ring (Fig. 258). These clods are balanced on the turret rim with the hind legs and propelled with the pygidium. Turrets are particularly common among species of *Anthophora* (Fig. 259) and *Diadasia* that nest either in horizontal or vertical surfaces. Figure 262 illustrates the turrets or chimneys of five species of *Diadasia* and points out the difficulties associated with assigning phyletic significance to biological characteristics. The species *afflicta* does not construct a turret, while that of *enavata* is erect and straight; in *consociata* and *mexicana,* the nest chimneys are erect and sharply curved apically, while in *olivacea* the entrance archway lies flat on the soil surface (see Linsley and MacSwain, 1957 for further details).

The height of the turret, in some species at least, appears to vary with the nesting site. Michener and Lange (1958d) report that *Megommation insigne* has turrets which range from 10 to 13 millimeters where the nests are located on bare ground, but these turrets reach 47 millimeters, or to the tops of the blades of grass, when the nests are located in grassy areas. In the perennial matrifilial colonies of *Halictus* (*Evylaeus*) *marginatus,* the turret is extended from year to year, reaching its maximum length of about 60 millimeters when the colony is about four years old (Fig. 260) (Quénu, 1957).

Nomia triangulifera constructs a turret under the tumulus that acts as a horizontal passage leading from the actual tunnel entrance to the edge of the tumulus. This is always plugged by the bee either as it leaves or as it enters (Fig. 255). A similar tumulus-turret pattern is found in *Halictus farinosus,* except that the lateral tunnel is always left open.

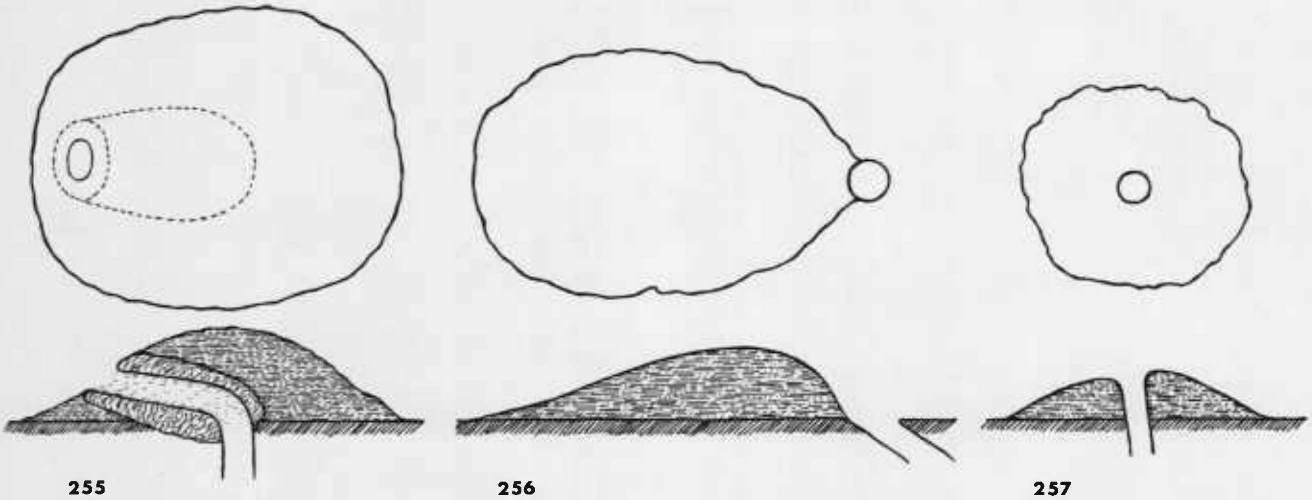
The soil mound of certain tumulus-making species will on occasion have a central "chimney" extending up through the tumulus as a continuation of the burrow. The chimney is, in many respects, typical of those constructed by the anthophorines, with a smooth, polished interior and a rough exterior, but it is very fragile and usually breaks when handled. This "pseudo-chimney" is often found in *Nomia melanderi* and *Andrena ovina* nesting sites. The structures are too uniform and too elaborately fashioned to be accidentally formed. In *N. melanderi,* the turrets are most evident at the time of burrow or cell excavation (Fig. 252).



252
Nomia melanderi

253
Nomadopsis scutellaris

254
Halictus succinctus

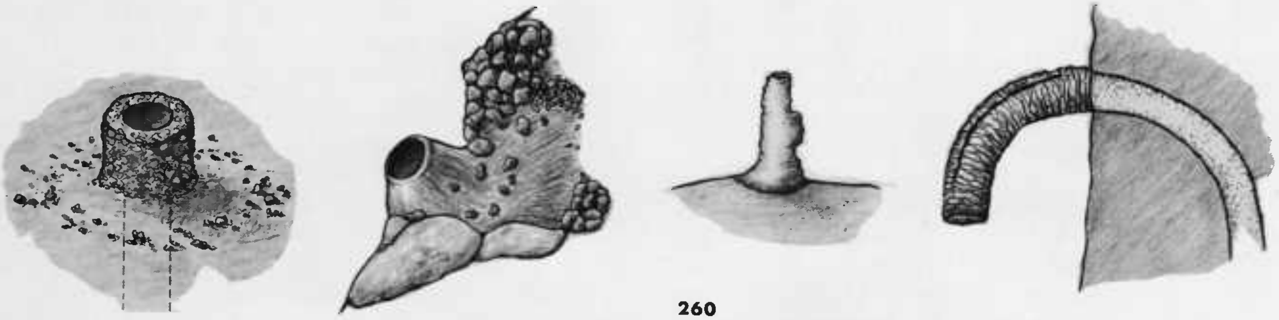


255
N. triangulifera

256
Hesperapis regularis

257
Andrena sp.

FIGURES 252-257. Top and sectional views of nest entrances and tunnels of six bee species.



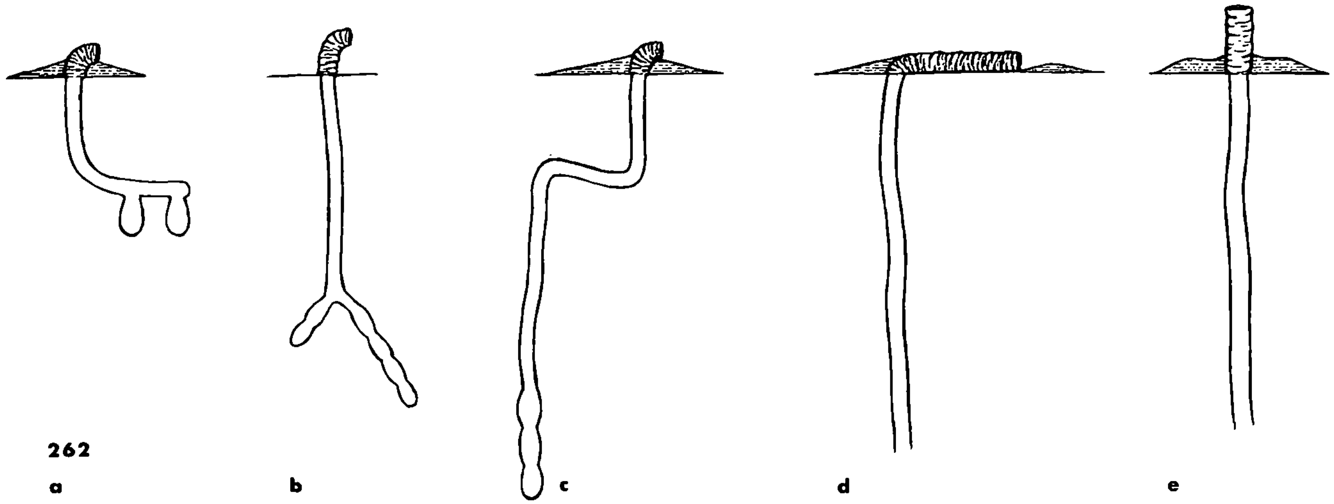
258
Ptilothrix

259
Anthophora

260
H. (Lasioglossum) marginatum

261
Anthophora occidentalis

FIGURES 258-261. Nest turrets of four bee species.



262

a
D. lutzi lutzi

b
D. consociata

c
D. mexicana

d
D. olivacea

e
D. enavata

FIGURE 262. Nest turrets of five species of *Diadasia.*

An interesting feature of turrets constructed by *Anthophora* nesting in vertical banks is a dorsal fissure (Fig. 261). It is incorporated into the structure but its function is obscure. For that matter, the function of the turret is obscure. In exposed situations many turrets are soon damaged or destroyed and most species do not repair or replace them. However, *Augochlorella striata* repairs damaged turrets if such damage occurs early in nest construction (Hicks, 1931).

It has been proposed that chimneys serve as protection against parasites and predators, but parasitism in turret makers seems to be at least as great as in non-turret makers. Malyshev (1935) suggests that chimneys have evolved to prevent nests from filling with dirt. Linsley (1958) feels that these structures might have some social significance since turrets are most common among groups of bees in which gregarious nesting is prevalent. It might well be that the tumulus does serve the purpose suggested by Malyshev in keeping burrows free of loose soil, and that such structures would be even more advantageous to species with gregarious nesting habits. For example, in densely populated artificial nesting sites of *Nomia melanderi* four inches of excavated soil was deposited on the soil surface. The apertures to each nesting tunnel were so close that excavation by one female resulted in the inadvertent addition of soil particles to adjacent tunnels. The presence of chimneys over each burrow prevented plugging of others (Stephen, 1960).

Some of the stingless meliponids (*Trigona*) construct a long waxy chimney at the nest entrance which permits them to defend their nest more readily against invaders. Such turrets are made of cerumen or other materials and extend outward from the nest or inward into the nest. They are usually lined with guard bees.

The outline on page 83 characterizes and classifies most of the entrance features observed at bee nests.

Communal nest entrances in solitary bee nests

Most species of bees have separate nest entrances, even when the nests are closely crowded. However, a few often use communal entrances from which individual nests branch an inch or more below the surface. *Andrena crataegi* females used the same entrance for as many as five nests in an area with hard-packed surface gravel in Logan Canyon, Utah. Rozen (1964) reported finding more than nine females of *Svastra o. obliqua* in a communal nest from which over 100 cells were removed. In those *Xylocopa* which also nest in a hard substrate, communal entrance shafts often extend into the timber across the grain, with separate nests turning parallel to the grain. Although a hard substrate may have some association with communal entrances, *Perdita maculigera maculipennis* was seen by Michener and Ordway (1963) to occasionally use communal entrances in sandy soil. The same species sometimes used several entrances for the same nest.

In the communal European *Halictus sexcinctus,* cells appear as direct offshoots of the main burrow and apparently each female constructs and provisions its own cell. However, there is no particular area along the main burrow that can be said to "belong" to any single female. Claude-Joseph (1926) reports that in certain communal cluster-forming species of *Corynura,* each female labors independently, constructing and provisioning her own series of cells. In other cluster forming species (*Halictus* (*Lasioglossum*) *duplex*), several females were observed provisioning a single cell. Since there is often only one cell open with a number of fe-

Classification of Nest Entrance Characteristics

- I. Without entrance features except plugged or unplugged exit-entrance hole. (Many lodgers and bees nesting in vertical surfaces.)
- II. With entrance tumulus, or turret, or both.
  - A. Entrance features on vertical or steep slopes.
    - 1. With entrance turret (usually no tumulus because of vertical surface). (*Anthophora, Melitoma.*)
    - 2. Without entrance turret (tumulus very asymetrical or nearly absent because of steep slope). (*Colletes ciliatoides.*)
  - B. Entrance features on flat or gently sloping ground (shape of tumulus not affected by slope).
    - 1. With turret.
      - a. Turret hidden by tumulus.
        - *1.* Turret vertical (*Nomia melanderi*).
        - *2.* Turret curved.
          - *a.* Excavated trail in front of tumulus (*Halictus farinosus*).
          - *b.* Without excavated trail in front of tumulus (*Nomia triangulifera*).
      - b. Turret exposed.
        - *1.* Turret curved (*Diadasia consociata,* Fig. 262b).
        - *2.* Turret straight.
          - *a.* Tumulus covering base of turret (*Diadasia mexicana,* Fig. 262c.).
          - *b.* Tumulus represented by pellets expelled at a distance from turret (*Ptilothrix* spp.).
    - 2. Without turret.
      - a. With closed exit-entrance hole (tumulus symetrical and without burrow). (*Nomadopsis, Calliopsis, Perdita,* some *Andrena.*)
      - b. With open exit-entrance hole.
        - *1.* Hole at or near center of tumulus (symmetrical). (Some *Andrena,* Fig. 257, *Halictus rubicundus.*)
        - *2.* Hole off-center on tumulus (eccentria). (*Anthophora bimaculata, Dasypoda plumipes, H. succinctus.*)
        - *3.* Hole at edge of tumulus (peripheral).
          - *a.* With excavated trail surrounded by tumulus. (*Anthophora pacifica.*)
          - *b.* Without excavated trail (*Hesperapis, Anthophora* (*Micranthophora*)).

males engaged in collecting provisions, it is assumed that not only cooperative provisioning but also cooperative nest burrowing and cell construction exist. Communal nests are constructed by some *Euglossa.* Roberts and Dodson (1967) reported that the *Bombus*-like cell clusters of *E. imperialis* and *E. ignita chlorosoma* have resin-lined communal entrance tubes which they close each night.

Although the occupants of most nests with communal entrances are probably not sisters, Michener (1956) and Michener and Lange (1958b) reported that sister bees of the halictine, *Pseudagapostemon divaricatus,* made separate nests from within the natal nests. In some cases the same entrances were also used by nonfilial bees. Michener considered that the principal advantage of the communal entrance in this case was the constant availability of bees to guard the entrance.

There have been reports of communal use of portions of the burrow attributable to circumstances resulting from the close proximity of a number of nesting females. Apparently, portions of the burrows of adjacent nests become fused and these areas of overlap are sequentially occupied by one or another female (i.e., *Perdita opuntiae*). In fact, there have been several records of the fusing of nests of two different species of halictine bees. Use of a common burrow by more than one species of bee has been observed for *Tetralonia speciosa, Tetralonia edwardsi,* and for *Hesperapis carinata* and *Perdita luteola.* In both cases it was obvious that the first species excavated the burrow and the other merely used the upper portion as a means of getting underground. In one instance we found *Megachile inermis, Anthophora* (*Clisodon*) *furcata terminalis,* and *Osmia* sp. using a communal burrow excavated by a beetle in an aspen log.

In contrast to communal entrances among solitary bees, a single nest having several entrances, has been reported for several species in a number of different genera: *Panurgus banksianus* (Nielsen, 1934); *Perdita maculigera maculipennis* (Fig. 232); and *P. opuntiae* (Rozen, 1967.)

Blind burrows

Blind burrows often occur as extensions of the main burrow, or less commonly as branches. These are particularly common in halictine nests (Figs. 235, 240, 248). Sakagami and Michener (1962) believe they serve as homeostatic structures to drain off excess water from the soil and to introduce moisture into the nest from deeper layers during periods of drought. They report that in *Halictus quadricinctus,* which nests in vertical banks, the blind burrow leads to the surface and forms a second entrance below the nest.

Blind burrows sometimes represent mine shafts for obtaining material to line the cells. In *Nomia melanderi* blind laterals were observed to extend several inches into an adjacent area of red clay from which material was taken to line the cells. Blind burrows or blind laterals are not universally present in the nests of the latter species, which would suggest that it is not a predictable characteristic, or possibly, that the structure itself is more evident at certain periods of the adult life.

Nest depth

Nest burrows vary in depth from slightly over one inch (some *Nomadopsis*) to nearly eight feet (*Hesperapis* sp.) (Stage, 1963, personal correspondence). Although some species may be characterized by the depth of their nests, individual variation is often considerable, especially in species that use a variety of soil types. For example, the nests of *Nomia triangulifera* vary from 13 inches deep in hard soil to 44 inches in sand. The alkali bee will not penetrate into extremely moist or poorly drained soil, nor will it penetrate compact clay layers. Its activity, in short, is restricted to soil conditions that are adequate for its occupancy. Very often, under natural conditions, the depth of the hard-pan over which the subsurface moisture is flowing will fluctuate from 6 to 18 inches below the surface. Where the hard pan is extremely shallow, the burrows will extend only two or three inches into the soil and the cell series will be constructed at about four inches. In optimal soils, dense concentrations of nests force some individuals to dig to 22 inches to find space for cell construction.

The overwintered female of *Halictus farinosus* places her cells about 4 inches deep, but her daughters in the same nest place their cells about 12 inches deep. This change in depth may be associated with deeper heat penetration or moisture recession or both, occurring in mid-summer.

Linsley (1958) states the *Xenoglossa fulva,* which nests in ground covered by dense vegetation, digs its tunnel almost three feet deep in an apparent attempt to avoid plant roots. The desert species *Andrena mojavensis,* which nests in sandy and well-drained soils, excavates a deep shaft in order to reach an appropriate moisture level to protect the developing larvae from dessication. Sakagami and Michener (1962) report that *Halictus* (*Lasioglossum*) *duplex* deepens the nesting tunnel as the season progresses, apparently in an attempt to establish the cells in regions of more favorable humidity and temperature. Michener and Lange (1958f) indicate that in *Halictus* (*Choralictus*) *rhytidophorus* nest depth appears to be correlated with the enlargement of the colony rather than with any variation in conditions in soil moisture content. They explain, however, that this may be attributable to the very frequent rains that occurred in the area in which this species was studied and the minor amount of variation in soil moisture that existed in these soils. In *Halictus* (*Evylaeus*) *marginatus* the depth of the nesting tunnel was associated with the age of the nest (Plateaux-Quénu, 1959). The queens of this species may survive for four or five years, in which case the nest becomes progressively deeper extending from approximately 14 inches its first year up to 24 inches by the third year.

Burrow diameter

Burrow diameter is generally determined by the diameter of the adult bee. However, halictine and nomiine bees excavate a main burrow that is somewhat larger than the branch burrows (which have a "normal" diameter). The same subfamilies constrict the "throat" of the main burrow which, as a result, is very close to the diameter of the bee. Legewie (1925) considers the constriction to have evolved along with the defense displayed by members of this group. Sakagami and Michener (1962) report that in *Halictus* (*Lasioglossum*) *duplex* the diameter of the constriction is larger during the spring and smaller during midsummer, apparently to accommodate the change in size of succeeding populations. The ability to modify the diameter of both the nesting burrow and the entrance has been shown to occur in a number of halictine species; rapid repair is made on burrow and burrow entrances when they have been artifically enlarged by investigators. Constriction of the nest aperture and lining of the burrows with soil is believed by Michener to be a usual occurrence among the halictines.

Legewie (1925) reports that the main burrow of *Halictus* (*Evylaeus*) *malachurus* increases in diameter from 5 to 10 millimeters during successive broods in the course of one year. Other investigators have reported no progressive enlargement in other species of the same genus.

Vestibules

The main burrows of burrowing bees frequently have small enlargements, pockets, or short blind-side tunnels near the entrance. The purpose of such enlargements has been variously ascribed to provision of space for turning around, mines for obtaining soil used in lining the burrows and cells, and simply abortive laterals. Since halictid nests often have enlargements near the entrance but do not require them for turning, their use for this purpose is questionable. When enlargements form complete, short loops, as they sometimes do in chamber-making halictines, these would seem to be early or abandoned stages in chamber construction. However, their most common use is probably as soil mines.

Nest cavity linings

As mentioned earlier, many species of burrowing bees line the main burrow with fine particles of soil, probably tamped into place with their pygidium. Nonburrowing bees nesting in tubular cavities often do not make a lining unless the cavity requires modification. *Osmia lignaria,* for example, brings in mud to reduce the diameter of the nest enclosure when necessary, or to smooth out irregularities. When such modification is necessary, the same materials used for making cells or partitions are also used to fill in pockets or to narrow the nest diameter. At least one nonburrower, *Chelostoma minutum,* lines its burrow with a transparent varnish that appears to be secreted. An Australian hylaeine, *Meroglossa torrida,* not only lines its cavity with a transparent secretion but also uses this solution to streak the outside of twigs it inhabits (Michener, 1960a).

Both the burrowing *Colletes* and the nonburrowing *Hylaeus* line part or all of the burrow with a cellophane-like material secreted by glands located in the head, and applied to the nest with the broad bifid tongue. These cellophane-like linings are attached to the cell walls but are not totally infused with the substratum throughout their area of contact.

Lining the main burrow with fine soil particles appears to be the rule among the halictines. Many other bees may do the same thing, but definite evidence is not available. Apparently the "necks" leading into the cells and the "throats" leading into the main burrow are built up and maintained by the addition of soil particles to the respective areas.

Nest plugs

Nonburrowing bees that habitually use existing cavities are particularly consistent in providing nest plugs. This suggests that the plug serves primarily to prevent re-use of the nest hole before the progeny emerge. *Megachile rotundata* has been observed to clean out and re-use completed nests in which a plug had not been constructed or from which one bee had emerged. In such cases, existing cells and prepupae were removed from the nest.

The nest plugs of nonburrowing bees take many forms. The usual *Megachile* nest is plugged with a series of closely spaced circular leaf pieces with the uppermost flush or nearly flush with the surface of the substratum (Fig. 219). *Osmia* has a similar habit, completing the tunnel with macerated leafy material or with cemented soil particles. An interesting habit of some genera is the use of several different materials in sequence. For example, many *Anthidium* use plant down for a centimeter or two above the last cell and then fill the rest of the cavity with gravel. *Dianthidium* often uses loose seeds and small sticks between layers composed of resin and gravel. *Ashmeadiella* sometimes superimposes gravel over a leaf mastic plug.

Burrowing bees usually use substrate materials with which to plug their nests. Burrowing megachilids, of course, are exceptions, although they sometimes use substrate materials in part. A *Megachile* (*Derotropis*) nest burrow was found to contain a few petal pieces about an inch above the cell, with the remainder of the burrow above the petal pieces filled with sand and a few larger objects taken from near the nest entrance.

Hylaeus nearly always seals its burrow entrance with a secreted "cellophane" partition and frequently places another one a few millimeters deeper. This use of a double plug is also common among many megachilids that use partitions for this purpose (*Osmia, Megachile* (*Sayapis*), *Dianthidium*). The usual *Megachile* nest, however, is plugged with a single series of closely spaced, circular leaf pieces.

Many species of burrowing bees make no effort to seal or plug the entrance to the nesting tunnel upon its completion, although it is usually sealed through the action of wind and rain. In some species of *Ceratina* and *Xylocopa,* the proximal partition of the last-formed cell serves as the nest plug.

The extent to which burrows are plugged is highly variable among the burrowing bees. It may consist of plugging (1) the area immediately above each cell (usually a sublateral), (2) the laterals except for the main burrow, (3) the laterals and the main burrow to a point above the last-formed cell, or (4) an area at or near the entrance. Sometimes only the first type of plug is made (*Nomia melanderi*); sometimes the second and fourth types (*Nomadopsis*); sometimes the first and fourth (*Nomia triangulifera*); sometimes the third alone (*Andrena viburnella*); and sometimes the fourth alone (*Ptilothrix*). *Nomia triangulifera* uses the entrance plug only during the period of nest structure and while foraging. In *Nomadopsis,* some other panurgines, and many *Andrena,* the entrance plug is composed of the loose, dry soil in the tumulus "crater." This remains permanently in place and the bee digs through as it enters and leaves the nest but never removes the plug. Many *Anthophora* and some *Colletes* pack the soil of the nest plug tightly upon nest completion, while others merely brush loose soil particles into and over the hole. A few of the halictines, particularly the ones that are subsocial, seal the tunnel entrance from within by plugging the entrance aperture with uncemented bits of soil from the tunnel walls. Malyshev states that this is also true of *Andrena ovina,* but it is certainly not a common practice among solitary bees.

