9-21-1990

Classification of the Apidae (Hymenoptera)

Charles D. Michener

University of Kansas

Recommended Citation

Michener, Charles D., "Classification of the Apidae (Hymenoptera)" (1990). *Mi.* Paper 153.
https://digitalcommons.usu.edu/bee_lab_mi/153

THE UNIVERSITY OF KANSAS
SCIENCE BULLETIN

Vol. 54, No. 4, pp. 75-164 Sept. 21,1990

Classification of the Apidae[1] (Hymenoptera)

BY CHARLES D. MICHENER[2]

Appendix: *Trigona genalis* Friese, a Hitherto Unplaced New Guinea Species

BY CHARLES D. MICHENER AND SHÔICHI F. SAKAGAMI[3]

CONTENTS

---

[1] Contribution number 2031 from the Department of Entomology, University of Kansas, Lawrence.
[2] Departments of Entomology and of Systematics & Ecology, and Snow Entomological Museum, University of Kansas, Lawrence, Kansas 66045.
[3] Kita-ku, Ainosato 1-Jo 6-chome, 2-2-610 Sapporo, 002 Japan.

ABSTRACT

This is a review of the classification of the family Apidae. Alternative phylogenies for the subfamilies are presented. The Meliponinae is considered in greatest detail; 21 genera are recognized. Keys are provided for genera and subgenera. Male genitalic characters, worker sting rudiments, and worker palpal characters have been little used in the past and are incorporated in this work. An African group of genera that has been regarded as ancestral in the past is here considered to be derived from an American group of genera. A new subgenus, *Papuatrigona* Michener and Sakagami, is described for *Trigona genalis* Friese from New Guinea. The subfamilies Euglossinae, Bombinae, and Apinae are treated in less detail, but with keys to genera and synonymies.

INTRODUCTION

This is an account of the classification of the family Apidae in the sense of Michener (1974), Sakagami and Michener (1987) and many others. So understood, the Apidae includes four taxa here considered subfamilies: the Meliponinae (stingless honey bees), Euglossinae (orchid bees), Bombinae (bumble bees), and Apinae (honey bees). As explained by Sakagami and Michener (1987), the Apidae appears to be the sister group of the Xylocopinae, which is currently usually included in the Anthophoridae. This arrangement probably will be changed when studies of the higher categories of bees are finished. If the Anthophoridae is then united with the Apidae, the Apidae in the present sense will probably become the subfamily Apinae, and the four current subfamilies will be tribes. The classification would then be that of Michener (1944). But for the time being it is sufficient to note that the Apidae in the present sense appears to be a holophyletic clade unless its complex pollen-manipulating behavior and associated structures arose independently in two or more subfamilies. This possibility seems unlikely because of other synapomorphies.

The following character states are well known synapomorphies of the Apidae, although they have been lost in parasitic genera and in queens of highly social forms (Meliponinae and Apinae): Corbicula present on outer surface of hind tibia in females. Rastellum (comb of setae across inner surface of apex of hind tibia) present in females (weak in some Meliponinae). Hind basitarsus of female articulated near anterior end of apex of tibia. These character states are, of course, associated with the pollen-carrying and manipulation behaviors which are distinctive for Apidae (Michener, Winston and Jander, 1978). Other synapomorphies of the family are: Basitibial plate completely absent. Pygidial plate completely absent. Maxillary palpus reduced, one or two segmented. Nests usually constructed in large or irregular cavities, cells built up rather than excavated in the substrate. (In most other bees although not in many Megachilidae cells and burrows are excavated into a substrate. Sakagami [1966] has pointed out that the ability to excavate in substrates, so obvious in Anthophoridae, is virtually absent in Apidae. This is presumably a synapomorphy, although Bombinae and Meliponinae often enlarge subterranean cavities and young queens of the former excavate hibernacula in the soil.)

Listed below are other character states that show that the four subfamilies of Apidae are related to one another, i.e., that no one of them is an anthophorid group that has convergently evolved the external features of Apidae. These characters suffer from not having been examined in many species; yet they have been examined in various species of each subfamily and appear to be family characteristics.

Cephalic salivary glands present and formed of many alveoli. In other families these glands are tubular (sometimes locally expanded) or absent (Cruz-Landim, 1967).