The main tunnels of the panurgines *Psaenythia bicolor, P. interrupta,* and possibly some *Pseudopanurgus* are open but are characterized by the presence of one or more earthen septa along their way. Each system consists of a short length of loose soil, held in place by a narrow layer of more consolidated soil (Rozen, 1967).

Nest concealment

Malyshev (1935) considers entrance plugs to be a form of concealment, but it is not known to what extent this characteristic applies. Sphecid wasps, such as *Am-*

mophila and *Bembix,* carefully brush and tamp the area around their completed nests, effectively hiding them. Comparable behavior is not known among the bees. However, many species seek concealed places in which to establish their nests (under leaves, boards, or clumps of grass). One of the more unusual methods of nest concealment is reported by Malyshev for the European *Osmia bicolor.* This species uses land snail shells as a chamber for its nest and seals the mouth of the shell with the typical green macerated plug. It then proceeds to cover the entire shell with vegetative matter, such as pine needles or grass stems, arranged in a routine plan so as to form a kind of hut over it. Another snail-shell nester, *O. rufohirta,* drags or rolls the shell under a tuft of grass or to an area that provides equally effective concealment, while *O. fossoria* digs a shallow hole adjacent to the shell containing the completed cells and buries it. Thus, in spite of the simplicity of the nest, certain species of *Osmia* display a variety of intricate methods for insuring its protection.

Re-use of the nesting burrows

Nest re-use does not seem to be prevalent among solitary bees. The few documentations on this aspect of bee characteristics do not indicate such behavior. *Nomia melanderi* re-uses the main burrow as a means of access to the soil layer in which a new chamber and a series of cells are constructed. However, the cells from which the adults emerge are firmly repacked with soil as the adults leave and become a part of the generalized substrate. Successive generations of *Exomalopsis chionura* and *Melitoma euglossoides,* both gregarious soil nesters, also utilize emergence burrows (Rozen and MacNeill, 1957). It is suspected that the phenomenon of main burrow re-use by gregarious species may be common.

Nest re-use is particularly prevalent among species that construct cells in substrates other than soil. The simple linear nests of the megachilids, *Colletes, Hylaeus,* some *Ceratina,* are regularly re-used by succeeding generations. The linear branched nests of *Xylocopa* generally become increasingly complex in successive years with additional branches added to accommodate the new brood.

Old cells and cell clusters are usually filled with soil or remain undisturbed. However, Claude-Joseph (1926) reports that old cells of *Corynura chilensis* are partly relined and re-used, while Michener and Lange (1958a) note that in *Augochloropsis sparsilis* cells within a cluster are regularly re-used. In the latter species the old wax is removed from the interior of the cell and replaced with a layer of new wax, beginning with the central cells of the cluster and working peripherally. The latter authors state that there is no evidence to indicate that the cells are not used repeatedly over a period of years. Sakagami and Michener (1962) comment that "reutilization of older cells is a remarkable advancement from the standpoint of labor economy. In the genuine social group (Apinae), bumble bees and stingless bees use their brood cells only once. Even among the honey bees, the Asiatic bee . . . *Apis cerana* Fabricius distinctly avoids the repeated use of old combs. . . .". Only in the genus *Apis* are the cells regularly re-used as brood cells, or as brood and storage cells interchangeably.

Cell Characteristics

The brood cells comprise the basic nest unit. The orientation, shape, and composition of the cells themselves are probably at least as valuable in architectural diagnosis as any other group of characteristics.

Orientation

Cell orientation is usually constant for a species and sometimes for a genus. For example, vertical cells with the posterior end down are characteristic for *Nomia,* some *Andrena,* and *Diadasia;* cells oriented obliquely downward are characteristic of *Nomadopsis* and *Pseudopanurgus;* and cells oriented horizontally are characteristic of some *Halictus.* Worker and drone cells of *Apis* are directed obliquely upward. The brood cells in the genus *Trigona* are usually vertical; however, in at least one meliponine species, *Dactylurina staudingeri,* the cells are almost horizontal (Figs. 221, 222).

The uniformity of cell orientation breaks down at the subfamily level, for all of the above types of orientation are found among the Halictinae and most are found among the Anthophorinae. Cell orientation is particularly variable in species that nest in stems, branches, logs, and human dwellings. Lodger bees generally accept suitable tubular cavities with little regard to their direction. Burrowers in wood orient themselves with the grain without regard to gravity, but at least one species of *Ceratina* was seen to nest only downward into vertical and subvertical stems. Both *Xylocopa* and *Megachile* have been seen to nest in "hanging" holes, thus making it necessary to pack their food up against the "top" of the cell and deposit their egg upside down.

Cell shapes and their purposes

The cells of solitary bees may be barrel shaped, cylindrical, vasiform, or irregular in shape. Among the soil burrowing bees, the brood cells are often pandurate (fiddle-shaped), although in some species the constriction at the upper end is not apparent and this shape is more nearly oval with a flattened or slightly concave top. Among the Halictinae the brood cells are remarkably similar in overall shape. The only obvious difference occurs among some of the social species where there is a size difference in the cells between those used to produce workers and those used to produce queens. Michener (in Sakagami and Michener, 1962) states that a flattened lower surface to the cell is evident particularly in those species in which the brood cells are located in a horizontal position. However, even among species that locate their cells vertically, one of the sides of the cell is always flatter than the other (Fig. 263).

This led him to conclude that the primitive cell position was horizontal.

The cells of lodger bees are usually cylindrical, but if the cells are crowded into odd shaped cavities, their outside walls tend to conform with those of the cavity. Lodger species of *Osmia* accommodate to wide nesting tubes by placing their cell partitions closer together to form short wide cells. In these cases they may become transverse. Leaf-cutting *Megachile* adapt to larger holes by lining their cells with more leaf pieces and slightly shortening the cells. Malyshev (1935) reports that a number of species of *Osmia* construct a small rounded "threshold" or transverse partition at the entrance of what will ultimately be the completed cell. He states that this threshold, first reported by Fabre, is possibly a vestige of what was once a continuous longitudinal wall. In other words, it is an architectural mark as to where that particular cell must end (Fig. 264).

Megachilids nesting in the open (particularly the anthidiines) have roughly cylindrical cells which are usually irregularly placed in a cell group and more or less covered over by the nest-building material to form a single turtle-shaped structure (Fig. 217).

The brood cells of Apidae are usually oval, except in the genus *Apis* in which they are hexagonal-cylindrical. The queen cells of *Apis* are elongate-oval, pendant, and covered with shallow depressions (Fig. 265). In *A. mellifera* L. the male cells are larger than those of the worker, but this is not true in *A. dorsata*. *Bombus* brood cells, each of which usually accommodates several larvae, are irregularly dome-shaped when the larvae are growing (Fig. 223). Upon maturity each larva spins its own oval cocoon which, upon emergence, remains as a cellular vestige. Successive generations of bumble bees tend to have larger individuals; consequently, the cells in the upper layers of the nest are generally larger. Cells of the stingless bees (Meliponinae), unlike those of *Bombus*, are open until fully provisioned. The cells are almost round in some of the more primitive species of *Trigona* (Fig. 288), and more oval and elongate in others (Fig. 289).

Occasionally, blank cells appear interspersed in the cell series of certain species of tube-inhabiting megachilids, xylocopids, and colletids (Fig. 266). Malyshev (1935) considers the uninhabited cells in *Ceratina* as a device which helps the young to emerge from the nest without destroying the other immatures above. He postulates that these cells also may be a means of protecting the larvae against certain parasites. Otherwise, social apids are the only bees that use cells for purposes other than housing brood. *Bombus* constructs special waxen "honey pots" before making a pollen and wax mass in which the first eggs are placed. Later, some species make additional "honey pots" around the periphery of the nest, but most of the surplus honey is stored in the cocoons of emerged brood from which the wax has been stripped. Certain species also construct one or more special pollen storage tubes (Fig. 220).

Some Meliponini construct special pots for honey and pollen which are generally much larger than the brood cells. These pots are segregated in special areas outside of the brood ring (Figs. 221, 222). In some species such pots are also used for storage of pitch or other building materials.

Apis uses worker and drone cells interchangeably for pollen and honey storage or for rearing young. Normally, cells used for pollen surround the central brood area and those used for honey occupy peripheral cells in the central combs as well as the comb in the outer and upper portions of the colony. Frequently, pollen stored in cells is topped with honey, especially when large quantities of nectar are brought into the colony.

Cell caps

Bees that fashion complete cells from substrate materials (Andrenidae, Melittidae, Halictidae, most Anthophoridae) usually construct their cell caps in the form of flat spirals or as inverted conical plugs. In *Andrena viburnella* the inner surface of the plug is deeply concave and is composed of a series of superimposed concentric rings of soil (Fig. 268), whereas in *Nomia* the inner pattern of the cap is distinctly spiralled (Fig. 267). The cap is constructed by placing small strips of material on the upper rim of the open cell. More strips are added in spiral or concentric fashion until the final one placed at the center completes the ceiling. In *Anthophora occidentalis*, at least, the strips are first applied with the mandibles and then tamped in place and smoothed inside and out with the pygidium. Since the bee has difficulty reaching the inner surface of the latter spirals through the small remaining hole, this section of the inner ceiling wall is always somewhat rough. The cell caps of different groups, as seen from the cell, vary from sharply concave (*A. viburnella*) to slightly concave (*Anthophora occidentalis*, Fig. 272) to flat (*Anthophora pacifica*, *A. ursina*).

The pattern and shape of the inner surface of the cell cap is often characteristic at the species level, but at the subfamily level (at least in the Halictinae) both characters lack diagnostic value. Sakagami and Michener (1962) note that among the South American halictines some species fashion plugs with spirally arranged mortar or mortar with concentric rings, while others construct a simple homogenous mortar plug.

At least one genus (*Xylocopa*) that makes only partitions instead of complete cells, also constructs the caps in a spiral pattern from bits of sawdust glued with salivary material. The related *Ceratina* makes plug-like partitions which may simultaneously serve cells on either side, or which may act as a base or cap for only one cell in a series (Fig. 266).

In *Colletes* the "cellophane" cell cap is sometimes fashioned as a lid attached at one point to the neck of the cell before the cell is provisioned. In this position the lid serves as a door that remains open, or is opened each time the bee enters the cell during the provisioning process (*Colletes ciliatoides* (Fig. 274) and *inaequalis,* respectively). There are also reports of species that do not form a cell cap until after the egg is laid (Claude-Joseph, 1926).

Hylaeus apparently constructs the cell cap after the egg is laid. In some cases it is simply a transverse "cellophane" partition, with another partition constructed adjacent to it to form the floor of the next cell. In "oversized" cavities, *Hylaeus cressoni* was observed to merely pull one loose edge of the cell wall to the other side in order to effect its closure. Caps of *Megachile* cells (except in *Sayapis*) are composed of a linear series of circular leaf discs recessed slightly into the upper ends of the cells (Fig. 219). Each disc is glued to the margin of the cell cap. The cell cap of *Megachile* (*Sayapis*) *pugnata* is unique in that it consists of a single leaf disc glued to the margin of the cell wall which is superimposed with several thicknesses of masticated leafy materials (Fig. 269). Most other megachilids construct cell caps as monolithic partitions of masticated materials, apparently fashioned with the mouth parts. The cap of such a cell is fastened to the inside of the cell rim.

In most incomplete cells (i.e., those that lack fabricated cell walls), a separate partition is made for each end of each cell. However, in a few cases (*Osmia lignaria*), the cap of one cell forms the floor of the next. According to Fischer (1955), *Heriades variolosa* supports its cell plug with a ring of secreted "cellophane-like" material placed just inside the partition. This species is also remarkable in making its partitions in two zones, an outer ring of cemented soil particles and an inner disc of resin (Fig. 317).

The social apids form dome-shaped cell caps from masticated wax. In *Bombus* the "cap" is punctured and closed each time provisions are added; in the meliponines the cell is capped after it has been provisioned and the egg laid; and in *Apis* the cell is capped after the larva is full grown. Many social apids construct wax caps over most of their storage cells.

Cell caps or plugs are the rule among the nonparasitic, cell-constructing bees. Except for *Corynura herbsti* and *Colletes inaequalis,* the cell cap or plug is put in place only after oviposition has occurred. Claude-Joseph (1926) reports that *herbsti* plugs the cell immediately after construction, opens it to provision it, and then reseals it after oviposition. However, two solitary species, *Halictus* (*Sphecodogastra*) *texanus* (Kerfoot, 1967) and a tropical colletid, *Ptiloglossa* sp. (Roberts, 1967), and four species of social halictines, *Halictus* (*Evylaeus*) *marginatus,* (*E.*) *malachurus,* (*E.*) *cinctipes,* and (*E.*) *pauxillus,* are known that do not construct cell caps or plugs. Both solitary species construct laterals from the main burrow, each of which terminates in a single cell, and both species backfill the lateral with soil to a point near the cell entrance (Figs. 270, 273). The halictines, on the other hand, have open laterals and the queen and/or workers "tend" the mature larvae, removing feces, dead larvae, and inquilines to one of the basal nest branches (Plateaux-Quénu, 1959; Knerer and Plateaux-Quénu, 1966).

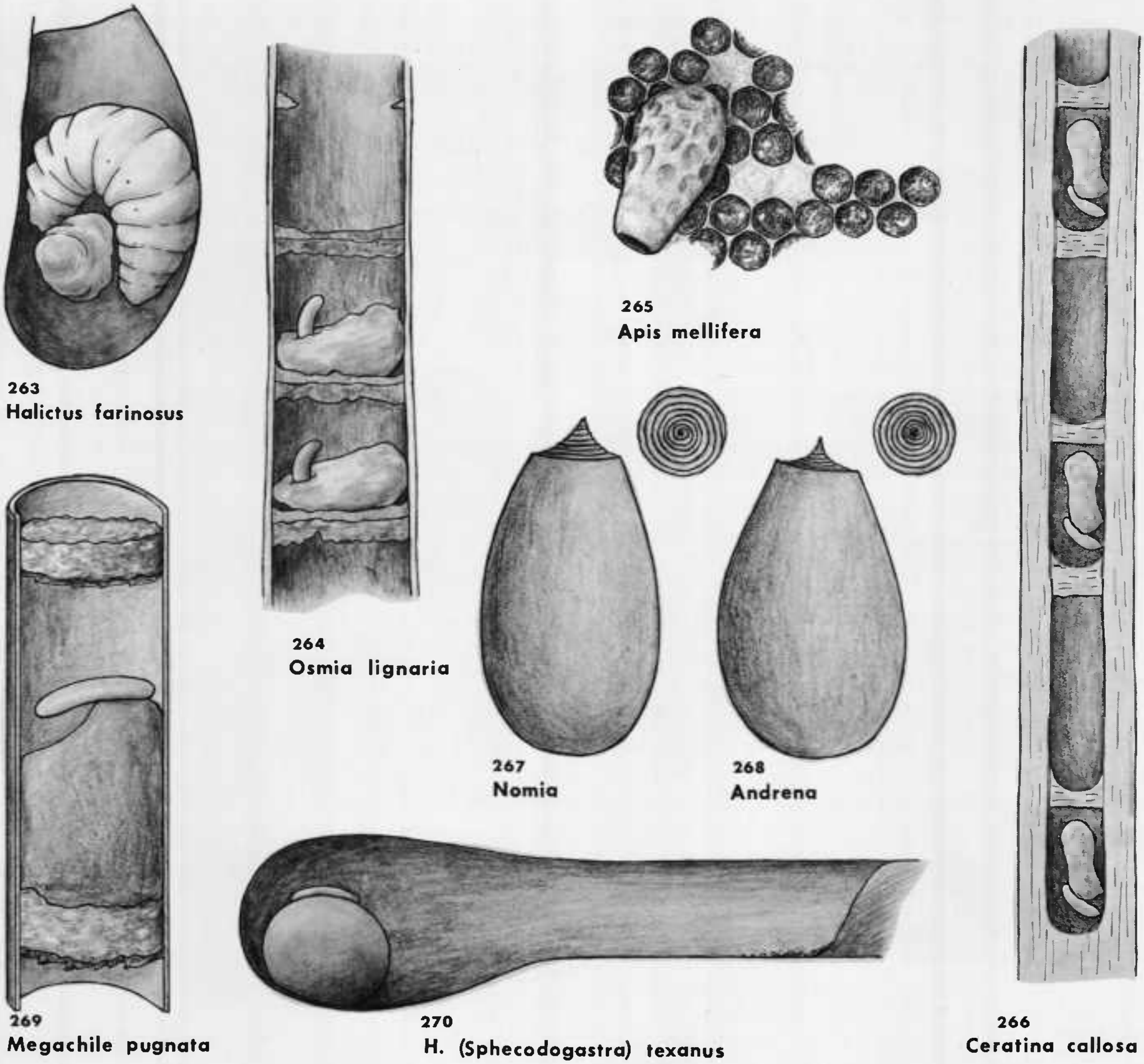
Composition of cells

Cell building materials belong to three categories: secreted, substrate, and foreign. The secreted materials include: (1) True wax used by social apids to construct their cells and other accessory structures. The wax is secreted by plate-like glands on the sterna (*Apis*) or terga (*Bombus,* meliponines), and is molded and applied with the mandibles. (2) A wax-like material used by the Anthophorinae and other bees to line their cells. This "wax" is apparently secreted from the accessory glands of the reproductive tract and is applied with the pygidium. (3) A material used by many andrenids, halictids, melittids, and anthophorids as a thin varnish to the interior surface of their cells. The origin and method of application of this material have not been determined. (4) A cellophane-like material used by colletids to construct their cells and line portions of their burrows or nest cavities. It has been assumed that the salivary glands of this group secrete a liquid material which solidifies as it is applied by the glossa. Daly (1966) described a series of glands on the basal abdominal sterna of *Ceratina dallatorreana* which he believes secrete the invisible waterproof lining of their cells. This may represent a fifth method of lining the cells.

Three additional substances that may prove to be secreted are "metabolic" water used by *Anthophora* (*Micranthophora*) and others to make "cement" for their cells, a glue-like material used by *Megachile* to cement leaf cuttings, and the cellophane-like material used in the cells of *Heriades variolosa* as a "support" for the capping partition (Fischer, 1955).

Cell lining materials are also secreted by larvae. *Colletes ciliatoides* Stephen larvae coat the inner wall of the fecal envelope with a transparent coating, apparently secreted by the malpighian tubules (Torchio, 1965). *Svastra o. obliqua* larvae coat the inner wall of their cells with a smooth, brown anal secretion before defecation or cocoon spinning. The silk cocoon and the anal secretion of the larva, plus the cell lining produced by the parent, form a three-layered structure (Rozen, 1964).

Materials obtained from the substrate include soil (soil-burrowing bees) and plant products (wood-burrowing and lodger bees). The particles of soil or wood are cemented together with water gathered from sources outside of the nest (probably some *Anthophora* and some *Ptilothrix*), with "metabolic" sources, or with substrate moisture. The cemented material is carried in the mandibles and troweled into place with the pygidium. It is interesting to note that *Anthophora* (*Clisidon*) *furcata* and probably *Augochlora* and *Augochlorella* utilize sawdust from their wood substrate to line their cells, which they subsequently coat with a wax-like



263
Halictus farinosus

264
Osmia lignaria

265
Apis mellifera

267
Nomia

268
Andrena

269
Megachile pugnata

270
H. (Sphecodogastra) texanus

266
Ceratina callosa

FIGURES 263-270. **Halictus farinosus* cell with one side flattened—cells are normally horizontal (263); *Osmia lignaria* cell series with threshold marking the apical end of new cell (264); *Apis mellifera* queen cell (265); *Ceratina callosa* cell series with blank cells interspersed (266); *Nomia melanderi* cell and inner view of cell cap with its spiral structure (267); *Andrena viburnella* cell and inner view of the cell cap composed of a series of concentric rings of soil (268); *Megachile pugnata* cell with cell cap composed of one leaf disc and masticated leaves (269); and *Halictus* (*Sphecodogastra*) *texanus* cell and lateral without cell cap (270).**

(*A. furcata*) or varnish-like (*Augochlora* and *Augochlorella*) material.

Foreign materials are gathered in the field for use in cell construction by all nonparasitic megachilids and euglossines, as well as by many *Centris*. Megachilids gather and transport resin, plant down, pebbles and other small objects, mud, leafcuttings, and leaf pulp with their mandibles and/or front two pairs of legs. Euglossines and *Centris* carry resinous materials on their hind tibiae, a characteristic resembling that of apines and meliponines. As indicated in the following outline, these foreign substances may be used singly (*Anthidium*, *Ashmeadiella*) or in combination (*Dianthidium*, some *Osmia*). In some species they are intimately mixed (mud and leaf pulp partitions of *Osmia californica*), whereas in others they are joined but not mixed (the leaf piece and resin cells of *Trachusa* and the leaf piece and mud-resin partitions of *Megachile* (*Sayapis*). Among the megachilids, the same materials are usually used to construct the cells as well as the other nest components.

Summary Outline of Cell Characteristics

I. Cells made of wax and not embedded in, or closely surrounded by, substrate.

- A. Brood cells for males and sterile females hexagonal; those for queens elongate oval and pendant; cells for honey and pollen storage same as those for males and sterile females (*Apis*).
- B. All brood cells oval, usually upright.
  - 1. Brood cells preformed in final position and capped as soon as eggs are laid (Meliponinae).
  - 2. Eggs laid in communal chamber and brood cells continually enlarged and shifted outwardly as larvae grow (*Bombus*).

II. Cells constructed of colorless, transparent (cellophane-like) material closely invested in but not intimately joined with surrounding substrate (Colletidae).

- A. Cells shaped according to previously constructed burrow and with inner walls somewhat pandurate (*Colletes*).
- B. Cells with shape accommodating to preformed tubular holes of various sorts—usually cylindrical or irregular —not pandurate (*Hylaeus*).

III. Cell or cell partitions composed of substrate soil, or "sawdust" from substrate wood or pith.

- A. Inner wall with a visible lining of a secreted material.
  - 1. Lining of a transparent silk-like material insoluble in ether, chloroform, or sulphuric acid.
    - a. Earthen wall of cell stronger than substrate (*Diadasia, Melitoma*).
    - b. Earthen wall of cell little, if any, stronger than substrate.
      - *1.* Lining mixed with soil particles (some halictines).
      - *2.* Lining not mixed with soil particles (*Andrena, Halictus, Tetralonia, Panurginus*).
  - 2. Lining wax-like, opaque, soluble in ether, chloroform, sulphuric acid.
    - a. Earthen wall of cell considerably stronger than substrate (*Anthophora*).
    - b. Earthen wall of cell little, if any, stronger than substrate (*Macropis*).
- B. Inner wall of cell normally without a visible lining.
  - 1. Cells complete (*Nomadopsis, Calliopsis*).
  - 2. Cells composed of transverse partitions (*Xylocopa, Ceratina*).

IV. Cells composed primarily of foreign materials brought into the nest. Cells of many species facultatively complete (enclosed in lining material) or incomplete (composed of transverse partitions only).
In other species the distinction is obligatory.

- A. Cells lined with fine fibers, usually plant down, always complete, (*Anthidium, Callanthidium*).
- B. Cells lined entirely with mud, usually incomplete, (*Osmia* s. str.).
- C. Cells lined with mixture of mud and leaf mastic, usually incomplete, (*Osmia californica*).
- D. Cells with leaf mastic lining surrounded by mud (*Osmia unca*).
- E. Cells lined with leaf mastic alone (many *Osmia*).
- F. Cells lined with resin alone, usually incomplete, (*Chelostomoides angelarum*).
- G. Cells lined with leaf pieces alone (most *Megachile,* some *Hoplitis*).
- H. Cells lined with leaf pieces and resin, complete, (*Trachusa*).
- I. Cells lined with pitch and gravel (*Dianthidium, Chelostoma minutum* Crawf.).
- J. Cell partitions composed of mud-leaf mastic and one leaf piece (*Megachile* (*Sayapis*) *pugnata*).

Nest building materials

In most cases the materials which bees use to fabricate cells are the same as those used to construct other portions of the nest. However, as indicated in the section dealing with nest plugs, other plugs, especially loose gravel and miscellaneous bits of debris, are used by some megachilids for plugging their nests. Furthermore, the social Apinae usually use other than cell-building materials in other parts of the nest.

Bombus usually establishes its nest within or adjacent to a supply of fibrous materials (rodent nests, car seats, buffalo robes, and so forth) with which it surrounds its nest. The fibers are separated and recombined as a fluffy envelope around the wax cells and canopy. When necessary, bumble bees shread fibers from such items as bark and cloth and transport them short distances to the nest.

Apis gathers resin (propolis) which it transports on its corbiculae and uses to seal off openings to the nest cavity or to wall off foreign objects such as dead mice in the nest.

Meliponines gather and transport a variety of substances including resins, grease, soil, excrement, and plant wax on their corbiculae. The resins and soils are often mixed with secreted wax to form the cerumen with which they make the cavitaceous envelopes surrounding the combs, the various struts supporting the nest complex, and the entrance turrets, if any. Resin of a particularly sticky nature is sometimes attached to the inner lining of the entrance.

Number of cells per nest

The number of cells per nest ranges from one to several thousand. Most solitary soil-burrowing species make only one nest, which contains as many cells as foraging conditions and the reproductive potential of the bees allow. Nests of *Nomia melanderi* may contain from 5 to 24 cells, depending upon the availability of forage and the quality of the substrate in which they are nesting. A few soil-burrowing species characteristically limit the number of cells per nest and make several nests. *Emphoropsis miserabilis* constructs only one cell per nest (Stephen and Torchio, 1961a) as does *Hesperapis regularis* (Burdick and Torchio, 1959), whereas *Ptilothrix sumichrasti* constructs up to about five (Linsley, MacSwain, and Smith, 1956).

The number of cells per nest constructed by the nonburrowing (lodger) bees is extremely variable between individuals because of the size variation in selected nest cavities. Some species of *Osmia* normally select small pockets in rocks that accommodate only one cell, but the same species may place several cells in somewhat larger holes. *Megachile rotundata* will accept tunnels which accommodate only a single cell but more commonly uses long tubular cavities in which it places as many as 20 cells. The reproductive potential of this species is even higher (up to 40 eggs), but there seems to be an upper limit to the number of cells it places in a single tube, independent of its length.

Social bees have a higher reproductive potential, but they usually make only one nest within a single season. Furthermore, more than one reproductive female may contribute to the number of eggs laid. Consequently, their nests usually have a much larger number of cells than do the nests of most solitary bees. In social halictines, the number of cells per nest varies according to the number of generations and the number and fecundity of reproductive individuals remaining with the colony. The cells are not re-used but are often filled to permit new cell excavations within the same general area in the same season. A total of 548 cells was recorded in one nest of *Halictus* (*Evylaeus*) *marginatus,* which also contained 209 active females at the time it was unearthed (Quénu, 1957).

In *Bombus* the number of cells per nest rarely exceeds a few hundred. Michener and Laberge (1954) reported a nest of *Bombus medius* from Brazil with 2,157 cells, of which 127 contained immatures. *Bombus* cells are not re-used for brood, but some of the old cocoons may be filled with honey or pollen and in this way add to the nest architecture. The queen is responsible for egg laying until late in the season, at which time some workers may lay unfertilized eggs.

The number of cells in *Apis* colonies is generally much greater than in those of *Bombus* or the halictines. Although only one individual (the queen) is normally responsible for egg laying, she is far more fecund than any other bee. Cells are re-used many times and both new and old cells are used for honey and pollen storage as well. Consequently, the number of cells per nest in use at one time is determined by the reproductive capacities of the queen and the foraging abilities of the workers. Large colonies of *Apis mellifera* may have hundreds of thousands of cells in use at one time. The nests of meliponines are highly variable in cell numbers; the nests of some species are little more populous than those of *Bombus,* whereas those of other species rival nests of *Apis* in total number of cells.

Perhaps one reason why social apids have developed more populous colonies than social halictines rests with the nature of the nesting material. As the social organization of the halictines has advanced, the nest has become comb-like and is often surrounded by an excavation. The fragile earthen cells and pillars restrict the number of cells that can readily be constructed in a single comb. Conversely, apid nests are not so restricted because of the relatively strong and light nature of the wax from which they are constructed.

Provisions

Bees can be distinguished from nearly all other aculeate Hymenoptera by their habit of providing their young with a diet of pollen or honey or both. Most wasps, on the other hand, provide their nests with material of animal origin. All of the known genera of the solitary vespoid wasp family Masaridae, except *Euparagia,* and all known species of the social vespid genus *Brachygastra* feed their larvae pollen. Pollen, often found in the nests of *Polistes,* is reported to be fed to the newly emerged young. Honey ants, *Prenolepis,* store honey using specialized members of their own colonies as honey "receptacles." A variety of other species of ants feed their young a partial diet of honey and pollen, but in none of them is this an exclusive habit.

Provisions for adults

Apis, Bombus, meliponines, and at least some xylocopines are the only bees known to store food in the nests for adult consumption. *Xylocopa virginica* was reported by Rau (1933) to store pollen cakes in its burrows during the fall for use by overwintering adults of both sexes. As far as is known, *Bombus* (Fig. 224) and the meliponines (Fig. 221) always store honey and pollen in separate cells, distinct and usually well removed (at least in the meliponines) from those used for brood. These stores are drawn upon by adults as well as larvae. *Apis* usually stores its honey in separate cells remote from the brood. These cells are capped with wax after they have been filled and the honey has evaporated sufficiently. The pollen of *Apis* is usually packed into cells in the area surrounding the "brood nest," whereas the cells filled with pollen remain uncapped. However, if only the basal half or two-thirds contains pollen, the remainder is filled with honey and the cell is capped. Apparently, nearly all of the food stored in *Apis* nests is destined for adult consumption, although pollen grains often appear in cells with larvae as well as in larval feces. Some apiculturists believe this represents accidental contamination rather than purposeful feeding of pollen to the larvae.

Provisioning for the larvae

It has been generally considered that two methods of provisioning exist among bees; progressive and mass. In progressive provisioning, the food is supplied to the larvae at intervals, the amount and interval of feeding corresponding to the needs of the individual larva. In mass provisioning, a full complement of food is provided each cell before the egg is laid. As indicated below, the distinction between the two types of provisioning is not nearly as sharp as the above definitions suggest.

Apis is the only genus of bees that feeds its larva exclusively or nearly exclusively with glandular food. The glandular food fed to the queen larva is called "royal jelly." Worker and drone larvae are fed royal jelly for the first two or three days and a somewhat different material called "worker jelly" thereafter. The degree to which "worker jelly" is supplemented with honey, and possibly pollen, has not yet been ascertained. Qualitative differences in the food of queen and worker larvae are apparently responsible, at least in part, for caste differentiation. In other social bees, caste differentiation appears to be based entirely on quantitative differences in feeding (*Trigona,* the halictines), or on hereditary factors (*Melipona*).

Progressive provisioning

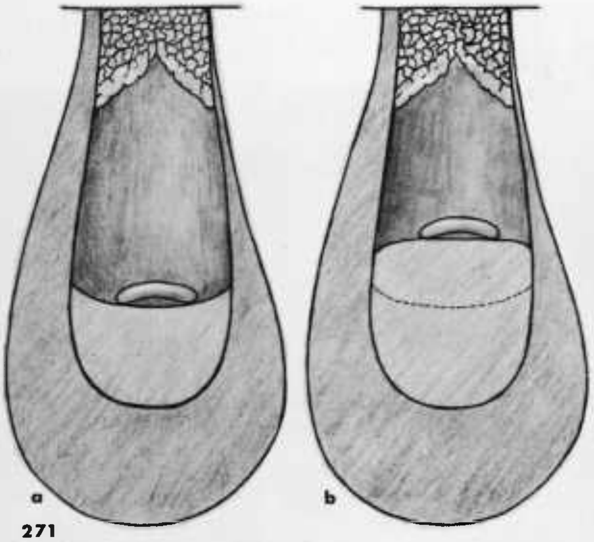
Apis feeds its larvae progressively in open cells, and there is no reciprocal passage of materials between larvae and adults as there is in most social insects other than bees. Worker and male larvae are fed more or less as need arises, but queen larvae are given large quantities of royal jelly in advance of their need, especially in later stages. This method of provisioning is intermediate to the mass provisioning characteristic of most bees.

Provisioning in communal chambers. Bombus and almost all Allodapini are the only taxa, other than *Apis,* known to practice progressive provisioning. In addition, the allodapines and most *Bombus* are unique in that they provision the larvae in communal chambers.

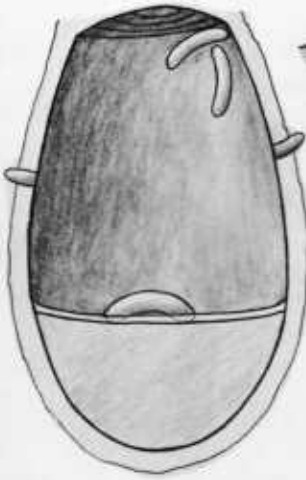
Bombus queens provision the egg chamber of their first brood before the eggs are laid, but they add more food to the cell before the larvae mature. The later egg chambers of members of this genus are provisioned in a variety of ways. Species of the subgenera *Fervidobombus* and *Alpinobombus* provide a pollen base to the egg cells on which the eggs are laid. The larvae are fed by means of pollen-pockets, in which the pollen is packed beneath them, or by wax-pollen pockets located on the side of the brood masses. The larvae develop communally and are fed honey by workers which bite holes in the cell cap and disgorge the honey directly into the cell. The holes are repaired immediately after the larvae have been fed. *Pyrobombus,* on the other hand, usually primes each of the egg cells with a layer of pollen, after which the larvae are fed both pollen and honey through holes cut in the cell surface.

The worker broods of the subgenera *Bombias, Bombus,* and *Cullumanobombus,* as well as the queen and male broods of *Fervidobombus* and *Alpinobombus,* contain eggs in unprimed cells (Hobbs, 1964). In the latter subgenera, the larvae are provisioned progressively from the time of eclosion until they are fully mature. Most, if not all, of the communally reared *Bombus* larvae are isolated from each other only after each mature larva spins its cocoon (Fig. 223). Thus, queens of all species of *Bombus* stock their first brood cells with quantities of pollen prior to oviposition. Subsequent brood cells may be partially provisioned with pollen (*Fervidobombus, Pyrobombus,* etc.) or may be unprimed (*Bombias, Bombus,* etc.). Aside from the first brood, definitive progressive provisioning occurs only in *Bombias.*

The allodapines, depending upon the species, feed their larvae individually and progressively, or provide a lump of pollen upon which the newly hatched larvae feed communally. Additional pollen is provided as the larvae develop. Those species that feed their larvae progressively from eclosion, first feed them a secreted fluid and later add pollen to their diet.

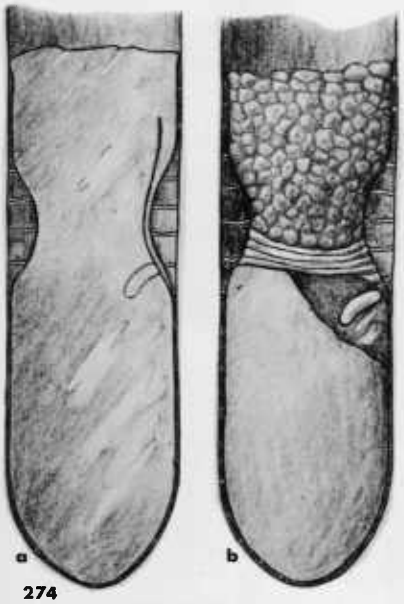


271
Svastra obliqua obliqua



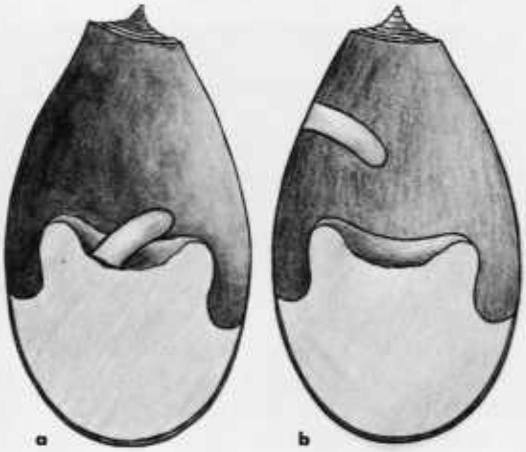
272
Xeromelecta californica and Triepeolus dacotensis eggs in Anthophora occidentalis cell

273
Ptiloglossa sp.



274
Colletes ciliatoides

275
Anthophora urbana



276
Andrena virburnella

FIGURES 271-276. *Svasta obliqua* completed cell (271a) and cell with provisions expanded due to fermentation (271b); *Anthophora occidentalis* completed cell (272) showing provisions layered with a film of nectar in which the host egg floats (eggs of the parasite *Triepeolus* are embedded in the cell wall and eggs of the parasite *Xeromelecta* are attached to the inside of the cell cap); *Ptiloglossa* sp. cell with fluid provisions on which the host egg floats (273); *Colletes ciliatoides* cells (274); unprovisioned cell with cellophane-like lining and cell cap of the same material folded back against the wall (274a) and completed cell sealed with several layers of secreted material superimposed with soil and sand (274b); *Anthophora urbana* completed cell (275); and *Andrena viburnella* completed cells (276): usual egg placement (276a) and egg placement when provisions are covered with water (276b).

Mass provisioning

Community provisioning. Meliponines (Fig. 264) and many semi-social halictines mass-provision brood cells and seal them as soon as the eggs are laid. In this way their provisioning habits resemble those of solitary bees. However, they differ in that more than one bee contributes to the provisioning of each cell. This is universally true of the meliponines but occurs only in the later generations and probably only in certain cells of the halictines.

Types of provisions. Food stored by bees ranges from liquid honey to nearly dry, friable masses of pollen. Mass provisioned food (except for the royal jelly fed to queen honey bee larvae) is always a mixture of pollen and honey, but it may include a glandular additive. The provisions may have the consistency of gruel, jelly, or dough, depending upon the concentration and quantity of honey they contain. Moisture may be absorbed or lost after the egg is laid (*Osmia* spp.), or the provisions may ferment (*Svastra*, Fig. 271), thus changing the consistency of the stores from one category to another.

Provisions may be packed into the bottom of the cell and thereby assume no form other than that of the cell. Usually such provisions are gruel-like or jelly-like (most Colletidae, Anthophorini, Eucerini, many megachilids) but occasionally they are dough-like (some *Osmia, Lithurgus*). Some species within this group add a thin liquid layer, presumably composed of nectar, over the provisions (Fig. 272). This may serve to prevent desiccation of the provisions as well as eggs and young larvae. The Anthophorini, most of which form such a nectar pool, are characterized by the cheese-like odor of their provisions. The same odor has been detected in the abdominal venter of the adult female, apparently associated with a series of glands (unpublished). There is some evidence that this odor serves as an attractant to the nesting site. Thorpe and Chemsak (1964) reported that provisions of *Melissodes pallidisignata* offer a moderately strong odor of fermentation.

The extremely fluid provisions of *Ptiloglossa* sp. are unusual among the bees. In this species the bottom half of the food mass consists of a ropy mixture of pollen, nectar, and presumably some fungal spores, while the upper half appears to consist of nectar (Fig. 273) (Roberts, personal communication).

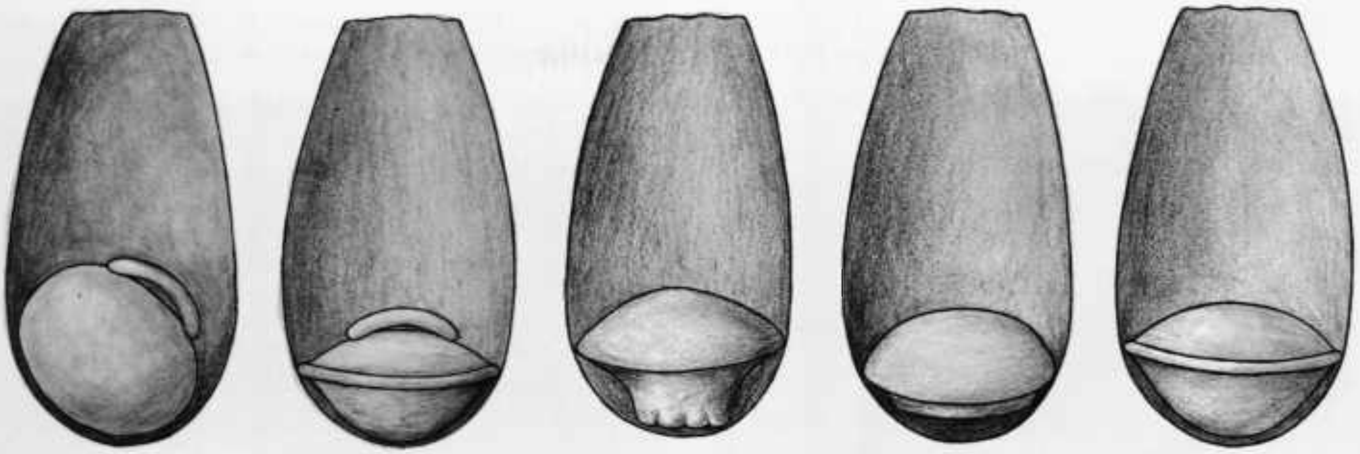
Except for *Hylaeus,* which transports pollen and nectar in its honey stomach and provides equally fluid material with each load, most bees add only a little nectar as the pollen store is being accumulated in the cell. Each female then gives the food mass a final soaking with nectar obtained on a field trip made essentially for that purpose. It is this behavior which is responsible for the surface pool of nectar over the pollen stores of species mentioned above. Cells in which provisions are packed in a moist condition, or to which surface nectar is added, usually have special linings that limit water loss or absorption to and from the surrounding substratum (colletids, *Anthophora,* Figs. 274, 275).

Many bee species mold their provisions into loaves (most *Xylocopa, Ceratina*), balls (halictids, melittids, most andrenids, *Dufourea*), or provide the food masses with special shapes or features (*Dasypoda, Exomalopsis, Xylocopa c. californica*) which limit contact of the provisions with the substratum and prevent water loss or absorption. In many *Osmia,* some *Megachile,* and some *Andrena* (Fig. 276) the food mass is only partially molded so that about half of its surface is in contact with the cell walls. Partially molded masses tend to be variable in shape and size within a species, whereas the size and shape of completely molded provisions are less variable infraspecifically.

Completely molded provisions would seem to limit the need for an impervious cell lining. However, *Andrena* and halictids, which usually have completely molded provisions, line their cells although they leave the cell caps unlined.

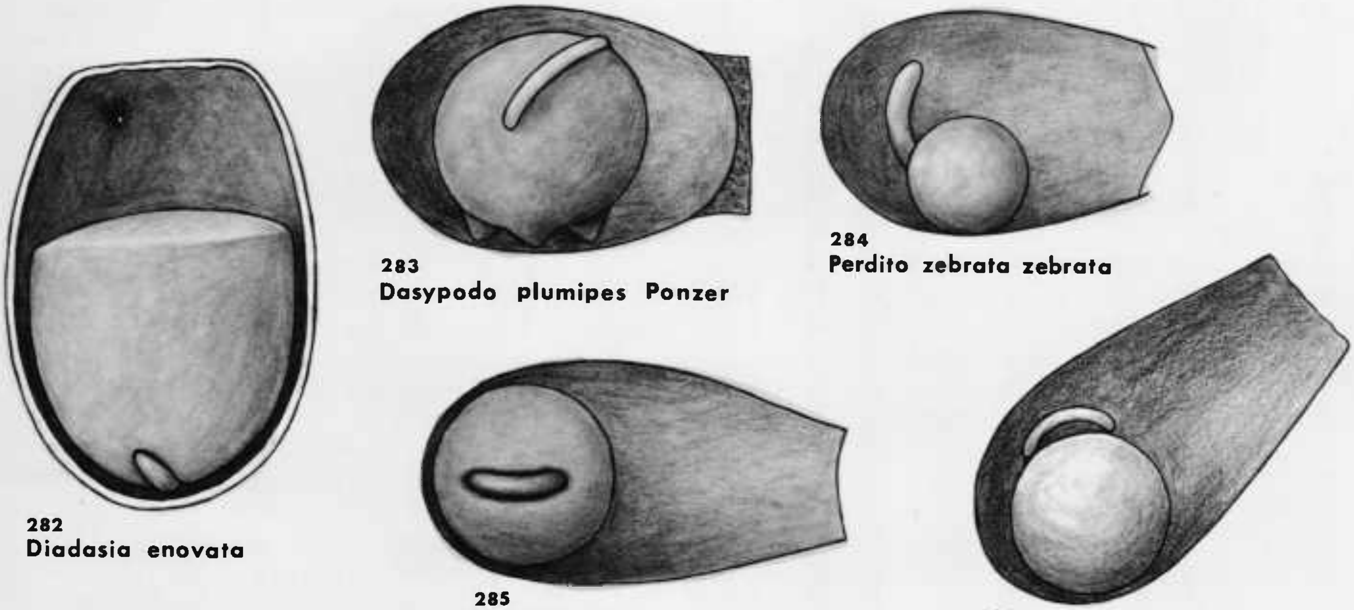
Cells of *Hesperapis* and *Perdita* have no waxy or water-impermeable lining, but their pollen balls are exceptionally smooth and, in *Perdita* at least, they are coated with a thin waxy layer. Other panurgine genera, *Nomadopsis* and *Calliopsis,* have both a waxy coat on their pollen balls and linings on the inner walls of the cells, although the cell lining is exceedingly thin in some species (Rozen, 1967). Females of the European melittid, *Dasypoda plumipes,* fashion three short "legs" at the base of the pollen ball which minimize contact of the pollen mass with the unlined cell wall beneath it (Fig. 283). Other specialized methods of limiting or restricting contact between provisions and cell wall include equatorial rims on pollen balls of *Nomia triangulifera, N. nevadensis,* and *N. heteropoda* (Figs. 278-281), which are the only portions in contact with the wall; and the dry crumbs of pollen with which several species of *Osmia* (*unca, rufa*) line the contact zone. All of the known emphorines shape their pollen mass to conform with the lower half of the cell (Fig. 282), but the mass contacts the cell walls only at a few points. This permits the female to place an egg at the base of the pollen mass in the manner discussed below.