Hypopharyngeal glands attenuate, usually pedunculate, each discharging through a single duct. In other families these glands are usually shorter, sessile, crowded against the hypopharyngeal plate or rods, the single duct at each side absent or hidden among the acini (Cruz-Landim, 1967).

Thoracic salivary glands made up of short, simple tubes, quite distinct from collecting ducts; cells cubical and secretory tubes formed by cuboid cells. In other families the tubes are of diverse types but not as in the Apidae (Cruz-Landim, 1967, 1973).

Larva (except in *Apis*) with small, conical dorsolateral tubercles on at least the thoracic segments (Michener, 1953).

In this paper the largest subfamily, Meliponinae, is treated in some detail because of new findings as to relationships within this group. The other subfamilies are treated in a more cursory way.

TERMINOLOGY AND MATERIALS

The terminology used is that of Michener (1944) with some modifications. The word *thorax* is used for the thorax plus the propodeum, while segments 2-9 of the abdomen are referred to as segments 1-8 of the *metasoma,* so that segment numbers will conform to those used in almost all taxonomic work on bees. It would be logical to use the word mesosoma for the thorax plus the propodeum, but no confusion results from use of the shorter and more familiar word, thorax. Confusion as to segment numbering would result if the word abdomen were to be used instead of metasoma, because the propodeum is the first abdominal segment. The abbreviations T1, etc., and S1, etc., refer to metasomal terga and sterna by number. The term *basal area of propodeum* is continued, as a convenience, even though the triangular area (which comprises most of the basal area in Apidae) is apparently the metapostnotum (Brothers, 1976). (The triangular area is vaguely defined if recognizable at all in Apidae; loss of the lines demarking the triangle also occurs in certain other bees.)

The word *keirotrichia* (introduced by Michener, 1981: 4) is used for the small hairs of uniform length, blunt or (in other families of bees) briefly bifid or spatulate, occupying part of the inner surface of the hind tibia. The area occupied, the *keirotrichiate area,* is of great importance in the classification of Meliponinae. Unfortunately nothing is known about the function of these hairs.

Several special terms are associated with the pollen carrying and manipulating structures of Apidae. All are unique to females of the family (see Introduction, above) or to parts of the family. They are absent in most parasitic or robber taxa, and in queens of highly social bees. The *corbicula* is the smooth, concave or sometimes flat area, surrounded by long hairs, on the outer surface of the hind tibia. The *rastellum* is the comb of strong, usually blunt tipped bristles across the inner surface of the apex of the hind tibia (Fig. 184). It is reduced to ordinary hairs in some Meliponinae; I have described it in such cases as a rastellum made up of hairs, or tapering (pointed) hairs. I could have said "rastellum absent" but since there are all degrees of reduction, it is hard to say at what point such a comment would be appropriate. The *auricle* is the posterior expansion of the base of the hind basitarsus for pushing pollen up into the corbicula. It is absent in Meliponinae. The *penicillum* is a compact tuft of strong bristles arising near the front of the apical margin of the hind tibia, usually directed posteriorly, sometimes almost parallel to the apical tibial margin (Fig. 184). It is found only in Meliponinae. The *anterior* and *posterior parapenicilla* are groups of bristles arising at the anterior and posterior apical angles, respectively, of the hind tibia of some Meliponinae. There are always hairs in these positions; how coarse they must be to be called parapenicilla is a matter of judgment. The posterior parapenicillum is developed only in the genus *Meliponula.* The anterior parapenicillum is more widespread. Since these terms are difficult to define, I have used them only sparingly.

I have described positions of structures on the legs in the traditional way. Some authors advocate standardization by considering all legs to project laterally from the body. The following tabulation shows equivalent terms for the hind tibia and basitarsus; I use those in the first column:

outer surface	anterior surface
inner surface	posterior surface
posterior margin	upper margin
anterior margin	lower margin

Following Plant and Paulus (1987), I use the term *lorum* in place of submentum as used by Michener (1944, 1985).

The lengths of the *jugal* and *vannal lobes* of the hind wing are both measured from the wing base to the most distal part of the lobe. The *gonostyli* (third valvulae or sting sheaths) of workers in Meliponinae commonly have strong *setae* arising from distinct bases. In some genera there are also, or instead of such setae, *minute hairs.* These are consistently much smaller than the setae and distinctive setal bases are invisible at a magnification of 160×.