The shape of the food mass is often characteristic of bee groups at the generic and/or specific level, but (like many other biological characteristics) there are too many exceptions to permit extensive generalization for the higher taxa. However, all of the known emphorini shape their provisions to conform with the bottom and sides of the cell and provide an elongate slot underneath the pollen mass for the reception of the egg. The Anthophorini and the Eucerini can be characterized similarly by the pasty or gruel-like unmolded pollen mass in the bottom half or more of each cell. At the generic level, the pollen balls of all known species of *Halictus* are remarkably similar in conformation. They are essentially circular in outline when viewed from above and are nearly always provided with a shallow



277 **Nomia melanderi**
278 **N. triangulifera**
279 **N. nevadensis arizonensis**
280 **N. nevadensis bakeri**
281 **N. heteropoda**

Figures 277-281. Provisions of five species of *Nomia.*



282 **Diadasia enavata**
283 **Dasypoda plumipes Panzer**
284 **Perdita zebrata zebrata**
285 **Halictus**
286 **Andrena**

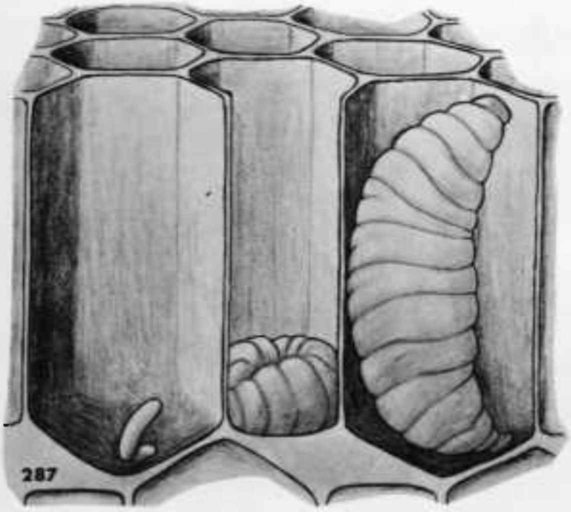
Figures 282-286. Provisions and egg placement in completed cells of five bee species.

"saddle" on the top in which the egg is placed (Fig. 285). The pollen balls of andrenids are formed as spheres (*Nomadopsis, Perdita,* Fig. 284, most *Andrena,* i.e., *bipunctata,* Fig. 286), or flattened spheres (*Panurgus,* most *Panurginus, Pseudopanurgus, Melitturga*). However, in certain species of *Andrena* (Stephen, 1965) and *Panurginus* (i.e., *labiatus,* Malyshev, 1924) the provisions are only partially formed and placed at the end of the cell. The pollen balls of *Dufourea mulleri* are also spherical, but many are provided with a shallow "saddle" on top of which the egg is laid. The groove is also formed on the upper surface of the ball and is nearly as wide as the egg, but only half as long.

With the exception of the colletids, shaping of the pollen mass is habitual with short-tongued bees. Almost all colletids provision the cell with a pasty or gruel-like pollen mass. There are, however, genera within the family (tribe Paracolletini) that form their provision into pollen balls similar to those of other short-tongued taxa (Michener and Lange, 1957). All known species of *Andrena,* except *A. viburnella, A. heterura,* and probably *A. perplexa,* mold their provisions into distinct spheres. These species pack a pasty pollen-nectar admixture into the bottom two fifths of the cell but mold the surface of the food mass. The pollen mass of *A. viburnella* bears a circular crater surrounding the egg (Fig. 276). The provisions of all known species of *Nomia* are completely molded into a form separate from, but resting on, the substrate. The pollen masses vary from the completely symmetrical flattened sphere of *N. melanderi* to the equatorially rimmed sphere of *N. triangulifera* and the keeled provisions of *N. nevadensis arizonensis* (Figs. 278, 279). Indeed, in the latter species there is a distinct and consistent difference in the pollen mass between the two subspecies, *bakeri* and *arizonensis* (Figs. 279, 280).

Summary of Types of Provisions of Individual Brood Cells

- I. Provisions provided more or less progressively to developing larva.
  - A. Provisions composed entirely or almost entirely of secreted material fed to developing larva in open cell (*Apis,* Fig. 287).
  - B. Provisions composed of admixture of pollen and nectar provided to developing larva(e) in sealed cell (later broods of *Bombus*).
- II. Provisions provided *in toto* prior to oviposition and cell closure.
  - A. Provisions unmolded; packed into cell with upper surface flat, irregular, or slightly concave.
    - 1. Provisions more or less homogeneous throughout, lacking special chamber or cavity for egg; egg exposed.
      - a. Pollen mass pasty or gruel-like but without a "pool" on its upper surface (eucerines, Fig. 271; most anthidiines; most colletids, Fig. 274; some *Trigona,* Fig. 288).
      - b. Pollen mass covered with a "pool" or thin liquid (most *Anthophora,* Fig. 272; some *Emphoropsis;* some *Trigona,* Fig. 289; some *Megachile*).
      - c. Upper half of provisions consisting of nectar, lower half of ropy pollen (*Ptiloglossa* sp., Fig. 273).
    - 2. Provisions homogeneous, except for a concealed egg chamber; egg completely concealed in food mass (*Lithurgus,* Fig. 290; *Osmia californica,* Fig 291).
  - B. Provisions with surface molded; lower half or more of food mass unshaped and in direct contact with cell wall.
    - 1. Food mass with median elevated, crater-like façade in which the egg is usually placed (*Andrena viburnella,* Fig. 276).
    - 2. Food mass with surface convex or irregular, but with a small pocket on upper surface for insertion of posterior end of egg (*Osmia* spp., Fig. 292).
  - C. Provisions completely molded; constructed into a complete form separate from, but resting on, the substrate.
    - 1. Underside of provisions with an elongate slot for reception of egg; provisions separate from, but shaped to conform with, bottom and sides of cell (Emphorini, Fig. 282).
    - 2. Provisions elongate or loaf-shaped.
      - a. Provisions contacting substrate at one or more specifically formed projections (*Exomalopsis,* Fig. 293; *Xylocopa,* Fig. 294).
      - b. Provisions somewhat irregular or with projections, but these apparently not designed as pedestals (Some *Ceratina,* some *Xylocopa,* Fig. 266).
    - 3. Provisions spherical, spheroidal, or elliptical, lacking ridges, rims, projections, grooves, or other irregularities.
      - a. Provisions symmetrical and spherical (*Nomadopsis; Perdita* (Fig. 284); *Dufourea;* most *Andrena*).
      - b. Provisions symmetrical, in form of flattened spheres (*Nomia melanderi,* Fig. 277; *Pseudopanurgus*).
    - 4. Provisions essentially circular in outline when viewed from above, but with ridges, rims, grooves, projections, or other irregularities.
      - a. With a horizontal equatorial rim.
        - *1.* Underside essentially like upper side, not produced (*Nomia triangulifera,* Fig. 278).
        - *2.* Underside somewhat produced to form a broad pedestal (*Nomia nevadensis arizonensis,* Fig. 279).
      - b. Without an equatorial rim.
        - *1.* Upper surface of provisions with a broad, shallow saddle in which the egg is placed (*Halictus,* Fig. 285).
        - *2.* Under surface with a tripod arrangement of short projections (*Dasypoda,* Fig. 283).



287

Apis mellifera

288
Trigona australis

289
Trigona carbonaria

290
Lithurgus fuscipennis

Figures 287-290. *Apis mellifera* egg, young larva, and mature larva in unsealed cells (287); *Trigona australis* brood cells with egg inserted into semifluid provisions (288); *Trigona carbonaria* provisioned cells and two honey pots (289); and *Lithurgus fuscipennis* completed brood cell with egg concealed in chamber (290).

Oviposition and Development

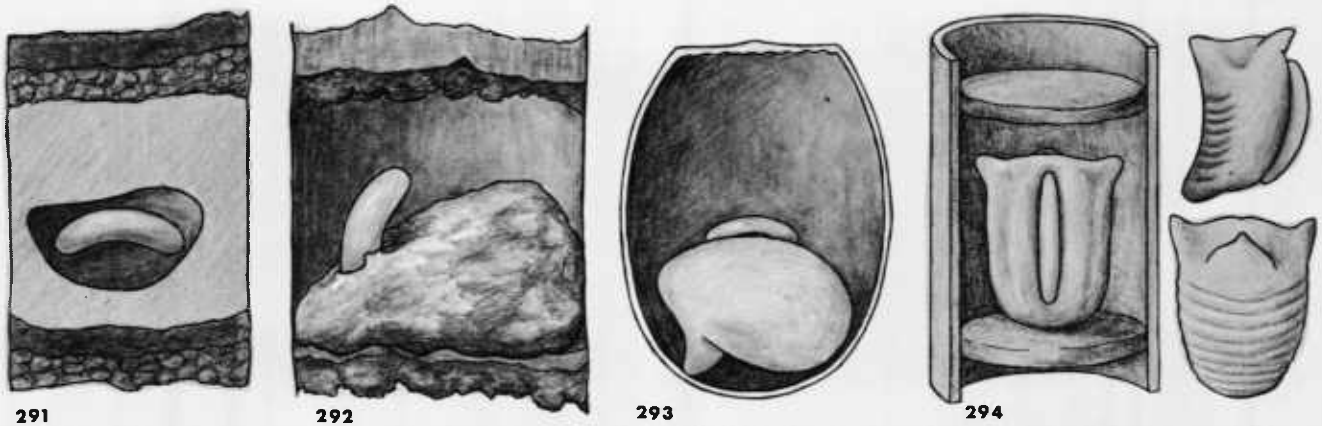
Oviposition

Except for *Apis, Psithyrus,* most Allodopini, and *Bombus* (*Bombias*) (other than the first brood), which oviposit in unprovisioned cells, provisions are always brought to the nest before any eggs are laid. The habit is consistent in *Apis* and *Psithyrus,* but the first generation eggs of all *Bombus,* including *Bombias,* are placed on a bed of pollen. The habit of ovipositing in cells before they are provisioned appears to be associated with bees that provision progressively. The allodapines feed their larvae progressively but do not construct cells, yet like *Apis* and *Bombus* they lay eggs and then provide food for the hatching larvae.

All other nonparasitic bees lay their eggs after the cells are fully provisioned. Solitary forms oviposit immediately after provisioning each cell, but the social halictines and meliponines may completely provision a number of cells simultaneously before any eggs are laid.

Most parasitic bees lay eggs after the host cell is fully provisioned. However, there are several known exceptions. Medler (1958) reported that a species of *Coelioxys* laid a single egg near the base of the host cell while it was being provisioned. On the other hand, Ferton (1897) noted that *Coelioxys afra* laid its egg with one end leaning on the egg of *Megachile albipila* on top of the host provisions (Fig. 295), and that *Coelioxys conica* thrust its egg through the leaf pieces of *Megachile circumcincta* cells so that the posterior ends projected into the cell almost reaching the surface of the provisions (similar to that illustrated in Fig. 296). Michener (1955b) observed that *Stelis lateralis* concealed its eggs in the food mass of *Hoplitis pilosifrons* near the basal end of the cell. Similar oviposition habits have been reported for other *Stelis* in Europe (Verhoeff, 1892; Hoppner, 1898). Eggs of *Triepolus concavus* have been observed embedded in the cell wall below the upper level of the provisions of *Svastra obliqua* (Fig. 298), and they may have been so placed while provisioning was in progress (Rozen, 1964).

Resealing of the host cell by the parasite is an uncommon occurrence among bees, yet it is known to occur in a few genera and suspected in another. *Melecta* and *Xeromelecta* oviposit after the cell caps are formed, for their eggs are sometimes suspended from the inner surface of the caps (Fig. 272). *M. pacifica* removes a portion of the cell cap of its hosts, *Anthophora pacifica pacifica* and *Emphoropsis cineraria,* and after oviposition seals the cap with soil particles. Eggs of *Zacosmia maculata* have been found on the side walls of the cell as well as suspended from the cap of its host, *A. Micranthophora) flexipes,* and are apparently laid before and after the host cell cap is made. *Psithyrus* takes over an established nest of *Bombus* and kills the queen. She substitutes her own eggs for those of the incipient queen, or constructs cells in which her own eggs are placed. In either case, the parasite seals the cell and its eggs are reared by the brood of its host. The female of *Stelis* (*Odontostelis*) *bilineolata* similarly takes over a cell cluster of the apid, *Euglossa,* driving the attendant female from the nest. She then opens the cells containing eggs or small larvae, removes and destroys them, and, after depositing her own egg, reseals the cell (Bennett, 1966). Single eggs of *Sphecodes* in cells of *Halictus,* with no trace of the host egg, raises speculation that adult



291 **Osmia californica**

292 **Osmia lignaria**

293 **Examalapsis chianura**

294 **Xylacopa californica arizanensis**

FIGURES 291-294. Cells, provisions, and egg placement of four bee species.

females of some species may remove the host egg before depositing their own (unpublished).

Eggs are laid in groups for subsequent communal provisioning only in the Allodopini (Fig. 225) and *Bombus* (Fig. 299). All other bees (except most parasitic species) lay but a single egg per cell. The nomadines, melectines, and parasitic megachilids often lay several eggs in a single host cell. This may represent oviposition by more than one individual, but cases of a single female laying more than one egg per cell have been observed (Michener, 1955b). *Sphecodes* apparently never lays more than one egg in each host cell.

In recapitulation, one egg may be placed in each cell (most bees), several eggs laid separately in the same cell (many parasitic genera), or groups of eggs may be laid in communal chambers (Allodapini, most *Bombus*, some *Psithyrus*). They may be laid in unprovisioned cells or chambers (*Apis*, *Psithyrus*, and *Bombus* (*Bombias*), or in provisioned cells (most bees). Several individuals may lay eggs in the same cell (some parasitic genera) or in the same communal chamber (Allodapini).

Egg placement

Eggs laid singly in unprovisioned cells are placed vertically in the bottom of the cell in *Apis*, and horizontally in *Bombus* (*Bombias*) (Hobbs, 1965). When laid in unprovisioned chambers as single clusters of eggs, they may be vertical (*Psithyrus*, some *Bombus*) or horizontal (some *Bombus*). In the Allodapini, where several groups of eggs may be laid by more than one bee in the same communal chamber, they may be in masses (Fig. 225) or in circular or spiral rows (Fig. 226) (Sakagami, 1960).

Eggs laid in provisioned cells occupy a wide variety of positions. The eggs of parasitic genera are usually concealed in some fashion in the cell walls (*Triepeolus*, *Nomada*, *Oreopasites*, *Holcopasites*, *Neolarra*), or the food mass (*Coelioxys*, *Stelis*), or suspended from the upper part of the cell (melictines). The nonparasitic species attach their eggs to the cell wall near the food mass (*Colletes*, Fig. 274) or place them on top of it (most bees), under it (Emphorini), or in the food mass (all others). Of the various positions described in the following summary outline, those in which the egg is on top of the food mass with both ends touching it are the most common. Generally, egg placement is a species-specific characteristic, although changes in the consistency of the food mass due to environmental factors may obscure the original orientation between egg and provisions. The accumulation of moisture on top of the pollen mass prior to oviposition in *Andrena viburnella* was observed to result in the female appending the egg to the cell wall above the pollen mass (Stephen, 1965, Fig. 274). In most cases, egg placement has generic or tribal significance, but the unique placement of eggs by certain species makes broad generalizations unreliable (*Andrena*, *Emphoropsis*).

Egg structure

Bee eggs are usually delicate, smooth, white, cylindrical, and elongate. They are without evident reticulation when viewed with a stereoscopic microscope, but they may show fine surface structure when viewed under higher magnification (90x and above) (*Nomia melanderi*; *Bombus californicus*, Fig. 309). Surface reticulation does not appear to be of generic significance, for in *Pseudopanurgus aethiops* and *P. timberlakei* the chorion is smooth but occasionally wrinkled, whereas in *P. boylei* it is distinctly reticulated (Rozen, 1967). With few exceptions, such as the parasitic nomadines, the eggs of bees are slightly arched on the side that is dorsal with respect to the hatching larvae. Most of the eggs are rounded at both ends, and one end is usually slightly smaller than the other. The degree of arching

Classification of Egg Placement

- I. Eggs laid in communal chamber or, if in separate cells, on a common food mass.
  - A. Eggs laid in an enclosed egg chamber, sometimes partitioned.
    - 1. Eggs laid on common food mass (first brood of some if not all *Bombus,* Fig. 299).
      - a. Eggs laid in partitioned chamber (some *Psithyrus;* first brood of some *Bombus,* Fig. 302).
    - 2. Eggs laid in unprovisioned, unpartitioned chamber.
      - a. Eggs laid in horizontal cluster (later broods of *Bombus nevadensis,* Fig. 299).
      - b. Eggs laid in vertical cluster (later broods of some *Bombus*).
  - B. Eggs laid in open chamber comprising entire nest (Allodapini).
    - 1. Eggs attached in spiral rows to wall of chamber (*Allodape pringlei,* Fig. 226).
    - 2. Eggs piled into bottom of chamber, not attached to walls (*Allodape sauteriella, Allodapula unicolor,* Fig. 225; *Exoneura* spp.).
- II. Eggs laid individually in separate provisioned or unprovisioned cells.
  - A. One egg laid in bottom of each unprovisioned cell.
    - 1. Egg attached vertically to bottom of cell (*Apis,* Fig. 287).
    - 2. Egg laid horizontally on bottom of each cell (first brood of *Bombus morrisoni;* Fig. 300).
  - B. One egg laid in each cell which is at least partially provisioned.
    - 1. Egg attached primarily to cell wall rather than food mass.
      - a. Egg attached to but not embedded in cell wall.
        - *1.* Egg attached to cell cap or immediately below it and remote from food mass (*Melecta; Xeromelecta,* Fig. 272).
        - *2.* Egg attached to cell wall near food mass (*Colletes,* Figs. 274, 301).
      - b. Egg embedded in cell wall.
        - *1.* Egg with at least one third exposed in cell cavity (inserted from outside cell, some *Coelioxys,* Fig. 296; inserted to substrate through cell wall, *Nomada,* Fig. 302).
        - *2.* Egg completely embedded in cell wall except for anterior end (egg straight, *Triepeolus,* Figs. 297-298; U-shaped, *Oreopasites*).
    - 2. Egg attached to both cell wall and food mass (*Ceratina australensis,* Fig. 305; *C. callosa*).
    - 3. Egg attached to or embedded in the food mass.
      - a. Egg placed in groove on underside of pollen mass (Emphorini, Fig. 282).
      - b. Egg completely buried in food mass.
        - *1.* Egg located in chamber (some *Osmia; Lithurgus,* Fig. 290).
        - *2.* Egg closely invested in food mass (some *Coelioxys; Stelis,* Fig. 306).
      - c. Egg attached to or partially inserted into top of food mass.
        - *1.* One end of egg free from food mass and cell wall.
          - a. Egg attached to provisions (but not inserted) by one tip (*Panurginus* spp., *Andrena* spp., Fig. 276; *Perdita zebrata zebrata,* Fig. 284).
          - *b.* Egg with one eighth to one half of lower surface in contact with food mass (*Megachile* (*Sayapis*); some *Anthidium,* Fig. 304).
          - *c.* Egg with one end partially inserted into food mass (some *Osmia,* Fig. 292; some *Trigona,* Fig. 289; some *Coelioxys,* Fig. 296).
        - *2.* Egg with both ends in contact with food mass.
          - *a.* Egg with lower face and tips partially immersed in food mass (*Anthophora* spp., Fig. 272; *Hylaeus; Megachile* spp., Fig. 295).
          - *b.* Egg barely contacting food mass along entire ventral side (egg curvature fitting ball, *Andrena* spp.; *Panurginus* spp.; *Systropha,* Fig. 308; egg in depressed saddle, *Halictus* spp. Fig. 285; *Xylocopa,* Fig. 294).
          - *c.* Egg arched away from food mass (Eucerini, Fig. 271; some *Emphoropsis*), or from surface of pollen ball (*Sphecodes* spp.; *Andrena* spp. Fig. 286; *Nomia,* Fig. 277; *Exomalopsis,* Fig. 293; *Nomadopsis*).
      - d. Egg floating on fluid or semi-fluid provisions (*Chilicola ashmeadi; Ptiloglossa* sp., Fig. 273).

varies considerably. Generally, eggs on gruel-like provisions are only slightly arched, while those on convex pollen balls are highly arched and usually attached to the ball only at both ends. Variation often occurs between species in the same genus, i.e., *Nomia melanderi* eggs are more distinctly arched than those of *N. triangulifera* (Figs. 277, 278). From the limited data available, it appears that the most slender eggs are always more strongly arched. The curvature of the egg is also affected by its maturity. As the embryo develops, the egg tends to straighten.

The eggs of many parasitic bees assume highly unusual shapes. Those of *Triepeolus* are straight and have a flat, slightly expanded anterior end flush with the inner wall of the cell (Figs. 297, 298). *Oreopasites* eggs are bent double and the enlarged anterior-dorsal end which is flush with the cell wall is granular. *Nomada* eggs are also enlarged anteriorly and are asymmetrically curved as a result of a sharp median ventral constriction where the egg is in contact with the inner lining of the cell (Linsley and MacSwain, 1955).

Egg size is extremely variable. Among nonparasitic bees, that of the honey bee (about 1.4 mm.) is probably the shortest in relation to the adult size. *Nomia triangulifera,* a slightly smaller bee, has an egg 3.7 millimeters long. The egg of *Diadasia enavata,* a bee about the size of the honey bee, has an extremely long, slender egg (at least 6 mm.). The largest bee eggs in relation to the size of the adult are undoubtedly those of certain species of *Allodape.* An unidentified species reported by Brauns (1926) had an egg equal to about one-third of the bulk of the mother. Probably the largest bee eggs are those of *Xylocopa,* for eggs of *X. californica arizonensis* are over 10 millimeters long. By comparison, the eggs of *Bombus* queens, the adults of which are comparable in size to *Xylocopa,* are only 2 to 3 millimeters long. The eggs of most parasitic bees are remarkably small. This is particularly true of nomadines.

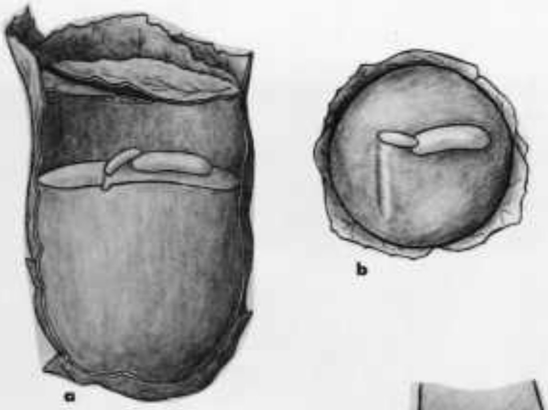
Incubation and hatching

The period of egg incubation for different species is largely influenced by the temperature at which the eggs are held. The incubation period varies from 1.7 days in *Megachile rotundata* to as long as 3 to 5 weeks in *Andrena ovina* (Malyshev, 1935). The honey bee and *Megachile rotundata,* both of which have relatively short incubation periods (3 days and 2 days respectively), normally incubate at rather high temperatures. Eggs of *Nomia melanderi* eclose in from 2½ to 3 days when held at 24° C., a temperature comparable to that of the soil of endemic nesting sites in the Pacific Northwest (Hackwell and Stephen, 1966). Vernal species of bees that nest deep in the ground have relatively long incubation periods (*Andrena viburnella* and *Emphoropsis cineraria*). The eggs of *Andrena viburnella* hatched in from 8 to 12 days in the laboratory when held at 8° C., the temperature of the soil at the nesting level (Stephen, 1965). There is considerable variability in the incubation period within a species when eggs are held at different temperatures. For example, in *Megachile rotundata,* the incubation period ranged from 1.7 days at 32° C. to 5 days at 21° C.

The early embryo of the honey bee lies in the chorion of the egg with its ventral side facing the dorsal surface of the egg (DuPraw, *in lit.*). Before hatching takes place, the embryo revolves 180°, allowing the larva to hatch with its ventral side down. The same phenomenon was observed in *Nomia melanderi* (Hackwell and Stephen, 1966) and *Megachile rotundata.* DuPraw (*in lit.*) states that before the chorion of the honey bee egg is sloughed, that portion adjacent to the spiracular line of the embryo is dissolved. The dorsal and ventral remnants are then pushed backwards by peristaltic waves. In *Megachile rotundata* which undergoes a similar process, the chorion is somewhat better developed and the ventral remnant remains attached to the ventro-apical end of the larva where it is eventually joined by successive larval skins. Hackwell and Stephen (1966) report that the first instar of *Nomia melanderi,* in which five larval instars are found, remains enclosed by the chorion of the egg except in the proximity of the head. Here the chorion is dissolved, or ruptured, and the mandibles can be observed moving free of the chorion, ingesting a fluid in their proximity.

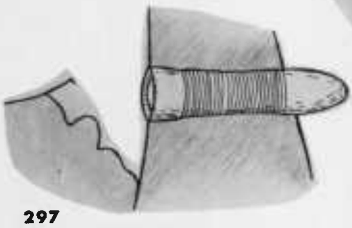
Eggs of most nomadines (*Triepeolus, Oreopasites, Neopasites,* and *Nomada*) hatch when the larva pushes through the head end of the egg and crawls out. In *Triepeolus,* at least, the egg has a cap-like structure that breaks away and sometimes remains attached at one edge as if by a hinge. The hatching method employed by nomadines may be characteristic of those bees whose eggs are closely invested in the substrate. Since the larvae of parasitic bees are unusually mobile and must usually reach and destroy the host or rival parasites in order to survive, the violent eclosion reflects their durability and capacity for strenuous activity.

FIGURES 295-309. *Coelioxys afra* egg leaning against egg of *Megachile albipila* (295); *Coelioxys elongata* eggs embedded in the provisions and through the leaf-cup of *Megachile japonica* cell (296); *Tripeolus* completely embedded in walls of host cells near the surface of provisions (297-298); two cells of *Bombus californicus,* each containing a cluster of eggs (299); *Bombus morrisoni* egg cell containing one egg (300); *Colletes inaequalis* completed cell with egg attached to cell wall and surface of provisions (301); eggs of parasitic bees, *Nomada* and *Neopasites,* partially embedded in cell walls of hosts (302-303); shaped pollen mass of *Anthidium emarginatum* with egg attached by one end (304); *Ceratina australensis* completed cell with one end of egg attached to cell wall and the other end leaning against pollen leaf (305); *Hoplitis pilosifrons* completed cell with egg of *Stelis lateralis* embedded in pollen mass (306); *Melitturga clavicornis* completed cell with one end of egg attached to pollen ball (307); *Systropha planidens* completed cell with one surface of egg in complete contact with pollen ball (308); and egg of *Bombus californicus* showing reticulated chorion (309). ▶

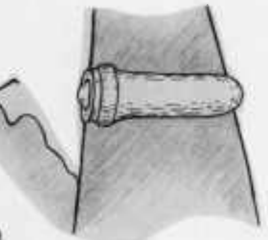


295
Coelioxys afra Lep.
in Megachile cell

296
Coelioxys elongata
on Megachile japonica



297
Triepeolus remigatus
in Xenoglossa cell



298
Triepeolus rufithorax
in Svastra cell

299
Bombus californicus

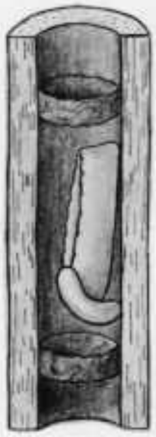
300
Bombus morrisoni

301
Colletes inaequalis

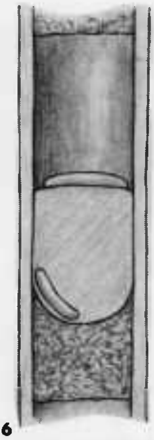
302
Nomada opacella
in Andrena cell

303
Neopasites in
Dufourea cell

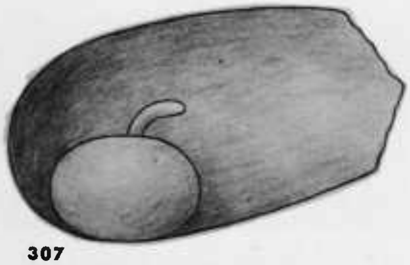
304
Anthidium emarginatum



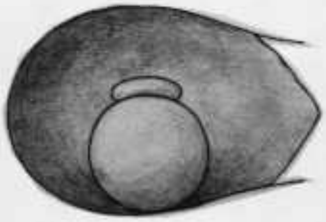
305
Ceratina australensis



306
Stelis lateralis in
Hoplitis pilosifrons cell



307
Melitturga clavicornis



308
Systropha planidens

309
Bombus californicus

Larval development

The caudal end of most first instar bee larvae remains at the spot where the posterior end of the egg was attached. According to Malyshev, the first instars of *Dasypoda* and *Systropha* drop to the base of the cell shortly after hatching and begin their food consumption at that point. As the larva matures, it retains the pollen ball within the confines of the growing U-shaped body, thus keeping it from direct contact with the cell wall. Observations on *Hesperapis carinata,* indicate that the first instar larva migrates only slightly, but that the second instar crawls down the side of the ball to its base, feeding as it moves (unpublished).

In species which provide a pool of liquid on top of the provisions, the first, second, and sometimes at least part of the third instars are spent feeding on it (*Anthophora occidentalis*). Usually very little feeding occurs in the first instar of this species and growth is slight. *Diadasia enavata* barely increases in size from the first to the second instar (2.3 to 2.7 cm. in total length and head capsule width from 5.0-5.2 mm.) (unpublished). *Megachile rotundata* larvae actually become shorter but slightly broader in the second instar, although the head capsule is distinctly larger.

The method of feeding differs according to the consistency of the food. Alkali bee larvae, which have a moist but solid food mass, make a small notch in the ball during the second and third instars. In the third instar, they begin to swing their heads from side to side in increasing arcs, consuming the pollen that can be reached by arching their bodies. This feeding pattern continues during the fourth instar, until the immobile caudal end is perched on a narrow summit. The larva usually attacks the ball during the fifth instar by "diving" downwards and wrapping itself about it as it increases in size and the remaining fragment decreases.

The larva of *Diadasia enavata,* like that of *Hesperapis,* begins to migrate as early as the second instar. It is long and slender and has a projection on the ninth abdominal sternum which it presses against the pollen mass as it moves. Since the lower parts of the pollen mass are gradually eaten away before the upper area is fed upon, it appears that the larva does not travel vertically as much as it does laterally around the lower part of the barrel-shaped mass. It maintains its position by pressing its dorsal surface against the cell wall, and as it grows the space between the food and the wall grows correspondingly greater. In the last instar, the larva begins to encircle the now oval-shaped ball, eating conspicuous vertical, parallel channels into it. The food mass retains its perfect oval shape until it practically disappears.

The larva of *Hesperapis carinata* crawls to the bottom of the cell, feeding as it goes, and assumes a C-shaped position lying on its side under the ball. Apparently, it juggles the ball around as it feeds by using the extension of the ninth sternum. At any rate, the larva maintains the same position under the ball, which in turn retains its spherical shape until its disappearance. Inasmuch as *Hesperapis regularis* (Burdick and Torchio, 1959) and *H. rufipes* (Michener, 1953a) prepupae do not have a prominent ninth sternum extension, the feeding habits described may vary interspecifically.

Megachile rotundata and *M. pugnata* do not change their position until they reach the fourth instar, at which time they "dive" into the food mass, eating away one side of it and then consuming it in a seemingly random manner.

Parasitic bee larvae of most of the Nomadinae and Melectini, but not Megachilidae, usually have greater elongated mandibles in the first instar, with which they destroy the host egg or young larva (Figs. 103, 104). *Stelis,* a megachilid parasite of other megachilids and some Apidae, has relatively unmodified mandibles in the first instar, possibly adapted to feed on pollen while burrowing toward the host. The larvae of *S.* (*Odontostelis*) *bilineolata* and *S.* (*Stelidomorpha*) *nasuta* do not kill their hosts directly, although the latter apparently consumes the food of the larger host larva so that it starves (Fabre, 1914). The mandibles of the second instar larvae of *S.* (*Microstelis*) *lateralis* and *S.* (*Stelis*) *minuta* are sharp but not elongated and are used to crush the head or body of the host. (Rozen, 1966b). The mandibles of *Coelioxys* are somewhat modified in the first instar but become extremely elongate upon molting into the second stadium (Figs. 105, 106). It is not known whether the first instar feeds on the host's provisions, but during the second instar, the elongate mandibles are used in a shovel-like manner to disturb the surface of the host's provisions. This activity disrupts the orientation of the host egg or early instar with its provisions and death ensues. Although other genera have only been observed to attack during the first larval instar, the fact that the second instar also has somewhat enlarged mandibles indicates that egg predation and inter- or intra-specific combat may also occur in this stage. Later instars of parasitic bees have relatively normal mandibles and feed on stored food. The shape of the mandibles is variable among both nonparasitic and parasitic bee larvae. This variation is probably associated in some way with differences in provisions and methods of feeding.

The rate of development of bee larvae, like all poikilotherms, is temperature dependent, proceeding most rapidly at an optimal temperature and progressively more slowly at temperatures above and below this optimum. In *Megachile rotundata,* development from egg to prepupa may occur in 8 days at 32° C., whereas it will require from 22 to 28 days when held at 22° C.

Larval instars

It is generally accepted that there are five larval instars in the honey bee, *Apis mellifera,* and this finding is generally accredited to Bertholf (1925). However, nowhere in the latter paper does the author state unequivocally that five instars exist, and his tabular data lack clarity on this point. Apparently there is a difference of opinion on this matter, for Bier (in Büdel-Herold, 1960) claims there are six moults from the egg to the adult honey bee: that is, four larval moults, one to the pupa, and the last to the adult.

Trigona is said to have five instars, but among other bees the number of larval instars is reported to be three or four. Four larval instars are recorded in the Australian ceratinine genus *Allodapula* (Syed, 1963), and this number is considered to be the rule among most bees. Linsley and others (1952) record three larval instars in the bee *Diadasia consociata.* In *Diadasia enavata,* the second instar larva is subequal in size to the first and is easily missed.

Recent detailed studies on the development of *Nomia melanderi* have shown the presence of five larval instars rather than four as previously considered (Hackwell and Stephen, 1966). The first instar is of very short duration and, except for the head capsule, it is entirely covered with the egg chorion. First instars of very short duration may also exist in other species of bees for which three or four instars have been reported.

In *Nomia,* as in most bees, two thirds to three fourths of the growth of the larva occurs during the last instar. Since the full-grown larva of *Nomia* is much heavier than the original pollen ball and egg, it must be assumed that the pollen absorbs considerable water from the substrate or the atmosphere, either at, or prior to, the time it is ingested.

Defecation

Insect scatology frequently serves as an excellent tool for determining the organismal associations in gregarious nesting sites of bees. In old nests, scavengers usually destroy dead bees, larvae, and even cocoons, but the excrement left by hosts, parasites, predators, and scavengers remains as telltale evidence for many years. Consequently, arthropod scatology has received some attention, but it deserves much more critical analysis.

It is well known that honey bee larvae do not defecate until they have finished feeding. The mid-gut, which contains the undigested and presumably as yet incompletely assimilated pollen, does not make a connection with the hind-gut until late in the last instar. This seems to be characteristic of most bees and it prevents contamination of the food. The family Megachilidae is characterized by earlier defecation. Most species begin defecating shortly after reaching the fourth instar, but *Megachile brevis* begins voiding feces during the third instar (Michener, 1953a) as does *M. rotundata. Stelis* was reported by Michener (1955b) to begin defecating as early as the second instar while burrowing through the pollen in search of the host. A species of *Osmia* has been observed in the laboratory to defecate in the first instar shortly after the first food was consumed. Even though most megachilids defecate while feeding, they usually prevent extensive contamination by spinning silk strands which entangle the fecal pellets and hold them away from the food, either at the top of the cell or against the lateral walls (Fig. 317).

Early defecation is also known to occur in the xylocopine genera, *Ceratina, Xylocopa,* and *Allodape* (Sakagami, 1960). Michener (1962c) reports that *Ceratina australensis* begins voiding feces during the early part of the fourth instar and the long oval pellets merely drop and accumulate in the bottom of the cell. In some *Allodape,* the adult bees remove the fecal pellets from the nest as they are voided.

The Emphorini defecate early. *Diadasia,* at least, begins to defecate soon after it reaches the last larval instar. In *D. enavata,* the fecal strips deposited while feeding can be distinguished from the post-feeding ones. Rozen (1967) notes that he has never seen fecal matter in cells of mature fall-collected prepupae of *Pseudopanurgus,* and suggests that members of this genus overwinter as predefecating forms.

Fecal material is usually of two main types. The bulk of it, extruded during or immediately after feeding, is composed primarily of empty pollen grains, although some unabsorbed residue and probably some malpighian tubule secretion is also included. The feces varies in consistency from a viscous fluid (most *Anthophora*) to long pasty ribbons (*Diadasia,* Fig. 310), or to short bacilliform pellets (*Osmia,* Fig. 312). In spite of a certain amount of collapsing of the pollen grains during digestion, it is often possible to determine the floral source of the pollen from fecal material almost as well as from scopal pollen. The larvae of *Nomia melanderi* begin defecating within one or two days after the pollen has all been consumed and about two to four days prior to the time of the formation of prepupae. During the latter part of the defecating process, a thin silk-like thread extrudes from the anus of the larva. It is transparent and in most cases difficult to observe because of the presence of the feces, but on close examination it can be found embedded in each of the fecal smears (Hackwell, unpublished). *Colletes ciliatoides* was observed by Torchio (1965) to produce a large quantity of viscous material one day after the last fecal pellet was deposited. This material was applied as a cocoon-like layer to the inner surface of the fecal layer.

The surface of each fecal pellet usually has longitudinal grooves or ridges impressed upon it from muscular action by at least the anal segment. The consistency of the feces is usually pasty at the time of extrusion but becomes firmer within a few hours and is eventually brittle in old cells. The length of the pellets is variable between and sometimes within species. Generally, the moister fecal material is extruded in longer ribbons. The feces of several species of *Stelis* are extruded as continuous strands and can thus be distinguishd readily from the short fecal pellets characteristic of other megachilids (Fig. 312).

Many larvae press the fecal pellets or strands against the walls of their cells as soon as they are extruded. This converts them into ribbons, streaks, or cakes, depending upon their original consistency and where they are applied. In *Nomia melanderi* the tip of the abdomen is flexed forward and upward from the bottom of the cell, and as it moves the fecal material is smeared up the side of the cell. A series of vertical ribbons is readily evident in the base of cells of this genus, and the gyrating larvae usually spread the ends of the ribbons into a basal fecal cup (Fig. 313). The vertical ribbons of *N. melanderi* extend further up the cell walls than do those of *N. nevadensis* (Cross and Bohart, 1960). *Triepeolus* deposits a nearly continuous fecal layer around the cell walls but leaves a particularly heavy concentration at the equatorial zone. Some *Anthophora* void a semi-liquid material which is left as a nearly homogenous, hemispherical cake in the bottom of each cell.

The fecal deposits of *Nomadopsis scutellaris* are similar to those of *Anthophora,* and each one has an amorphous blackish layer on top near its center (Fig. 315). This represents the final deposit, and is probably composed largely of material from the malpighian tubules. *Colletes* applies its feces as a thick uniform orange layer to the entire inner wall of the cellophane-like cell. This fecal layer turns dark brown within a few weeks. *Hesperapis carinata* and *H. regularis* partially flatten a mass of short, parallel strands slightly to one side of the cell base (Fig. 316). *Nomada* sp. speckles the cell walls with flattened oval pellets oriented in various directions (unpublished), whereas the defecating larvae of *Megachile rotundata* deposit their short, bacilliform pellets about the upper inner surface of the cell where they are held by fine silken threads (Fig. 314). The mature larvae of *Perdita* rest on their dorsum and extrude short fecal pellets which accumulate as a heap on their venters (Fig. 311) (Rozen, 1967).

Cocoon spinning

Cocoon spinning appears sporadically throughout the Apoidea and other Hymenoptera, and is thus extremely difficult to correlate with phylogeny. In the Megachilidae and Apidae, the cocoon habit is universal, whereas it is completely lacking in the Andrenidae, Nomadinae, and Xylocopidae. In the Colletidae, a few species of *Colletes* have been observed to spin thin cocoons and that of *Ptiloglossa* sp. is well formed (Roberts, personal communication). In the Halictidae, only the Dufoureinae are known to construct cocoons. Among the Melittidae, *Macropis* and *Melitta* are cocoon makers, whereas individuals of some *Hesperapis* spin poor ones and *Dasypoda* make none. Most anthophorids spin cocoons, but the Anthophorini is an exception. Some individuals of another anthophorid, *Exomalopsis chionura,* spin complete cocoons and others omit them entirely, even at the same nesting site (Rozen and MacNeill, 1957).

Bee cocoons probably serve to protect prepupae and pupae from various environmental factors. They may also offer resistance to predators, rapid changes in temperature and humidity, inoculation with disease organisms, and contact with potentially harmful materials such as feces and soil particles. Genera without well-formed cocoons or strong protective cells usually have rigid prepupae (andrenids, most halictids, most melittids, most nomadines) and/or overwinter as adults (some andrenids, some halictids, etc.). Those having strong cocoons usually have nonrigid larvae which may be slightly active (megachilids, eucerines, melectines) or else have flaccid larvae (*Bombus*). *Diadasia* and some *Anthophora* which have exceptionally flaccid prepupae, construct no cocoon (*Anthophora*) or only poor ones (*Diadasia*), but they have strong cells.

Cocoon spinning usually begins just before (*Dufourea* and *Centris*) or while the post-feeding larva is voiding its feces and continues for a period after defecation is completed. However, megachilid larvae produce variable amounts of silk during the feeding period of the last instar to separate the fecal pellets from the food. The cocoons of megachilids are usually quite tough, sometimes rather rigid, and usually composed of several layers. These include an outer shroud in which the fecal pellets are incorporated (Fig. 318), an intermediate dense fiber-like layer, and a nonfibrous, varnish-like material applied to the inner cocoon wall.

The cocoons of some groups of bees possess specialized structures by which they can be readily identified. Most megachilids make a nipple-shaped projection over the anterior end. The nipple is well developed in most anthidiines and poorly developed or absent in *Megachile* (Figs. 314, 318). *Coelioxys* cocoons can be distinguished from those of their host (*Megachile*) by the much coarser fibers around the cap. Eucerines spin a cap-like structure of several rather loosely connected layers of coarse silk (Figs. 319, 320).

The total amount of silk produced varies considerably even within the same species. This is probably due to a nutritional factor, as poorly fed larvae produce the smallest amount. For example, if the food of *Megachile rotundata* larvae dries before it is entirely consumed, the starved larvae spin very delicate or sometimes incomplete cocoons.

The silk used for making insect cocoons is usually produced by the salivary glands which open into the labium. However, cocoons of a few insects are made of silk produced by the malpighian tubules and spun through the anus (most neuropterans, some beetles, and chalcid wasps). In the bees, *Colletes ciliatoides* makes a delicate varnish-like cocoon that seals the fecal layer against the walls of the cell. The silk is produced from the anus as a fine, transparent ribbon after defecation is completed, and it has its origin in at least one pair of the malpighian tubules (Torchio, 1965). It is suspected that the varnish-like interior lining of megachilid cells is also secreted by the malpighian tubules, but this has not been confirmed.

310
Diadasia enavata

311
Perdita sp.

312
Osmia californica and Stelis sp.

313
Nomia melanderi

314
Megachile rotundata

315
Nomadopsis anthidius

316
Hesperapis

317
Heriades

318
Anthidium

319
Melissodes robustior

320
Melissodes

FIGURES 310-320. *Diadasia enavata* cell interior showing ribbons of fecal material applied to inner surface of cell by mature larva (310); *Perdita* sp. mature larva with fecal pellets held on its venter (311); *Osmia californica* (upper cell) cocoon with bacilliform fecal pellets on outer surface and *Stelis* sp. (lower cell) cocoon with long strands of fecal material (312); *Nomia melanderi* cell with bands of feces arising from cell base (313); *Megachile rotundata* cell with fecal pellets held at upper end of cocoon (314); top view of *Nomadopsis anthidius* cell showing fecal "cake" at bottom of cell (315); *Hesperapis regularis* cell with mass of near parallel fecal strips on one side of cell base (316); *Heriades variolosa* section (above) showing the narrow secreted rim below partition as well as use of different material for constructing the partition, and (below) short fecal pellets distributed uniformly over the outer surface of cocoon (317); *Anthidium* "nippled" cocoon composed of layers of silken material (318); and cocoons of two species of *Melissodes* (319-320).

Foraging

Foraged materials are consumed in the field or brought back to the nest as provisions or nest-building materials. Since most of the foraging takes place on flowers, we will first discuss the means by which bees recognize and distinguish between flowers.

Flower recognition

Bees locate and distinguish flowers through their ability to discriminate color, form, and odor. Frisch (1924, 1950) and Kühn (1924, 1927) independently concluded that the honey bee is receptive principally to four wave bands or colors: orange-yellow, wave lengths 6,500 to 5,300 Angstroms; blue-green, 5,100 to 4,800 Angstroms; blue-violet, 4,700 to 4,000 Angstroms; and ultraviolet, 4,000 to 3,100 Angstroms. Color discrimination by bees is shifted towards the shorter wave lengths of the color spectrum when compared to that of man. They do not distinguish red but clearly perceive ultraviolet. Consequently, pure red flowers are unattractive to them, but red flowers that reflect ultraviolet are readily seen. Some students believe that bees are unable to discriminate clearly among the various shades of colors that lie within each of the above spectral bands, and that those trained to yellow, for example, would go to yellow-orange or yellow-green. However, according to Kühn and Fraenkel (1927), honey bees are able to distinguish between many different shades in the orange-yellow and blue-violet spectra.