The male genitalia of Meliponinae sometimes have the gonocoxites opening basad, in a more or less straight line across the base of the genital capsule, as in most other bees. However, in some genera and in some preparations of others the capsule is split longitudinally from the base by a V-shaped incision and the gonocoxites open mesad along the arms of the V. To avoid repeated wordy descriptions, I call the former *rectigonal,* the latter, *schizogonal,* and forms believed able to exhibit both conformations are called *amphigonal.* The matter is discussed in greater detail under the subfamily Meliponinae.

The uses of certain other descriptive terms are indicated in the accounts of characters in Tables 1 and 2.

Except as otherwise indicated in the text, and except for some "subgenera" of *Bombus* and *Psithyrus,* specimens of the type species of each named supraspecific taxon (whether or not recognized as distinct) were examined. In the Meliponinae, the worker sting apparatus provides useful characters. The sting and associated structures were removed, usually with part of the metasoma, from relaxed specimens and placed for a few hours in a 10% solution of KOH at room temperature. Meliponines are weakly sclerotized; prolonged treatment and high temperature are not desirable. After passage through acidulated (with acetic acid) water and dissection as needed to reveal the structures, the material was placed in glycerin for study and eventually for preservation, like male genitalia, in microvials with the specimens from which they were taken. Mouthparts were similarly treated, sometimes without KOH, and sometimes were preserved in glycerin jelly on slides.

In my sketches of meliponine stings, the lateral parts of the sting apparatus give only a general impression of the first valvifer, base of the second valvifer, and their connections. These parts are weakly sclerotized, often difficult to see, and are often curved away from the observer. A new study, perhaps with uncleared material examined at right angles to the plane in which the structures lie, might reveal additional interesting characters.

By no means all species of each meliponine taxon were dissected, but divergent species of each were dissected where possible. Males are unknown for many species and three genera. It is often possible to verify major features of worker gonostyli and sting stylets, and of lancets if they are long, by opening the apex of the metasoma of a relaxed specimen, without dissection and clearing. This was done for various species to determine the consistency of character states found in dissected material of related species.

ANALYSIS OF RELATIONSHIPS AMONG APID SUBFAMILIES

Relationships among the four subfamilies, Apinae (A), Bombinae (B), Euglossinae (E), and Meliponinae (M), have been considered for many years and are discussed in several recent papers (Winston and Michener, 1977; Kimsey, 1984; Plant and Paulus, 1987; A. Weller, unpublished).

Unlike previous authors, I have ignored autapomorphies in this analysis. Although autapomorphies are important in showing monophyly of the subfamilies, inclusion of autapomorphies in a statistical analysis of relationships among subfamilies allows one to maximize the consistency index and thus improve the apparent strength of the analysis without really adding information on relationships among taxa. Each subfamily is quite distinctive and numerous autapomorphies could be listed, fewer for B than for the other three. Partly because the subfamilies are so different from one another, largely because of autapomorphies, structure in the relationships among them has been hard to establish.

Table 1 is a list of actual or potential synapomorphies that vary among subfamilies of Apidae. The apomorphous condition (1) was recognized by comparison with plesiomorphies (0) found in *Manuelia* (the base group of Xylocopinae, probable sister group of the Apidae, Sakagami and Michener, 1987) and other Anthophoridae, specifically *Exomalopsis* and *Anthophora*. Condition (2), when present, is presumably derived from (1), so that the codes for the states are ordered.

A few supposed synapomorphies that have seemed useful previously were omitted from Table 1. The stipital sclerite of the maxilla (Winston, 1979; called the subgaleal sclerite by Winston and Michener, 1977) was found to be strong with an anteriorly projecting angle at each end in M (as in *Xylocopa*), but relatively delicate in A B E. Because of similarity to *Xylocopa*, the strong sclerite was considered plesiomorphic, the delicate sclerite, synapomorphic for A B E. But *Xylocopa* was the wrong outgroup; *Manuelia* and other small Xylocopinae, and most other long-tongued bees, have a delicate sclerite and the strong sclerite in *Xylocopa* is probably related to the strength of the proboscis in that genus. The strong sclerite in M is therefore an autapomorphy, not a plesiomorphy.

Kimsey (1984) correctly points out that the loss of the basistipital process, as a synapomorphy of A B E as stated by Winston and Michener (1977), is an error because the process is present in B E, as in M. The loss is therefore an autapomorphy of A.

Kimsey (1984) described the sclerotic bridge below the foramen magnum (her postgenal lobes) as showing similarity between B and E. It is true that in these two groups the bridge is over half as wide as the foramen magnum whereas it is narrower in A; in M it is also usually narrow but is variable, so that I have chosen to ignore this feature for present purposes. In all four subfamilies the bridge includes a lightly sclerotized invagination, well illustrated for M by Camargo, Kerr, and Lopes (1967, pl. B). When the bridge is broad the invagination is large, especially so in E, but in no species that I have seen is the lower part of the bridge incomplete as illustrated by Kimsey for E. Plant and Paulus (1987) also did not consider this character state as a synapomorphy.

The slender base of the hind basitarsus of workers of Meliponinae (Figs. 184-187), i.e., the lack of an auricle in contrast to the other three subfamilies of Apidae (Figs. 188, 189), seems at first to be a plesiomorphy because other families of bees also lack an auricle and have a relatively slender basitarsal base. However, in all pollen collecting Apidae the basitarsus arises from near the anterior distal angle of the tibia, i.e., from near the anterior end of the apical tibial margin. In other families of bees the basitarsus arises nearer the median axis of the tibia. After discussion with Michael Prentice of the University of California, I believe it likely that the family characteristic of Apidae, anterior position of the hind tibiotarsal articulation, permitted development of the auricle by providing space for it. The auricle was later lost in ancestors of the Meliponinae when a different pollen manuipulating device (involving the penicillum) evolved, although the position of the tibiotarsal articulation was retained. Loss of the auricle is therefore an autapomorphy at the subfamily level and is not included in the cladistic analysis. Of course if this interpretation is incorrect, the meliponine condition probably would be plesiomorphic relative to other Apidae and a strong indication that M is the sister group of A B E.

Larval apids are not particularly similar to those of the outgroup, Xylocopinae, presumably because the latter have lost cocoon spinning behavior and correlated structures. The larval mandibles of A M are weakly sclerotized, the apices simple or with fine denticles. The larval mandibles of B E are robust, with considerable sclerotization, without denticles but with a strong tooth on the upper margins (Michener, 1953). Neither type of mandible occurs in the Xylocopinae but mandibles similar in general form to those of B E occur in various Anthophorinae. Nonetheless a decision as to which apid type is apomorphic is not clear, and I have chosen not to use this character in the cladistic analysis. The weak larval mandibles of A and M are quite different from one another and their weakness could be convergent, not synapomorphic.

For cladistic analysis the synapomorphies listed in Table 1 were plotted upon all possible topologically different dendrograms for the four subfamilies. Five of the results are shown in Figures 1-5. The character states of the four subfamilies are indicated in the same table by the initials (A, B, E, and M) indicated above.

The total number of character state changes, i.e., dendrogram length, as well as corresponding consistency indices, are indicated in Figures 1-5. The calculations were made by the computer program McClade version 2.1 (Maddison and Maddison, 1987) using a hypothetical outgroup consisting of all the plesiomorphies. The most parsimonious tree is Figure 1, which corresponds to the traditional view of apid classification (Michener, 1974).

Subsequently Michael Prentice and Howell V. Daly of the University of California kindly sent me their as yet unpublished analysis of subfamilial relationships of Apidae. They have found other subfamilial characters, the details of which they will describe and illustrate. Of their characters I found eight to be particularly useful and polarizable with some confidence, using the same outgroups that I used previously. These are four characters of the prosternum, which are particularly strong, one of the internal ridge in front of the middle coxa, two of the maxilla, and one of the pharyngeal plate.