Most studies indicate that *Apis* displays no obvious color preference and that its more regular appearance on blue and purple flowers is a result of a more striking contrast of these colors with the green of the foliage. However, according to Michener (1953d), *Megachile brevis,* when visiting a wide variety of hosts, preferred blue and purple flowers, was less attracted to white or greenish flowers, and visited yellow flowers least often. This preference occurred to a greater degree than could be explained by the relative abundance of flowers of the various colors. Counts made by Pedersen (1962, unpublished) in plots of white-flowered alfalfa of one clone and blue-flowered alfalfa of several clones showed that *Megachile rotundata* and pierid butterflies preferred the blue, whereas honey bees demonstrated no preference. Comparable studies conducted during a three-year period in Oregon using white- and blue-flowered alfalfa clones indicated that *Megachile rotundata* showed no color preference, whereas honey bees could be found principally on the blue.

Form perception by bees is apparently crude but sufficient to enable them to distinguish between adjacent flowers of different forms. In general, it appears that form is perceived primarily on the basis of the interruptedness of the outline (Frisch, 1950). Experiments by Frisch, as well as by Hertz (1933) and others, demonstrate that length of outline is important in pattern perception. Apparently, the more complex forms with more outline increase the flicker which is the characteristic to which the bees respond. Movement of the patterns in relation to the bee also increases perception by increasing the flicker (Wolf, 1937). Consequently, a bee is able to perceive form in a moving object better than in a still one and when the bee itself is moving rather than stationary. Obviously, flowers or flower clusters with complex form and long, flexible stems have an advantage in attracting bees over those with little pattern and a relatively immovable position.

Bees supplement their ability to distinguish among and between color and form with a well-developed sense of smell. Odor-perceiving organs are located in the eight terminal segments of each antenna of the honey bee. From a series of experiments (Frisch, 1919, 1921), the following conclusions were drawn: materials detected by humans can be detected equally well by bees; flowers that are unscented to humans are also unscented to bees; and thresholds for perception of various odors are similar in humans and bees. Ribbands (1953), in testing a series of aromatic chemicals perceivable by both bees and humans, concluded that the thresholds of response to all of the substances was considerably lower in the bee than in man. In addition to being able to discriminate among different odors, the honey bee is also able to retain the memory of an odor for long periods of time (Frisch, 1919).

Frisch (1950) and others indicate that bees are first attracted to flowers by their color, and then identify them by their form. Olfactory mechanisms usually take over as they come within odor-perceiving range. Ribbands (1953) provides a more extensive review of color, odor, and form perception among bees.

Foraging by parasitic bees

Parasitic bees are as well adapted as nonparasitic bees for securing nectar from flowers. Some have undergone changes in body size to adapt to the various host bees, and this has resulted incidentally in a change in floral adaptation. Parasitic bees have been considered to be nonspecific in their choice of floral hosts, but preferences do occur, and in some cases these preferences appear to be associated with those of the host bee.

Parasitic bees acquire the pollen required for nutritional purposes directly from the stamens or ingest it as a contaminant in the nectar. Thus they usually lack the long body pile for accumulating pollen or special devices for carrying it. Among the parasitic forms in the Northwest, only *Melecta* and *Psithyrus* have body pile of the length and density of nonparasitic forms. The parasitic *Halictus* (*Paralictus*), an eastern North American subgenus closely related to the nonparasitic *Halictus* (*Chloralictus*), has retained the tibial scopa but in a reduced form. *Lestrimelitta,* a social meliponine robber of *Trigona* and *Melipona,* has expanded hind tibae characteristic of the host genus, but it has lost the concavity, fringing hairs, and apical comb used for concentrating and carrying pollen. The expanded tibia is used for transporting propolis and cerumen from pillaged host nests. Pollen and nectar is pillaged from host nests and carried in a paste-like form within the "stomach" (Sakagami and Laroca, 1963).

Foraging by nonparasitic bees

Among nonparasitic bees, males resemble parasitic forms in their foraging habits and in the absence of structures for concentrating and transporting pollen. However, male bees are often nearly as hairy as females of the same species.

Males. Except for drone honey bees which are fed or which feed inside the nest, male bees are usually found on the same floral hosts as females of the same species. If the female uses separate hosts for nectar and pollen, the male is most likely to be found on the nectar source. Both sexes of *Emphoropsis miserabilis* take nectar from *Arctostaphylos* early in the season, but females subsequently utilize a number of other floral genera as they become available (Stephen and Torchio, 1961a). Males of the alkali bee, on the other hand, visit a wide variety of nectar sources, while females usually restrict their nectar gathering to the same plants from which they extract pollen. In some bees, such as many *Nomadopsis, Calliopsis,* and *Perdita,* mating takes place on the flowers and both sexes collect nectar from the same host plants.

Females. The foraging behavior of females is more complex than that of males, for they are responsible for gathering and storing quantities of pollen and/or nectar for the propagation of the species. The following sections on foraging apply principally to females.

Communication among foraging bees

Apis and the meliponines are the only bees known to communicate information concerning the location and nature of the forage they visit. The communication dances of *Apis mellifera* have been presented in detail by Frisch (1950). Lindauer (1961) discusses the dances of other species of *Apis* and methods of communication employed by the meliponines.

Returning foragers of *Apis,* before disposing of their nectar or pollen, perform a "dance" by which they communicate the direction and distance of the food source to other bees in the hive. The richness of the source is indicated in a general way by the vigor and longevity of the dance. The identity of the plant species is communicated primarily by proffering samples of nectar, although this information may also be obtained by smelling the pollen on the corbiculae of the dancer.

A more primitive method of communicating the source of forage occurs among some meliponines in the genus *Trigona.* Returning foragers place scented droplets from their mandibular glands onto various objects along the route between the forage source and the colony. By means of vibrations they create in the hive upon their return, the foragers alert other bees but do not communicate specific information concerning distance or direction of the source. The original forager then returns to her food source along the route established by the scent marks. Alerted bees follow her closely and become familiar with the scent trail at the same time.

Foraging flight range

Most studies on the distances bees fly to obtain forage have been restricted to the honey bee. Honey bees have been reported flying as far as 15 miles, but this occurred under extreme stress conditions where closer forage was not available. Apiculturists generally consider that nectar-collecting bees can rarely, if ever, balance hive consumption when they fly to forage more than two miles from the hive. Apparently, most bees fly only as far as necessary in order to reach forage. Upon reaching the foraging area, different species of bees vary greatly in the distances they travel while accumulating a load. Since honey bees tend to distribute themselves uniformly on the forage, their flight range is strongly influenced by their population density. Therefore, the flight range in *Apis* is a function of the population density at a given locale in relation to the amount and condition of the bloom available to them.

Among solitary bees, the larger species are generally stronger and faster fliers, and the flight range is, to some extent, associated with body size. The alkali bee first orients on the nectar and pollen source nearest the nesting site, and the population gradually increases its range by extending in increasingly broad, concentric circles away from the nesting site (Stephen, 1959). The foraging behavior of *Megachile rotundata* differs sharply from that of *Apis* and *Nomia* for it tends to collect pollen and nectar from the nearest suitable source regardless of the population density that may exist.

Many bees attempt to govern the distances they must fly by establishing their nests close to suitable forage (see Site Selection, page 73). This is particularly prevalent in *Bombus,* but since the queens are confined to the nest for much of the season, the colony overcomes a local food shortage when workers take increasingly longer flights. If local pollen sources for many of the solitary species disappear while the female is still gravid, many (especially *Megachile*) abandon the nesting site and move to a more productive floral area.

Limiting forage areas

Individual honey bees, once they have begun foraging, tend to confine their activities to a small radius and to return to the same area repeatedly until it becomes unprofitable (Crane and Mather, 1943; Bateman, 1947; Singh, 1950). It is also believed that this radius tends to become larger as the bloom becomes more sparse, or when individual flowers become less productive. Levin (personal communication) suggests that honey bees return more faithfully to areas along the edges of alfalfa fields than to areas toward the center and are especially prone to return to discreet patches rather than to areas of similar size in larger fields. Observations on several species of *Bombus, Anthophora, Emphoropsis,* and *Osmia* indicated that they returned to individual shrubs in a hedgerow more often than to small areas in large, more or less undifferentiated tracts of *Astragalus* (unpublished).

Fidelity to floral source

Since Aristotelian days it has been known that individual honeybees tend to confine their visits to a single species of plant while on a foraging trip and to return to the same species until it becomes unproductive. The foraging force of a single colony of honey bees may visit dozens of flower sources, but each individual normally confines its activities to a single species. This fidelity is all the more remarkable in the light of the extremely wide host range of the species, as discussed in subsequent sections.

Grant (1949) documents an instance in which honey bees segregated into two foraging populations on three subspecies of *Gilia capitata* that he had interplanted in a garden. Plant breeders trying to achieve complete hybridization of two or more clones of alfalfa in a cage have experienced difficulty because the honey bees used as pollinators did not move freely from one clone to the other. It is apparent that interfertile species and subspecies of flowers growing side by side can maintain a degree of genetic isolation even in the presence of such a wide-ranging pollinator as the honey bee.

The extent to which individuals within wild bee species demonstrate fidelity to a particular plant species within their host range is not well known. Bees which have been studied in this regard (*Bombus, Nomia melanderi, Megachile rotundata*) are less faithful than honey bees to one floral source on each foraging trip or from one foraging trip to another, even though their host range as a species is much smaller. In one area from which a large number of alkali bee cell provisions were studied, a total of six plant species was determined by pollen analyses, but four and occasionally five of these species were represented in a single pollen mass (unpublished). While this observation does not reflect the usual host fidelity among members of this species, it illustrates the variability displayed by many solitary oligoleges. The greater fidelity of individual honey bees to particular food sources may be associated in some way with their well-developed communication system in the hive.

Floral preferences

Loew (1884) was one of the first to recognize that insects demonstrate varying degrees of host plant preferences. He used the term "heterotropy" for this phenomenon and divided it into three types as applied to flower-visiting insects: monotropy for insects consistently visiting only one species of plant; oligotropy for those visiting several related species of plants; and polytropy for those visiting many species of unrelated plants. Loew failed to recognize that many bees, while restricting themselves to a small number of flower species as pollen sources, would secure their nectar from a wide variety of flowers. Robertson (1925), recognizing that specific bee:flower relationships could only be determined on the basis of pollen collection, proposed the terms, "monolecty," "oligolecty," and "polylecty" to apply specifically to the pollen source preferences.

Pollen source preferences

The honey bee has a wider known range of pollen sources than any other bee. When it is rearing brood and pollen sources are not available, it will collect such items as fungus spores, grain millings, and coal dust. If the honey bee is used as the standard for polylecty, all other bees must be spoken of as oligolectic in varying degrees. If a bee such as *Diadasia australis,* which apparently collects pollen only from *Opuntia* and rarely visits other plants even for nectar, were used as the standard for oligolecty, then the great majority of bees would have to be designated as polylectic. Even monolecty, as it is usually applied to bees and flowers in a single area (for example, *Dufourea versatilis* on *Mimulus nanus*) would become meaningless in most cases if all species of the host genus were made available to the bee.

It is obvious that the above terms are relative and must be used in comparison with patterns known for other species. The alkali bee readily collects pollen from several genera of legumes, from mints, and from such unrelated plant genera as *Cleome, Cuscuta,* and *Convolvulus,* but it rarely collects from other hosts normally adjacent to its nesting sites. However, when its preferred hosts are limited, it will collect pollen from Canada thistle (*Cirsium arvense*); or when its preferred sources are absent, it will broaden its range to include rabbit brush (*Chrysothamnus*) (unpublished). The alkali bee is, therefore, intermediate in its pollen host preference and can be referred to as polylectic or oligolectic, depending on the frame of reference.

The ability of most bees to broaden their host range under stress further clouds the meaning of such terms as oligolecty and polylecty. Possibly, only the "preferred" hosts of those freely visited in competition with other acceptable hosts should be considered when discussing lecty.

Megachile rotundata, within its broad geographical range, has been reported collecting pollen from various species in seven different families. In the Pacific Northwest each of four isolated populations were observed collecting pollen from a different plant species representing a different family. This suggests that population differences in host specificity exist in *Megachile rotundata* and that the species could be considered facultatively oligolectic (Stephen and Torchio, 1961b). The above differences in host preference could be explained by larval conditioning to particular pollens, but such conditioning has yet to be demonstrated.

Well-developed oligolectic behavior is found among all families of bees, but it is better represented in some than in others. For example, it is common in Andrenidae and unusual or poorly developed in Apidae. On the basis of the North American fauna, it would appear that the families could be ranked from those with the highest percentage of oligolectic species to those with the lowest: Melittidae, Andrenidae, Colletidae, Megachilidae, Anthophoridae, Halictidae, and Apidae. At the subfamily level, the degree of oligolecty or polylecty is often quite marked. Within Colletidae, oligolecty is much better developed in the Neotropical Chilicolinae than in the Colletinae, and more prevalent in Colletinae than in Hylaeinae; in Andrenidae it is somewhat better developed in Panurginae than in Andreninae; and in Halictidae it is much better developed in Dufoureinae than in Halictinae (oligolecty of Nomiinae is intermediate but more like that of Dufoureinae). Some of the outstandingly oligolectic bee genera in the Northwest include *Perdita, Nomadopsis, Dufourea, Peponapis, Proteriades, Anthedonia, Diadasia,* and *Hesperapis*.

In the genus *Anthocopa,* oligolecty is evident at the subgeneric or species-group level, with each taxon exhibiting a definite preference for a different floral source (Hurd and Michener, 1955). *Perdita* is remarkable for the extent of oligolecty shown at the subgeneric and species levels (Linsley, 1958). In many other genera, one or several species may exhibit oligolectic tendencies while the rest may be polylectic. For example, *Colletes aestivalis* is specific on *Heuchera hispida,* whereas most other species show limited oligolectic tendencies.

A few genera noted for their polylectic habit are exemplified by *Apis, Halictus,* and *Ceratina.* A striking feature of most social and subsocial species as compared to solitary ones is their greater polylecty. This is probably accounted for in part by their generally longer foraging season. Unfortunately, since degree of polylecty is itself a relative matter and since the pollen preferences of the species in most genera are poorly known, it is impossible to discuss with precision the degree of polylecty demonstrated by most taxa.

Oligolecty is generally accepted as having risen through the fractionation and subsequent isolation of portions of an extensive interbreeding population into small breeding communities. This classical manner of bee-flower isolation and adaptation, however, does not provide a satisfactory explanation for the *Proteriades-Cryptantha* relationship. There are ten species of *Proteriades* near Riverside, California, which compete on the same species of *Cryptantha,* during the same season of the year, at the same time of day, and at the same place. The flight period of these species does not even coincide with the main bloom of *Cryptantha* in the area in which the observations were made (Hurd and Michener, 1955), suggesting that the apparent *Proteriades-Cryptantha* relationship may be purely adventitious in origin.

Factors leading toward the development of oligolecty may involve characteristics other than those directly associated with flower visitation. Linsley (1958) suggested that the small size and weak flight of *Perdita* may have accelerated the oligolectic process and resulted in its great proliferation of oligolectic species. However, *Halictus* (*Chloralictus*), which has numerous species of small size, is not remarkable for its oligolecty.

Much has been said about the evolutionary significance of restrictive pollinator-plant relationships. Many plant taxa are obviously better adapted for pollination by some types of pollinators than by others, just as many bees are obviously better adapted for collecting pollen and/or nectar from some flower types than others. To what extent foraging behavior and associated structures in bees evolved in direct response to the presence of particular flower types is debatable, just as is the reciprocal problem concerning the structure and "behavior" of flowers. A fruitful discussion of these problems would require detailed analyses of particular pollinator-flower relationships, which is beyond the scope of this bulletin. Early general compilations and discussions by Darwin (1876), Muller (1883), Kerner (1894), Knuth (1906), Lovell (1914, 1918), Robertson (1925, 1928, 1929), and Clements and Long (1923), provide wide-ranging but sometimes uncritical information on the subject. Recent papers by Grant (1949, 1950, 1965), Linsley, MacSwain, and Raven (1963, 1964), and Hurd and Linsley (1964), present more critical analyses of specific relationships and evolutionary pathways.

Adaptations for pollen collecting

Bees generally visit flowers in such a way as to obtain as much pollen as possible. The method used depends on the structure of the flower, and bees with a predilic-tion for a particular flower type are often remarkably skillful at manipulating it. For example, *Anthophora* and *Bombus* visit tomato flowers readily and vibrate them rapidly and efficiently to shake pollen from the anther tubes, whereas honey bees, which visit tomato flowers only when other pollens are not available, shake the flower slowly and only after much probing and hesitation. On alfalfa, many kinds of moderate-sized to large bees trigger a special mechanism when they thrust their heads into the flowers and push the wing petals laterally with their legs. The triggered sexual column of the flower strikes the bee in the fossal area, daubing it with pollen, and at the same time showering the bee with additional pollen over a larger area. While the flower is still open, the bee scrapes the stamens with its forelegs to obtain additional pollen.

Bees attracted to legumes, such as many megachilids and anthophorids, are extremely adept at this maneuver, even when their size is small. Honey bees are only moderately skillful at collecting pollen from alfalfa, and some *Halictus* trip the flowers with the greatest of difficulty. Many small species of bees cannot "trip" the flowers, but glean what pollen they can from tripped flowers by scraping around the stamens where they are pressed against the standard petal. *Perdita hurdi* cuts holes in the corolla tube of the unicorn plant, *Proboscidea arenaria,* to extract pollen from the hidden stamens (Hurd and Linsley, 1963). Many other examples of primarily behavioral adaptations for collecting pollen could be cited. In most such cases, the bee effects cross pollination as it collects its pollen, but in the last two cases mentioned above, the plant does not benefit.

Structural adaptations for collecting pollen may be general or specific. The long, branched hairs possessed by most bees can be considered as a general adaptation for accumulating pollen. The abdominal scopae of megachilids and the accessory scopal brushes of many andrenids and halictids often receive pollen directly from the anthers. These bees collect pollen from many composites by "wading" across the flower heads, thus forcing pollen directly into the abdominal propodeal and femoral scopae. *Hesperapis regularis* collects pollen from *Clarkia unguiculata* directly into the scopae, but it first pulls the stamens to the scopae (Burdick and Torchio, 1959).

A more specific adaptation occurs in *Proteriades*. It has hooked hairs on the maxillae which are used to extract pollen grains from the small, slender corolla tubes of *Cryptantha*. The foretarsi of *Calliopsis* (*Verbenapis*) are provided with a series of curled bristles, an adaptation which permits the bee to insert its forelegs into the flower of *Verbena,* scrape out the pollen, and deposit it in a regular pollen-carrying apparatus. In *Verbena,* normally a moth-pollinated flower, the anthers are hidden in a slender tube beneath a circle of hairs, and most bees that visit the flowers acquire only limited amounts of pollen on their proboscides.

Adaptations for pollen transport

After collecting pollen, most bees transfer it to the specific organs in which it is carried. *Hylaeus* and other members of the Hylaeinae transport an admixture of pollen and nectar from the flowers to the nest in their crops or honey stomachs. All other bees in the Northwest collect and transport pollen externally. The means by which the pollen is transferred from the various parts of the body on which it is received is imperfectly known. In many bees it is scraped from the body with the forelegs and possibly the midlegs and passed to the hind legs which pack it into and onto the definitive pollen-transporting organs.

The two main areas of pollen transport on the bodies of bees are the abdominal venter and the hindlegs. Megachilids, which use the abdominal venter exclusively, pack pollen between transverse series of stiff hairs on each sternite. Other bees use the outer surface of the tibia and/or the metatarsus of the hindlegs. Some bees, besides using the tibial and metatarsal scopae, also carry pollen on the abdominal venter (Fideliidae and the colletid subfamily Chilicolinae), the sides of the abdomen (*Nomia triangulifera* and some halictines), or the sides of the propodeum, the hind femora, and the trochanters (*Andrena and Protoxaea*).

The hairs of the tibial scopae of some bees have undergone considerable modification to accommodate the various sized pollen grains that they must carry. In the genus *Diadasia* the majority of species collect pollen from Malvaceae and are characterized by moderately branched scopal hairs. *D. enavata,* an oligolege on Compositae, has fine, densely plumose hairs on each scopa adapted to transport the relatively small pollen grains common to this family. *D. angusticeps* is the only species of the genus found on Onagraceae, and its tibial scopae are composed of stiff nonplumose hairs that transport the cobweb-like pollen masses of its host family. Such unrelated groups as *Anthedonia, Diandrena, Anthophora,* and *Tetralonia* have members which are oligoleges on *Oenothera.* All of these bees possess sparse, simple scopal hairs to accommodate the large *Oenothera* pollen grains interconnected by viscid threads.

The family Apidae is characterized by the development of a corbiculum and pollen comb on the hind tibia. The corbiculum is a concave, polished expansion of the tibia, fringed by long and incurved bristles. The comb at the apex of the tibia is used to force pollen from the inner surface of one leg onto the corbiculum of the other.

Most bees carry pollen as a dry powder which adheres to the transport area as a loose mass because of its sticky nature. Apids and most panurgines moisten the accumulated pollen with nectar. The apids convert it into a moist lump in the corbiculum, and the panurgines fasten it to the long, sparse hairs of the tibial scopa.

Nectar collecting

Honey bees not only collect nectar from every kind of flower from which they are physically able to obtain it, but they also collect such diverse sugary materials as granulated cane sugar, juice from decaying fruit, honey dew, and nectar from extrafloral nectaries of plants. Although no other bee visits such a wide variety of sources for carbohydrates, most bees visit more plant species for nectar than for pollen. The range of flowers visited for nectar nearly always includes the pollen sources. *Apis* stores large quantities of nectar for consumption throughout the year and must visit flowers more often for nectar than for pollen. Emphasis on nectar collecting applies to a lesser extent to all other social members of the Apidae. Other bees, including both social and solitary forms, require nectar only for immediate consumption and for mixing with pollen in the brood cells.

Many flowers visited by honey bees and other bees for nectar have special mechanisms for showering or daubing them with pollen. In the course of a single foraging trip, the honey bee will transfer this pollen to the corbiculae and return to the nest. Under these circumstances, the returning honey bee has a full crop but only a partial pollen load. A few kinds of pollen, such as cotton, are actively rejected by honey bees even when showered upon them. *Melissodes,* visiting blue curl

(*Trichostema* sp.) for nectar, has the pollen deposited on the apical abdominal tergites from which it cannot be successfully transferred to the scopae (unpublished). Many kinds of bees visit *Asclepias* for nectar but not for pollen which is enclosed in pollinia and cannot be utilized. Some flowers are used only for pollen because they lack nectar (*Rosa, Quercus*) or because the nectar is unavailable to the bee at the time of its visitation (*Halictus* (*Chloralictus*) visiting "tripped" flowers of alfalfa).

Many bee species that exhibit oligolectic tendencies when collecting pollen, also take their nectar from a limited number of host plants. Restriction to nectar sources, however, is rarely as well developed as it is to pollen sources. For example, *Andrena anograe knowltoni* restricts its pollen collecting to *Oenothera* but also visits the crucifer, *Stanleya pinnata,* for nectar (unpublished). *Osmia lignaria* collects pollen and nectar from a variety of plants having small, smooth pollen grains but also visits *Taraxacum, Agoseris,* and other composites with spined pollen grains for nectar (unpublished).