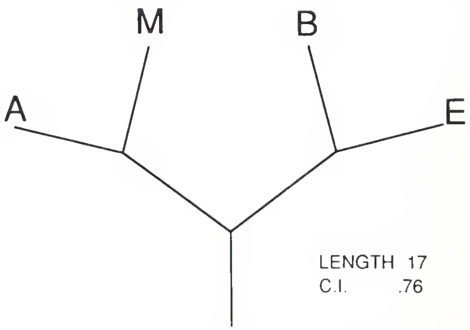


Figure 1. Dendrogram showing possible cladistic relationships among subfamilies of Apidae. A = Apinae, B = Bombinae, E = Euglossinae, and M = Meliponinae. Length = total number of character state changes in 12 characters. CI = consistency index.

Analysis using the parsimony computer program PAUP version 2.4 (Swofford, 1985) (hypothetical ancestor, all plesiomorphies) yielded (for my original 12 characters) dichotomous trees like Figure 1. However, for all 20 characters, the result was like Figure 3. PAUP version 3.0 gave two equally short trees for all 20 characters; one was dichotomous like Figure 1, the other had a branching pattern like Figure 3 (tree length 28, consistency index .786, retention index .714).

I believe that the evidence is strong that the A and M are sister groups, as indicated by Figures 1 and 3. This is not in agreement with the recent views of Winston and Michener (1977) and Kimsey (1984), who regarded M as the sister group to the clade of A B E, as in Figures 4 and 5. Some common character states for A and M, i.e., states that support the sister group relationship of these subfamilies, are losses. However striking, they might be independently evolved in A and M. Examples are: reduction of man-

TABLE 1. Characters used in cladistic analysis of subfamilies of Apidae. Distribution of character states is indicated thus: A = Apinae; B = Bombinae; E = Euglossinae; M = Meliponinae. (0) = the plesiomorphous character state; (1) = the apomorphous alternative.

Character 1. Body size. (0) Small to middle-sized and often rather slender (A M). (1) Large and robust (B E). Polarization is based on the small size of *Manuelia* but since some anthophorids are large, it may be incorrect.

Character 2. Papillae on distal parts of wings. (0) Absent (A M). (1) Present (B E). In various groups of bees, large sized taxa have evolved, and they often (although not always) have papillate wings. There is no certainty that these character states are homologous in the large Apidae (B E). Moreover, since large body size and wing papillae are often associated, this character suffers from the same problems as character 1; neither is a strong character.

Character 3. Grooves and ridges on outer surface of mandible. (0) Present (Figs. 173, 174) (B E). (1) Absent (Fig. 175), or in M with a single groove (Fig. 172) apparently not homologous to grooves of other bees (A M). A M are almost the only bees with greatly reduced mandibular grooves (Michener and Fraser, 1978). Therefore loss of grooves is likely to be homologous. However, as in all loss characters, convergence is possible and seems more likely because the highly social bees (A M) are the ones in which extensive nest structures of wax are made. Possibly relatively weak and more or less grooveless mandibles are adequate for such work, especially since these bees do not excavate burrows and cells.

Character 4. Mentum and "lorum" (= submentum). (0) United (E). (1) Separated (A B M). Plant and Paulus (1987) showed that these sclerites which have been regarded as primitively separate but united in most bees (Michener, 1985) actually evolved in the opposite direction and are separated only in A B M. It appears to be a strong character.

Character 5. Arolia. (0) Present (A M). (1) Greatly reduced (B). (2) Absent (E). This reduction and loss could have occurred independently, since arolia are lost in diverse groups of bees. The character states are ordered.

Character 6. Upper margin of main axis (basal part of malus) of strigilis. (0) Not expanded and without an apical prong (Fig. 176) (M). (1) Expanded (anterior velum of Schönitzer, 1986) and ending in a short prong or lamella above the pointed apex of the malus (Fig. 177) (A B E). The expansion is weakly developed in some Exomalopsini, Centridini, etc., but otherwise appears to be a synapomorphy for A B E. A distinct possibility, however, is that the expansion was lost in M, and the polarity therefore reversed.

Character 7. Hind tibial spurs. (0) Present (B E). (1) Absent (A M). Since the apomorphy is a loss, it might have arisen twice rather than once. Loss of tibial spurs is exceedingly rare in other bees, however.

Character 8. Stigma. (0) Large, several times as long as prestigma (Figs. 162-171) (M). (1) Small, shorter than prestigma (Figs. 178-182) (A B E). Stigmal reduction occurs in such a wide variety of bees that there is no strong evidence of its homology in A B and E. Alternatively, enlargement of the stigma occurs in minute Hymenoptera (Danforth, 1989), perhaps including minute meliponines, so that the polarization shown here may be wrong.