Honey bees and some halictines are the only bees that gather sugary liquids from sources other than flowers under field conditions. Honey bees collect nectar freely from the extra-floral nectaries of cotton, preferring it, in Arizona at least, to that from floral nectaries, probably because of its higher sugar concentration. *Halictus* (*Chloralictus*) sp. was observed visiting sugar syrup sprayed on vegetation in Logan, Utah, and a number of species of halictines of both sexes were seen taking fluids from broken watermelons at Davis, California (Bohart, 1950).

Adaptations for collecting nectar

The most common morphological adaptation for nectar collecting, and one that appears repeatedly through many genera of bees, concerns the length of the proboscis. Even among short-tongued families, some species such as *Dufourea versatilis, Nomadopsis zonalis,* and *Perdita albipennis* have developed long proboscides enabling them to take nectar from flowers with long, slender corolla tubes. Each of these bees is adapted to taking both nectar and pollen from the same plant. Many bees in long-tongued families, such as *Anthophora occidentalis* and *Bombus fervidus,* have unusually long tongues which enable them to collect nectar from flowers with long, slender corolla tubes. These species, however, do not necessarily collect pollen from the nectar hosts. Extremely small bees are usually found on correspondingly small flowers (*Hylaeus* is partial to umbellifers), but in some cases small body size allows the bee to crawl down the narrow corolla tubes for nectar (*Trigona* in flowers of *Convolvulus and Nicotiana*). Conversely, large bees have difficulty exploiting small flowers for either nectar or pollen unless the flowers are aggregated in a head to afford adequate support. *Xylocopa* is particularly restricted to large flowers because of its large body size and broad mouthparts.

A few groups of bees are able to reach the nectaries of slender corolla tubes by cutting holes at the bases of the tubes. *Bombus,* especially the relatively short-tongued species, use their mandibles to cut holes at the base of the corolla tubes of such flowers as red clover (*Trifolium pratense*) and hairy vetch (*Vicia villosa*). *Xylocopa* uses its maxillary blades to cut the corolla tubes of *Ipomopsis,* which has an extremely long, slender corolla tube. Nectar-collecting honey bees are quick to exploit holes cut by bees in both of these genera, and if a hole is not available on hairy vetch, they may force their heads into the flower until the corolla tube is split open (unpublished).

Water collecting

Honey bees and some of the other highly social apids take foraging trips specifically for water collection. The water is added to honey as a diluent or used for evaporation as a means of temperature regulation in the colony. *Ptilothrix,* some species of *Anthophora,* and several other bees collect water to assist them in digging or fashioning portions of the nest, particularly in hard clay soils. Water, when foraged, is taken into the glossa from shallow films on a solid substrata (apids and *Anthophora*) or from a body of water while "skating" on it (*Ptilothrix*).

Foraging for nest building materials

Apids, megachilids, and some anthophorids (*Centris*) forage for nest and cell building materials as well as for food. The propolis used by apids and *Centris* is generally taken from resinous exudates of plants with the mandibles and transferred to the hind tibiae. Various meliponines collect such oddments as excrement, paint, and tar by the same methods. *Bombus* shreds bark and cloth with its mandibles in which it transports the resultant fibers. Within Megachilidae, different taxa specialize in materials they collect for nest building (see outline, page 100). They gather nesting materials with the mandibles, which are often highly adapted for that particular purpose. For example, *Anthidium,* which strips fibers from woody plants, has strongly serrate mandibular edges; *Dianthidium,* which gathers resin and pebbles, has smooth mandibular edges; and *Megachile,* which cuts leaf pieces, has serrate and cusped mandibles. Osmiines, most of which masticate leaf materials, have mandibles similar in structure to those of *Megachile.*

Flight Periods

Seasonal flight

In general, the foraging season of oligolectic bees is shorter than that of polylectic species, principally because adult activities of the former are adapted to the restricted flowering season of their pollen hosts. The environmental factors that trigger plant growth and maturity appear to be the same as those that trigger bee activity. Therefore, bees with different temperature-threshold responses emerge at different periods throughout the blossoming season.

Among oligolectic species, syncronization of the appearance of the bee with the first blossoms of its host plant is remarkably accurate. Thus, in some of the larger bee genera, we find different species occurring in each season and utilizing entirely different pollen sources. For example, at Logan, Utah, *Anthophora pacifica* appears in April and early May on such flowers as *Astragalus* and stone fruits; *Anthophora bomboides neomexicana* in June on *Trifolium, Medicago,* and *Vicia; A. occidentalis* in July on *Cirsium;* and A. *flexipes* in August on late summer composites.

Seasonal differences among different species using the same host plant have probably evolved as a means of avoiding competition. Among the species using annual sunflower, *Helianthus annuus,* as their major pollen source in northern Utah, *Dufourea marginata* and *Dianthidium curvatum sayi* appear in July; *Diadasia enavata* and *Svastra obliqua* appear in late August; and *Hesperapis carinata* is present in September.

Bees with multiple generations visit several distinct floral successions for pollen. *Andrena candida* first appears on the earliest flowering plants, such as pussy willow (*Salix discolor*) and *Lomatium.* The second generation appears in the late spring on chokecherry (*Prunus melanocarpa*) and *Allium.* Conversely, some species may remain in a dormant stage for two or more years if the weather is unfavorable for host-plant flowering. Adults of a large nesting population of *Halictus* (*Evylaeus*) *aberrans* failed to appear in 1961 when their only host plant, *Oenothera latifolia,* failed to develop. In 1962, when *Oenothera* bloomed profusely, adults were again present but in reduced numbers. This example would suggest that environmental factors responsible for triggering bee activity and plant growth are at least similar.

Daily flight periods

The daily flight periods of bees are associated with the pollen and nectar production of their host plants. All social and semisocial bees, as well as many species of solitary bees, usually forage actively from dawn to dusk. However, within a single colony of honey bees, individuals may fly only during that time of day that nectar and/or pollen are being produced by the host plant to which they are oriented. For example, individuals that fly early in the morning for poppy pollen are not the same individuals that collect alfalfa nectar during most of the day or greasewood (*Sarcobatus*) pollen late in the day. It has not been determined to what extent this is true of other bee species. In the extreme northern latitudes, where daylight may extend to 24 hours for short seasons each year, some species of *Bombus* have been noted to fly and forage continuously. In lower latitudes, other species, such as *Melissodes* and some *Diadasia,* fly only for parts of each day, usually the mornings and early afternoons, and they are rarely seen in the field after 2 or 3 p.m.

There are, in addition, a number of species that are either matinal (collect their pollen in the early morning hours prior to or just following sunrise), crepuscular (collect their pollen at dusk), or nocturnal (fly and forage at night). In general, flowers with matinal or crepuscular blooming habits are visited by bees having corresponding flight periods. Among the matinal bees, *Xenoglossa* collects pollen from flowers of *Cucurbita* at dawn; *Peponapis* works the same flowers in the early sunlight hours; and such polylectic species as honey bees and *Agapostemon* collect nectar from the same flowers until they close (Bohart, 1964). *Halictus* (*Hemihalictus*) *lustrans* is a matinal oligolege on *Pyrrhopappus carolinianus,* the flowers of which close shortly after the sun strikes them early in the morning (Michener, 1947). The subgenus *Andrena* (*Onagrandrena*) comprises a number of matinal and crepuscular species. Species identity within this group is more readily determined on the basis of their host relationship and flight periodicity than on their morphological characteristics (Linsley and others, 1964). Malyshev (1935) reports that *Ptiloglossa ducali* is both matinal and crepuscular, flying at dawn and at dusk in South America.

Members of the halictine group, *Halictus* (*Sphecodogastra*), are the best known of the crepuscular bees. They collect their pollen in the early and late evening from evening primrose, *Oenothera.* As a rule, crepuscular and nocturnal species are characterized by extremely large ocelli. The subgenus *Perdita* (*Xerophasma*) has at least two nocturnal species with pale, almost whitish integument. Females of the halictid genus *Megalopta* have been collected pollen-laden at night, and a series of *M. genalis* collected in the Canal Zone had pollen from four different plant species, indicating that this species is not an oligolege. The entire subgenus of *Xylocopa* (*Nyctomelitta*) consists of nocturnal Indomalaysian species reported to fly all night on bright moonlight nights, and *X.* (*Proxylocopa*) includes only crepuscular or nocturnal forms. All reports made on the habits of bees that fly while the sun is not visible indicate that their flight is characterized by a loud buzzing noise. It has been suggested that this is a sonar-like device to provide sound reflection from objects about them (Linsley and MacSwain, 1958).

Parasitic Bees

It is generally conceded that parasitic forms have arisen many times in the evolutionary history of the bees, each parasitic segregate originating from a nonparasitic relative. From this origin, it is to be expected that each phyletic group of parasitic genera will resemble its pollen-collecting progenitor (and likewise the derived pollen-collecting contemporaries in the same lineage) most closely. The obvious affinities between *Coelioxys* and *Megachile, Stelis* and anthidiines, *Psi-*

thyrus and *Bombus,* and *Sphecodes* and *Halictus* lend credence to the rather recent independent origin of the parasitic habit in these groups. The degrees of phenotypic divergence and intra-group diversity have proved to be valuable criteria in establishing the antiquity of the parasitic group.

Refinement of the parasitic mode of life in bees has led to the loss of certain morphological characteristics once essential to the construction and provisioning of cells. These include (1) loss of scopae, (2) loss or reduction of long plumose body hairs, and (3) loss of basitibial plates. Parasitic life has also led to the development of certain positive characteristics shared by most parasitic bees and usually not present, or at least more poorly developed, in their nonparasitic relatives. These include (1) development of a long sting, (2) elongation and increased flexibility of the apical abdominal segments, and (3) increased thickness of cuticle and coarseness of body sculpturing.

The most diverse group of parasitic bees, and the one in which parasites and hosts are least obviously related, is the Nomadinae. This phyletic group is believed to have been derived from a primitive anthophorid. Among extant nomadines, *Triepeolus* adults most closely resemble other anthophorids and are usually parasitic on members of that family. *Triepeolus,* as well as various other nomadine larvae, however, exhibit larval characteristics in common with those of the more primitive halictine-andrenid group. Although this seems to throw some doubt on the supposed anthophorid origin of the subfamily, the resemblance of the larvae may merely express convergence. As indicated in the host-parasite list which follows, the nomadines attack a wide range of bee genera but have not become adapted to certain important and widespread taxa such as the Apidae, Megachilidae, Halictinae, and Hylaeinae.

Host specificity is a prominent feature among parasitic bees. In many cases the parasitic genus attacks only one host genus, or its selection may be confined to a single subfamily or family of bees. One of the few exceptions is the genus *Nomada* which attacks Andrenidae (*Andrena*), *Panurginus, Nomadopis,* and Halictidae (*Nomia* and *Halictus*), as well as the Eurasian Melittidae (*Melitta, Dasypoda*). However, by far the majority of species are parasitic on *Andrena.* Some of the reported cases of a single genus of parasite-attacking bees in several families are quite possibly based on faulty observation or chance cases of "mistaken identity" on the part of the parasite. On a few occasions, where the alkali bee and *Melissodes* coinhabited a single nesting site, larvae of *Triepeolus,* normally parasitic on *Melissodes,* were found in alkali bee cells. Some parasitic bees may be restricted to a single species of host, but this is probably rare.

"Incipient parasitism" of various forms has been noted in several groups of bees. In *Osmia,* for example, Bohart (1955) noted the gradual supersedure of an individual (*O. californica*) over another individual (*O. lignaria*) in a single nest. Michener (1961a) reported the ceratinid, *Allodapula associata,* to be a social parasite having normal scopae but apparently laying eggs in the nests of related species. Whether they also contribute food to these nests is not known. Queens of many *Bombus* species take advantage of nests begun by other individuals of the same or different species by killing the queen and taking over the nest. The progeny of the deposed queen sometimes care for the young of the invader. Early nests of *Bombus huntii* have been seen to be occupied successively by four or five queens under greenhouse conditions (unpublished). A recent paper by Knerer and Plateaux-Quénu (1967) describes the facultative parasitic behavior of *Halictus scabiosae* on *Halictus* (*Evylaeus*) *nigripes.* In one observation they noted a *scabiosae* egg on top of a *nigripes* pollen ball.

Robbery is commonly undertaken by most alpine genera, both within and between species and genera. The only important behavioral difference between *Lestrimelitta* and some species of *Trigona* seems to be that *Lestrimelitta* is an obligatory robber and has lost the instinct to forage from flowers, whereas *Trigona* is a facultative robber. Honey bees frequently turn to robbing when normal forage becomes scarce, but they apparently take only honey from other colonies. *Trigona,* on the other hand, sometimes steal nesting materials as well as food from other nests.

The following summary of parasitism among bees is based largely on biological characteristics. To a degree it also reflects the development and antiquity of the parasitic habit among the various groups.

I. The adult parasite lays one or more eggs in the host cell but only one first instar larva survives. The first or second instar destroys the host egg or early instar larva and then completes its development on the host provisions.
   A. The parasite normally hatches before the host and the first instar larva eats the host egg, progressing through one or two instars in the process.
      1. The eggs are inserted into the wall of the cell.
      2. The eggs are fastened to the surface of the cell wall or ceiling.
   B. The parasite may or may not hatch before the host. It destroys either the host egg or larva, whichever it encounters. It does not mount the host or feed on it.
      1. The first instar larva has moderately enlarged mandibles and the second instar has greatly enlarged mandibles with which it churns up the pollen and destroys the host egg or young larva (*Coelioxys*).
      2. The first (and possibly second) instar larva has small but sharp mandibles and kills the host larva (some *Stelis* and probably *Protostelis* and *Dioxys*).

II. The adult parasite lays her eggs in the host nest, but the first instar larva has no occasion to destroy the egg or young larva of the host.

   A. The parasite egg is substituted on the pollen ball for that of the host. It is not known whether host or parasite seals the cell (*Sphecodes* and some *Stelis*).

   B. The parasite eggs are laid in specific cells within the colony. The parasite larvae are cared for by the host (*Psithyrus*).

   C. The parasite eggs are laid in the same communal nursery with the host eggs and larvae and are cared for by the adult hosts (parasitic Allodapini).

III. The parasite population progressively takes over the host nest, either removing its food and building materials for its own nest or modifying it to its own nest pattern (*Lestrimelitta*).

Northwestern parasitic bees

The list on the next page includes the northwestern genera of parasitic bees and a few examples of other parasitic and host genera (in parentheses when not represented in the Northwest).

Natural Enemies of Bees

Bees are adversely affected by a wide variety of organisms acting as parasites, predators, and competitors. Relationships between bees and their enemies are extremely varied and often fit poorly into categories as usually defined. The principal groups of organisms involved include viruses, fungi, bacteria, protozoans, nematodes, arthropods, and chordates.

Microorganisms

Although diseases of honey bees have been studied extensively, little is known about diseases of other bees. Sac brood, the best known virus of honey bees, invades mature larvae, converting the latter into watery black bags. Certain diseased conditions of *Nomia* and *Diadasia* larvae, for which organisms have not been isolated, are suspected to be caused by viruses. The only definitely known virus of adult bees causes paralysis of honey bees.

Bacterial infections of honey bees include brood diseases (European foul brood, caused by *Bacillus alvei* Cheshire and Cheyne, and American foul brood, caused by *Bacillus larvae* White) and adult diseases (septicaemia, caused by *Bacillus apisepticus* Burnside). An organism similar to *B. apisepticus* is known to attack mature larvae of *Nomia melanderi* in Wyoming. Probably most kinds of bees, especially in the larval stage, are at least occasionally subject to bacterial diseases.

Various yeasts and molds, as well as bacteria, are of great importance in the spoilage of pollen and honey. Although stored honey and pollen shows some apparent antibiosis, its spoilage by microorganisms is perhaps the most important biotic factor contributing to early mortality of bees. The role of fungi in the brood cells of bees is often unclear. When the cells are in moist soil, dead larvae (and pollen in cells with dead larvae) are normally overgrown with various fungi. In some cases it may be impossible to tell whether the organism had initially spoiled the food and thus caused the larva to die, had attacked the organism directly as a parasite and later assumed a saprophytic role, or had developed secondarily after mortality of the larva had taken place (*Aspergillus flavus* (Link)). However, *flavus* is known to parasitize both honey bee larvae and adults.

Nosema apis Zander is a spore-forming protozoan found in the intestinal tract of adult honey bees, and *Nosema* organisms found in bumble bees are probably the same species. In the honey bee, *Nosema* is thought to be responsible for considerable mortality of workers and queens, especially in the early spring when many of the bees are old and cleansing flights have been restricted. Two other less serious protozoan diseases of honey bees are enteric amoebiasis (*Entamoeba apis* (Leidy) and Malpighian amoebiasis (*Malpighamoeba mellificae* (Prell). *Xylocopa* has been found with gregarine protozoans (*Leidyanna xylocopae* Bhatia and Setna) tightly packing the mid gut but not causing any obvious damage. Batra (1965) has recorded the presence of another gregarine protozoan in the hind gut of *Halictus zephyrus*. Little is known about protozoa in other kinds of bees but they are doubtless prevalent.

Nematodes

The best known nematode parasite of bees is *Sphaerularea bombi* Duford which attacks overwintering queen bumble bees and renders them sterile. Infested queens dig small burrows as overwintering hibernacula, and as the parasites become gravid, they reinfest the soil. A similar nematode has been found in the haemolymph surrounding the ovaries of overwintered *Halictus farinosus*.

Arthropods

The arthropod enemies of bees include both arachnids and insects. Centipedes may also play a minor role as general predators. Among the arachnids, spiders are often conspicuous predators of bees. The most commonly seen are crab spiders (Thomisidae); they lie on flowers, waiting for unwary visitors.

Mites are more common enemies of bees than spiders, but less conspicuous. Examination of a collection of pinned bees quickly reveals many species and genera of mites still clinging in death to the preserved bodies of their hosts. In many cases, the mites appear to act as harmless scavengers in the cells (Scutacaridae and Caloglyphidae) and use the adult bees merely as a means of transportation. However, it is possible that such mites are significant in the mechanical transmission of disease organisms.

A List of Parasitic Bees and Their Hosts from Northwestern America

PARASITE		HOST	
Family	Genus	Genus	Family
Halictidae			
Halictinae	*Sphecodes*	*Halictus* (s. l.), *Augochlorella*	Halictidae
		Calliopsis (?)[1], (*Melitturga*)[2]	Andrenidae
	Halictus (*Paralictus*)	*Halictus* (*Dialictus*)	Halictidae
Megachilidae			
Megachilinae	*Coelioxys*	*Megachile*	Megachilidae
Anthidiinae	*Stelis*	*Anthidium, Heriades, Hoplitis*	Megachilidae
		Osmia, Proteriades, Anthocopa	Megachilidae
	(*Heterostelis*)	*Ashmeadiella, Chelostoma*	
		(*Trachusa*)	Megachilidae
	S. (*Odontostelis*)	(*Euglossa*)	Apidae
	Protostelis	*Dianthidium?*	Megachilidae
	Dioxys	*Anthidium, Callanthidium*	Megachilidae
		Anthocopa, Hoplitis, Osmia	Megachilidae
		Megachile?	Megachilidae
Anthophoridae			
Anthophorinae	*Melecta*	*Anthophora, Emphoropsis*	Anthophoridae
	Xeromelecta	*Anthophora*	Anthophoridae
	Zacosmia	*Anthophora* (*Micranthophora*)	Anthophoridae
	(*Ericrosis*)	(*Anthophora* (?)) (*Centris*)	Anthophoridae
	(*Thyreus*)	(*Anthophora*)	Anthophoxidae
Nomadinae	*Nomada*	*Andrena, Panurgus, Nomadopsis*	Andrenidae
		Nomia, Halictus	Halictidae
		(*Melitta*), (*Dasypoda*)	Melittidae
	Epeolus	*Colletes*	Colletidae
	(*Isepeolus*)	*Colletes*	Colletidae
	Triepeolus	*Melissodes, Svastra, Anthophora, Xenoglossa*	Anthophoridae
		Nomia	Halictidae
		(*Ptiloglossa*)	Colletidae
		(*Protoxaea*)	Oxaeidae
	(*Biastes*)	(*Rophites*), (*Dufourea*)	Halictidae
	Oreopasites	*Nomadopsis, Perdita*	Andrenidae
	Holcopasites	*Pseudopanurgus*	Andrenidae
		Calliopsis, (*Hypomacrotera*)	Andrenidae
	Neolarra	*Perdita*	Andrenidae
	Townsendiella	*Conanthalictus?*	Halictidae
		Hesperapis?	Melittidae
	(*Odyneropsis*)	(*Ptiloglossa*)	Colletidae
	(*Hexepeolus*)	(*Ancylandrena*) ?	Andrenidae
	Neopasites	*Dufourea*	Halictidae
	(*Ammobatoides*)	(*Melitturga*)	Andrenidae
	(*Parammobatoides*)	(*Camptopeum*)	Andrenidae
Xylocopinae	(*Inquilina*)	(*Exoneura*)	Anthophoridae
	(*Allodapula*), some	(*Allodapula*), some	Anthophoridae
	(*Eucondylops*)	(*Allodape*)	Anthophoridae
Apidae			
Bombinae	*Psithyrus*	*Bombus*	Apidae
	(*Aglae*)	(*Eulaema*)	Apidae
(Euglossini)	(*Exaerete*)	(*Euglossini*)	Apidae
(Meliponini)	(*Lestrimelitta*)	(*Trigona*), (*Melipona*)	Apidae

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[1] Uncertain host-parasite relationship.

[2] Genera not represented in the northwest are parenthetically enclosed.

Mites of the family Anoetidae feed through the integument of the prepupae, but even when abundant, they have not been seen to cause significant injury. Acarid mites, frequently seen in the phoretic stage on megachilid adults and in the larval stages in megachilid food stores, often destroy the pollen before the bee larva develops fully. The enormously swollen bodies of pyemotid mites of the genus *Pyemotes* are occasionally found feeding on and destroying prepupae of ground-nesting as well as twig-nesting bees and wasps. Bumble bee nests are often inhabited by several species of mites which act as scavengers and probably consume some stored food as well. When very abundant, they are presumed to be harmful to the colony.

Several species of mites of the genus *Acarapis* live on the bodies of adult honey bees where they feed on the blood through intersegmental membranes. One species, *Acarapis woodi,* invades the tracheae, where it interferes with respiration and causes considerable mortality. This disease is largely responsible for strict quarantines on the movement of honey bees into uninfested countries (United States and Australia).

Insects are the most varied and the best known enemies of bees. There are general predators, specific predators, general scavenger-predators, specific "despoilers" or "depredators," parasitoids of several categories, and internal parasites. The bees are invaded or attacked primarily in the egg, mature larval, and adult stages.

General insect predators of sufficient size and agility frequently include bees in their diets. Among these are chewing insects such as dragonflies, mantids, tiger beetles, and sphecid and vespine wasps. Tiger beetle larvae are the only known larval insects to capture and prey on active adult bees. The bees are seized when they pass near the tiger beetle burrow entrances. Asilid flies and some reduviid bugs, which are likewise general predators of bees, pierce the bees' integument and drain the haemolymph. Bee larvae sometimes fall prey to the larvae of scenepinid flies (in wood) and bibionid flies (in the soil).

The vespines (especially *Vespa*) are often serious enemies of honey bees, seizing them at the hive entrance and carrying them to their brood.

Specific predators of bees include such piercing and sucking insects as ambush bugs (Phymatidae), bee assassins (Reduviidae-*Apiomerus*), and some asilid flies (*Promachus, Diagmites, Stenopogon, Proctocanthus, Sarapogon, Bombomima,* etc.). *Bombomima,* for example, is both a mimic and a predator of bumble bees. However, most of the supposedly specific bee predators also capture other insects on flowers when the opportunity presents itself. The most specific predators of bees are sphecid wasps (*Philanthus* and some species of *Cerceris*). These wasps capture a variety of bees on flowers and provision their cells with them. *Philanthus triangulum,* the "bee wolf" of the Old World, is a serious predator of honey bees. *Philanthus gibbosus* in this country sometimes provisions a single nest with as many as 200 small bees.

Among parasites of adult bees, the strepsipteran family Stylopidae is among the most highly specialized. The first instar larvae are injested from flowers by bees and carried in their honey stomachs to the cells where they are regurgitated on the pollen mass. One or more larvae penetrate the bee egg where they remain without molting until the prepupa is formed. They reach maturity at the same time as the host, but the female parasite remains in the abdomen of the bee in a larva-form condition. Hundreds of eggs hatch in her body and the larvae issue forth to the bee's abdomen and from it to each flower visited. Bee genera in the Northwest parasitized by stylopids are *Andrena, Pseudopanurgus, Dufourea,* and *Halictus.*

The best known internal insect parasites of adult bees are Diptera, family Conopidae (*Conops, Physocephala, Zodion, Myopa, Dalmannia*). The female fly seizes a bee usually in flight, on a flower, or at the nesting site and inserts an egg between its abdominal segments. The larva develops on haemolymph and fat body and keeps its posterior spiracles attached to the host tracheal trunks. The host is sterilized by the time the parasite reaches the third instar and dies just before the conopid forms a puparium which fills and distends its abdomen.

In Europe honey bees are invaded by a miltogrammine sarcophagid fly, *Senotainia.* The fly larviposits on the neck of the adult bee and the maggot develops in the thorax, finally leaving as a mature maggot from the bee's neck without killing it. Surprisingly, the other known species of *Senotainia* act as "cuckoo" parasites in the nests of aculeate wasps.

The fly genera *Melaloncha* (Phoridae), *Rondanioestrus* (Tachinidae), and *Myiapis* (Sarcophagidae) also oviposit or larviposit on adult bees, the larvae developing on the internal tissues.

Many insects act as more or less general scavengers and facultative predators in and near the nests of bees. When they penetrate a bee cell, they may consume the stored food, a dead larva, or even a living larva. Often the same species are pests of stored products. Included among them are dermestid beetles (*Trogoderma, Anthrenus*), grain beetles (*Tribolium*), and several well-known moth larvae such as the Indian meal moth, *Anagasta interpunctella,* the Mediterranean flour moth, *Anagasta keuhniella,* and the almond moth, *Anagasta cautella. Vitula edmandsii* and the lesser wax moth, *Achrona grisella,* are commonly found in the nests of both bumble bees and honey bees. These larvae often web over a bumble bee nest, destroying it completely late in the season. The greater wax moth is very destructive of honey bee nest combs; it is able to digest them, along with some pollen. Ants should also be mentioned in this category, although their relationships with bees are variable. Harvester ants (*Pogonomyrmex* spp.) steal pollen from unsealed cells of ground-nesting bees; argentine ants (*Iridiomyrmex humilis*) and others take honey from honey bee hives; and *Formica* spp. stand guard on flowers and prevent bees from landing on them. Certain species of formicine ants have been observed removing mature *Megachile rotundata* larvae from their nesting tunnels.

The many kinds of more specific depredators in the nests of bees are often spoken of as parasites. They differ from the previously mentioned insects in that they lay eggs in the nests of bees or where the first instar larvae can crawl into or be carried into the cells.

Clerid beetles of the genus *Trichodes* lay eggs on flowers, and young larvae are carried by various aculeates to ready-made holes in wood or clay banks. Once in the nests, the larvae feed on pollen and host larvae, moving freely from cell to cell and even from nest to nest when the hosts are gregarious. Some species, such as *ornatus,* prey widely on many aculeates, but others (like *similator*) restrict themselves to a single genus or family of bees in spite of their active larval life.

Meloid beetles of the genera *Nemognatha, Gnathium,* and *Zonitis,* like clerids, lay their eggs on flowers from whence the young larvae are carried to bee nests. After reaching the cell, they feed on the egg and then the stored pollen. The larvae of some species invade a second cell where they probably have to subdue a growing bee larva before they can feed on the pollen. After the second instar, however, meloid larvae are relatively inactive.

Other meloid genera gain entry to bee cells in various ways. For example, *Lytta* and *Meloe* lay their eggs in the soil and the larvae of the latter climb to flowers and from there are carried to nests by bees. *Hornia,* a specific parasite of *Anthophora,* lays its eggs in the bee cell in which it developed, and the young larvae crawl to the surface of the nesting site where they grasp passing bees. *Tricrania* oviposits on the soil surface and the larvae seek out their hosts.

The feeding habits of most parasitic bees are similar to those of meloids, but their eggs are laid in the cell with that of the host (or in place of it, as in the case of *Sphecodes*). Although the first instar cuckoo bee is moderately mobile (except in *Sphecodes*), succeeding instars are nearly immobile and never leave the original host cell. The bumble bee parasite, *Psithyrus,* like *Sphecodes,* has a relatively immobile first instar larva since it has no need to seek out and destroy a host egg or larva. The vespoid wasp genus *Sapyga,* a parasite of megachilids, is very similar in habits to most cuckoo bees, although the first instar larva does not possess long, pincer-like mandibles for destroying the host egg.

Sarcophagid flies (*Euphyto* and related genera) and anthomyid flies (*Hammomya*) also destroy the host egg and then feed on the stored pollen. The former larviposits in the host's nest entrance and then the maggots crawl to the open cells, and the latter lays its eggs on the host's pollen mass as it is being carried into the entrance. Apparently, the bee egg is not a nutritional necessity but is usually sought out and destroyed. Unlike clerids, meloids, and cuckoo bees, several maggots of these muscoid fly genera can mature in the same cell. Phorid flies (*Megaselia*) crawl directly into the cells and lay their eggs in the pollen mass. The tiny larvae feed only on the pollen, and occasionally the host bee larva is able to mature and actually eat the phorid maggots, thus neatly turning the tables.

Braulid flies (*Braula coeca*) are wingless creatures that inhabit honey bee nests. The larvae feed on nectar and pollen in the comb and the adults live on the bodies of the bees, stealing glandular food as it is being passed from bee to bee. They are most numerous on queens since the latter are the principal recipients of this food.

A large assemblage of insect parasites feeds directly in or on the bodies of mature bee larvae or young pupae. The adult parasite lays its egg in the cell (various Hymenoptera) or in the nest entrance (Diptera-Bombyliidae, the Mutillid-*Photopsis*). The hymenopterous groups include Leucospidae (*Leucospis*), Tiphiidae (*Brachycistus*), Pteromalidae (*Epistenia*), Mutillidae (*Dasymutilla, Photopsis*), Chrysididae (*Chrysura*), Gasteruptionidae (*Gasteruption*), Eulophidae (*Tetrastichus, Melittobia*), Torymidae (*Monodontomerus, Diomerus*), and Encyrtidae (*Coelopencyrtus*). Most of them thrust the ovipositor through the wall of the cell, or even through the nesting material and cell (*Leucospis*), to reach the larva, but the encyrtids and eulophids enter the cell first. Only one leucospid, tiphiid, mutillid, chrysidid, or gasteruptionid develops per host, but several to many eulophids, torymids, and encyrtids can develop on a single host. Most of the above forms feed externally, but *Coelopencyrtus* develops internally in *Hylaeus* after first undergoing polyembryony. *Tetrastichus megachilidis,* a parasite of *Megachile,* also develops internally.

Bombyliid flies (*Heterostylum, Anthrax, Villa*) are important parasites of bees that resemble the hymenopteran groups mentioned above in that they feed on the mature larva or young pupa. However, their maggots crawl through the nest and gain entry to the cell before it is sealed or crawl through cracks in the cell cap. They wait there until the host larva has almost completed its development before implanting on it. Only one maggot develops on each bee, and, in some cases, it migrates to another cell to partially consume a second host. Bombyliid pupae bore their way through the soil to the surface, and the adult females scatter their eggs into or close to the host nest entrances.

The rhipiphorid beetle, *Rhipiphorus,* exhibits a unique method of parasitism. *Rhipiphorus* (like meloid beetles) lays its eggs on flowers, and the larvae are carried to the bee cell. After dropping off the bee, the first instar *Rhipiphorus* enters the bee egg and remains there without molting until the host is nearly ready to break diapause as a prepupa. Then it develops internally to the third instar and emerges to complete its development wrapped around the neck region of its host.

Vertebrates

The most important vertebrate enemies of bees are toads, lizards, birds, skunks, field mice, and man.

Apicultural literature often refers to the giant toad (*Bufo marianus*) as an enemy of adult honey bees; large specimens station themselves by a particular hive until the bee population is decimated. Lizards have a similar habit, but they tend to move about more and feed on bees on a more occasional basis. Fence lizards have been seen to eat many leafcutting bees where nest shelters are easily reached. Horned toads (lizards) often consume alkali bees when they inhabit areas near nesting sites.

Birds are among the more important enemies of bees in some areas. King birds and flycatchers are especially well known as honey bee predators, but the list of birds that at least occasionally eat honey bees is a long one. On alkali bee nesting sites horned larks, blackbirds, and magpies have been seen to gather in large numbers to eat bees. Under some conditions, they probably eat enough of the bombliid parasites, *Heterostylum robustum,* to be more beneficial than harmful to the bee population. Areas within a nesting site that have a heavy concentration of larval bees are sometimes betrayed by the presence of holes made by the bills of curlews.

Skunks are important enemies of honey bees. They often station themselves by a hive and scratch on it to drive the bees out. Skunks are also serious predators of the larvae of ground-nesting bees. They have been seen to virtually plough an alkali bee site out of existence and to scratch away nests of *Anthophora occidentalis* in clay banks. Bears often cause havoc to apiaries in forested areas where they overturn entire hives to eat honey, adult bees, and larvae.

Defense Against Natural Enemies

Nest concealment is one of the most obvious defense mechanisms against natural enemies. Most nongregarious species place their nests near the crowns of plants or in depressions where some concealment is afforded. In gregarious species this tendency is usually less pronounced. For example, *Nomia melanderi* pioneers choose new nesting places primarily on the basis of soil conditions (including moisture, texture, and at least partial exposure to the sun). Given these conditions, they prefer to nest near plant crowns or at the edge of flat rocks or cow chips. As the nesting population increases and sheltered situations are largely pre-empted, completely exposed sites are readily accepted. The most striking form of nest concealment is that practiced by *Osmia rufohirta* which, as mentioned previously (page 78), drags its snail shell domicile to a depression and covers it with debris.

Architectural protection

Many architectural features of bee nests provide protection from both physical and biotic factors. These include cell walls and caps, burrow plugs, and entrance enclosures. Entrances may be closed with each departure and entrance (many panurgines), at night or during inclement weather (many halictines and other bees), or only when the nest is completed (most megachilids). It is probably impossible to determine which of these aspects of behavior have been fixed in response to physical hazards and which to biotic hazards. Perhaps both were responsible in many cases.

Some bees not only plug the entrance when the nest is completed but also camouflage the area over and around it. *Anthophora pacifica,* for example, carefully fills the nest, using soil around it for this purpose. Then it bites off the edges of the crater thus formed and, finally, drags soil back from several inches away to fill the crater. Even its cleptoparasite, *Melecta pacifica,* replugs the entrance and drags in soil from the surrounding area to make a uniform surface (unpublished). Such camouflaging efforts certainly seem to be directed against insect parasites or predators.

The function of entrance turrets on the nests of soil-inhabiting bees is not clear, although it is usually assumed that defense against parasites is involved. Entrance turrets of meliponine nests obviously function as a defense against insect predators and invading bees from other nests. In addition to restricting access to the nest, many meliponine turrets are lined with a sticky material which acts as a "tanglefoot" to invaders (Friese, 1914, *in* Schwarz, 1948).

Some bees close their uncompleted nests with their bodies rather than with a plug of soil. Halictinae is the best known group of soil-burrowing bees to employ nest guards of this type. Most species block the nest entrances with their heads, and all of them constrict their nest entrances. It is thought that the two habits are associated. Although the entrance constriction is evident in spring nests, it is more pronounced in summer nests, apparently to correspond with the smaller heads of the daughter bees (Sakagami and Michener, 1962). An extreme case is that of *Halictus malachurus* whose spring nest entrance diameter of 7 to 8 millimeters is reduced to 2.5 millimeters in late summer nests. The "neck" of halictine nest entrances is fashioned from soil brought from within the nest and pressed against the burrow wall with the abdomen. The lining is often hardened with a "salivary" substance (Sakagami and Michener, 1962). When an entrance is artificially enlarged, the lining is soon replaced by the bee guarding the entrance (stated for various species by Sakagami and Michener, 1962, and for *H.* (*Chloralictus*) *zephyrus* by Batra, 1964). Halictine nest guards are usually preforaging workers (reported for *H.* (*Chloralictus*) *inconspicuus* by Michener and Wille, 1961, and for *H.* (*C.*) *zephyrus* by Batra, 1964). According to Batra (1964), the nest entrance of *zephyrus* is constricted until it precisely fits the head of the nest guard. Although this type of relationship may exist for many species with a more or less circular head (for example, *Halictus* (*Halictus*) *ligatus* and *H.* (*H.*) *tripartitus*), the nest entrance of *Halictus* (*H.*) *farinosus* remains conspicuously larger than the head. In the latter species the nest guard is sometimes moderately aggressive and bites at a piece of straw thrust in her nest, but at other times she retreats as soon as she detects movement near the entrance. Apparently some halictines (*H.* (*Evylaeus*) *nigripes*) do not guard the entrance at all (Knerer and Plateaux-Quénu, 1967).

Similar nest constrictions or collars are common to the Australian and Asiatic species of *Allodapula.* Members of this genus restrict the interior diameter of the pithy stems that they occupy by cementing particles of pith, wood fibers, or other materials into a sharp restriction near or well below the entrance into the burrow. Upon disturbance of the nest, a female occupant will appear at the entrance and may bite the invader. On further disturbance, the bee retreats to immediately below the collar and positions herself so that the opening in the collar is blocked by the flattened posterior dorsal part of her abdomen (Michener, 1962b).

Individuals of the genus *Ceratina* also block their nest entrances, but in this genus the posterior portion of the abdominal dorsum is used as a plug. Furthermore, unlike Halictinae, the nest entrances usually are not constricted. Perhaps the somewhat "bell-bottomed" shape of the abdomen makes this unnecessary.

Less obvious, and perhaps less effective, is the nest blocking done by *Megachile rotundata* and, presumably, other species of the genus. At night the female rests with the tip of her abdomen near the nest entrance but not actually blocking it unless the nest hole diameter is nearly as small as that of the bee. In the morning she backs out, turns, backs in, and faces the entrance for a short period before taking her first flight (unpublished).

Osmia nigrifrons blocks the entrance to each unfinished cell (as well as the subsequent nest plug) with the tip of her abdomen. This behavior is most obvious when the female chooses holes of large diameter in which to nest. Before provisioning a cell, the cell cap is constructed so that only a small, off-center hole remains to be blocked.

Although the blocking of nest entrances with a portion of the body is apparently a defense mechanism against nest invaders, this behavior could have also evolved as a method of protecting the nest against rain damage or stabilizing humidity and temperature within the nest.

Avoidance and repellency

Other than nest entrance blocking, nonviolent forms of nest defense against natural enemies include avoidance and repellency. *Halictus rubicundus* is parasitized by the anthomyid fly, *Leucophora* sp., which oviposits in the pollen load of its host. The bee usually refuses to enter the nest when the fly is in close pursuit but, rather, takes long circling flights until the fly can no longer follow. It is usually another fly perched motionless near the entrance that succeeds in ovipositing (unpublished).

Many species of bees produce specific odoriferous compounds in their mandibular glands. According to Hockings, (1884, *in* Schwarz, 1948), species of *Trigona* with a strong odor are avoided by birds. Marianno (1910, *in* Schwarz, 1948), states that nearly all *Trigona* secrete odoriferous compounds that are repellent to other insects and birds alike. Although repellency is a likely role for the odoriferous mandibular gland secretions of bees, much more study is needed for valid affirmation. The secretion of a repellent odor probably serves for nest defense as well. Wheeler (1913, *in* Schwarz, 1948) induced the production of a strong rancid butter smell by thrusting his forceps into a swarm of *Trigona amalthea.*

Combat with the invader is a much more important nest defense mechanism among social apids than it is among solitary bess or halictines. Under crowded nesting conditions in a greenhouse, normally nongregarious species, such as *Anthophora pacifica,* sometimes attempt to enter each other's nests. If the nest occupant is at the entrance, she pounces on the would-be invader and attacks with her mandibles. If the invading bee gets into the nest, the owner drags her out and then attacks with her mandibles. This species likewise ejects the cleptoparasite, *Melecta pacifica,* but does not handle it as roughly. Under the same conditions, *Anthophora urbana,* normally a gregarious species, ejects another *urbana* when it actually enters her nest, but seems to pay no attention to its cleptoparasite, *Xeromelecta californica.*

Most nonsocial bees appear to pay little or no attention to either large or small insect parasites. For example, *Leucospis affinis* and *Sapyga pumila,* two hymenopterous parasites nearly as large as their host, *Megachile rotundata,* enter and leave host nests with apparent impunity. When a parasite is pushed out of a nest entrance, it seems to be merely because there is not enough room for host and parasite at once. Yet, this species, like those of *Anthophora,* becomes highly aggressive if a female of her own species attempts to usurp her nest.

The nonsocial bees likewise show no combativeness toward vertebrates. Birds may fatten themselves with bees on a nesting site of *Nomia melanderi* or in front of a *Megachile rotundata* shelter and the surrounding bees show no reaction. It appears that in such cases the stinging response is reserved for strictly personal defense and is not invoked until the bee is captured. The same noncombativeness is exhibited by the social halictines. Although *Halictus* (*Chloralictus*) species sometimes sting humans, this apparently results when the bee is trapped against the skin while imbibing perspiration.

Stings of nonsocial bees are generally much less painful to humans than those of social species of a corresponding size. In addition, the effects are less long-lasting, except in rare cases of specific allergies. An exception is the extremely painful sting of *Eulaema,* a bumble bee-sized euglossine.

Combativeness among social apids is highly developed. Colonies respond to invaders both individually and in concert, although the methods and tenacity of defense are variable between species and even within a species, depending upon the nature of the invader and the condition of the colony being invaded.

Apis and *Bombus* sting to protect their nests from insects and vertebrates, but the meliponines are stingless. *Apis* workers have a barbed sting which remains in its victim and continues to inject venom. Thus, for *Apis,* stinging is a sacrificial act committed in defense of the nest. The stings of most social Hymenoptera have long-lasting effects and have, thus, specifically evolved for nest defense rather than for personal defense.

Apis employs a special group of workers as entrance guards. These guards challenge approaching animals and usually admit only bees belonging to the colony. Once a guard has stung an invader, a gland associated with the sting releases an alarm odor which excites the other guards and tends to initiate a chain reaction. The notoriously fierce *Apis dorsata* and the central African honey bee, *A. mellifera adansoni,* are apparently no more readily aroused initially than other *Apis,* but the chain reaction following the first sting is more swift and far reaching.

Irritability of guard bees is increased by disturbance of the hive, by robber bees from other colonies, and by the presence of a large force of bees of foraging age not actively engaged as foragers. The last condition can be brought about by a cessation of a "nectar flow," inclement weather, or exceptional colony population. Strains of honey bees differ greatly in their prediliction for stinging, and "gentleness" is a factor sought after by bee breeders.

Species of *Bombus* vary in their likelihood to sting. *B. fervidus,* for example, is combative, whereas *B. morrisoni* is relatively passive. In a bumble bee nest, the larger workers are usually more aggressive than the smaller ones which often hide between the cells when the colony is disturbed. Bumble bees have the curious habit of lying on their backs and spreading their mandibles when they are alarmed but not aggressive enough to attack.

Although meliponine bees are stingless, they are not defenseless. Apparently, all species try to repel robbing attacks of other bees by biting their wing bases. Many species also defend their nests aggressively against vertebrates, biting at the roots of hairs and withers and crawling and biting ears, nostrils, and eye corners. Other species are so passive that they never attack man even when their nest is broken open.

Social apids have other forms of combative defense in addition to stinging and biting. Bumble bees often daub invading queens or *Psithyrus* with honey, rendering them nearly immobile. *Apis* often daubs invading insects such as *Psithyrus* with resin (propolis), although it is not clear whether the material is applied before or after the invader is killed. Several species of *Trigona* daub sticky fluids (resins?) on their enemies, especially invading bees (Drory, 1872, *in* Schwarz, 1948).

Trigona (*Oxytrigona*) expel a vesicating fluid from their anus which is capable of blistering human skin. The fluid is usually released at the time of biting, which increases the irritation (Drory, 1873, *in* Schwarz, 1948).

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Sources of Figures

The sources of many of the figures included in the text of this bulletin are as follows: Figures 5, 6, 7, 8, 9, 10, 12, 18, 21, 22, 23, 24, 26, 27, 28, 31, 34, 36, 51, Michener (1944a); 25, 82, Snodgrass (1956); 58, 59, 60, Stephen (1954); 61, 62, 63, 70, 71, 72, Mitchell (1960); 64, 65, Rozen (1958); 76, 77, 78, Stephen (1957); 84, 85, 86, 89, 90, 92, 94, 95, 96, 97, 98, 99, 100, 101, 102, Michener (1953a); 91, Burdick and Torchio (1959); 217, Fischer (1951); 220, 222, Kerr and Laidlaw (1956); 221, 288, 289, Michener (1961b); 225, Michener (1962b); 226, Sakagami (1960); 227, 266, 283, 290, 308, Malyshev (1935); 228, 276, Stephen (1965b); 229, 234, 245, Sakagami and Michener (1962); 230, Michener and Rettenmeyer (1956); 231, Michener and Lange (1957); 232, Michener and Ordway (1963); 233, Michener (1963); 235, 236, Kerfoot (1964); 237, 244, 246, Claude-Joseph (1926); 238, Michener and Lange (1958g); 239, 240, 247, Michener and Lange (1958d); 241, Friese (1923); 243, Michener and Lange (1958c); 248, 270, Kerfoot (1957); 251, Hurd (1958); 258, Linsley, MacSwain, and Smith (1956); 260, Plateaux-Quénu (1959); 262, modified from Linsley and MacSwain (1957); 271, Rozen (1964); 273, Roberts (1967); 274, Torchio (1965); 279, 280, Kerfoot (1964); 284, 311, Rozen (1967); 293, Rozen and MacNeill (1957); 295, 296, Ferton (1897); 305, Michener (1962c); 306, Michener (1955b); 307, Rozen (1965b); 317, Fischer (1955); 319, Linsley, MacSwain, and Smith (1955).

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