Character 9. First recurrent vein. (0) Longer, more oblique, not angulate or in B moderately so (Figs. 178-181) (B E). (1) Short and angulate (Figs. 162-171, 182), sometimes absent in M (A M). This character seems strong but may be in part related to size. As Danforth (1989) has shown, oblique veins tend to be more transverse (hence shorter) in small forms and more longitudinal (hence longer) in large forms. The angulation seems to remain as an indication that the condition is homologous in A and M. The states could have been considered as a developmental series from E → B → A M but evidence for the origin of the short, angulate vein of A M from the longer and somewhat angulate vein in B is lacking; I have therefore recognized only two states for this character.

Character 10. Jugal lobe of hind wing. (0) Present (Figs. 162-171, 182) (A M). (1) Absent (Figs. 178-181) (B E). This loss could have occurred independently in B and E. However, it did not occur in other bees. Plant and Paulus (1987) depreciate the loss as a synapomorphy, noting that in E the jugal lobe is replaced by a row of bristles. This is true, but the presence of bristles does not show that the lobe was not first lost.

Character 11. Gonobase of male. (0) Well developed (Figs. 189, 190) (B E). (1) Absent or nearly so (Figs. 138-161, 183) (A M).

Character 12. S7 and 8 of male. (0) Well developed (B E). (1) Much reduced or S8 almost absent (A M). Characters 11 and 12 involve reductions and losses that could have occurred independently, especially considering the great morphological differences between A and M in these features. However, loss of the gonobase is rare among bees and is therefore possibly homologous in the Apidae.

---

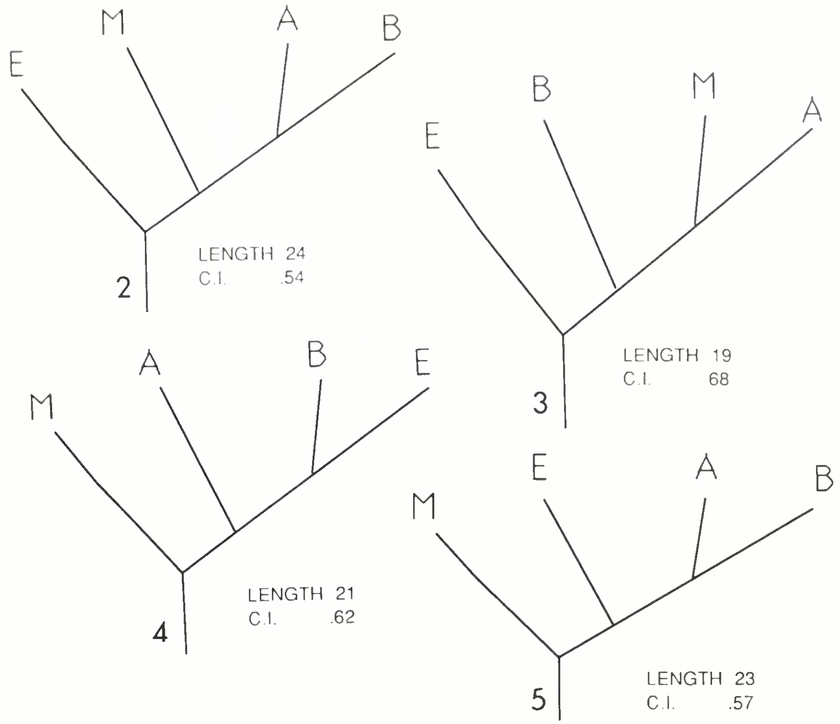
dibular grooves (3, Table 1), loss of hind tibial spurs (7, Table 1), and reduction of hidden sterna and most male genitalic parts (11, 12, Table 1). Some prosternal synapomorphies, however, such as its slender body, large anterior region and anterolateral processes, elongate groove instead of round apophyseal pit, etc., are not loss features and seem unlikely to have evolved convergently. Another such synapomorphy of A and M is the broad pharyngeal plate with transverse (rather than longitudinal) fields of sensilla (to be illustrated by Prentice and Daly).

The choice between a cladistic pattern like Figure 1 and a pattern like Figure 3 is not clear. To support the latter, one needs strong synapomorphies for the clade A B M. The articulation of the lorum and mentum (4), unique among bees, is the only strong, convincing character state of this sort, although one prosternal character state and states of the mesepisternum (in front of coxa 2) and pharyngeal plate also support A B M as a clade; these and others will be described and illustrated by Prentice and Daly. In support of the alternative, the dichotomous pattern of Figure 1, are apparent synapomorphies of B E. Body size and papillate wings (1, 2) perhaps are not polarized correctly, and the presumed derived conditions appear repeatedly among other bees, so might have arisen independently in B and E. Large size and papillate wings are often correlated among bees. The great reduction or loss of the jugal lobe of the hind wing (10) is unique among bees and thus strongly supports the sister group relationship of B and E, although the actual condition is rather different in the two subfamilies. Likewise, the great reduction in B and loss in E of the arolium and associated structures (5) supports the sister group relationship of these taxa. Both of these are losses and of course could have evolved independently.

Some apparent plesiomorphies appear in M, their corresponding apomorphies characterizing A B E. These are responsible for the trees such as Figures 4 and 5, showing M as the sister group for A B E, as advocated by Winston and Michener (1979) and Kimsey (1984). One such character is (6), the simple main axis of the malus of the strigilis in M, contrasted with the expanded lamella or prong (anterior velum of Schönitzer, 1986) found on the velum of A B E. An approach to such a structure occurs in some anthophorids such as *Epicharis*, although in most bees including *Manuelia* it is simple. If Figures 1 and 3 represent the most probable cladistic patterns, the strigilis of M probably represents a reversion. Likewise the large stigma of M (8) seems to be plesiomorphic relative to the reduced stigma of A B E, since large stigmata generally characterize the more primitive bees, including *Manuelia*, etc. As is well known, however, relative stigmal size is negatively correlated with body size in aculeate Hymenoptera (Danforth, 1989). The reduced wing venation of M suggests that this group originated as minute bees, which may therefore have had an enlarged stigma as a reversion that has been retained along with reduced venation even in larger meliponines. Finally, the slender base of the hind basitarsus of workers, i.e., the lack of an auricle, long seemed to me an important plesiomorphy contrasting with the unique synapomorphy, presence of an auricle, in A B E. For reasons discussed above I now regard loss of the auricle in M to be an autapomorphy or reversion. These same comments apply to the Plant and Paulus (1987) diagram of relationships (Fig. 2), except that in place of A B E, one should read A B.

A cladogram with M as the lowest branch (sister group to A B E) seems reasonable because we know that M is old (Cretaceous; Michener and Grimaldi, 1988a, b). M is also the most widely distributed; in appropriate climatic zones it occurs worldwide. The other three subfamilies are all geographically limited—A to Eurasia and Africa before being dispersed by man, B to the Holarctic, Oriental (montane) and Neotropical regions, and E to the Neotropics. Such distributions might indicate groups less old than M.

It will probably be possible to greatly increase the number of characters showing the similarities of large, robust taxa (B E) as opposed to the small bodied taxa (A M). For example, the lateral promotor of the mid coxa in B E is V-shaped and the lower branch extends forward behind the second and third pleuroaxillary muscles. In A M this muscle is much smaller, not or scarcely V-shaped, and does not extend so far for-



Figures 2-5. Dendrograms showing possible relationships among subfamilies of Apidae. Explanation as for Figure 1.

ward (Wille, 1956). Likewise the dilator of the salivary syringe has its origin below the posterior lateral margin of the prementum in B E, on the anterior lateral margin in A M (Wille, 1971); the latter condition is considered derived by Wille. These internal characters and characters 2, 8, and possibly 9, Table 1, are likely to be related to size and robustness rather than phylogeny.

The number of plesiomorphies that unite B and E could be augmented, but the corresponding presumed apomorphies of A and M are not necessarily homologous. Besides characters 3, 7, 9, 11, and 12, such plesiomorphies include (a) the form of the penis valves, which are very divergently modified in A and M; and (b) the presence of volsellae in the male (see discussion of Bombinae), which are absent in A and M. Characters 11 and 12 are actually divisible into several such states that may have evolved independently.

While Figures 1 and 3 appear to represent the best cladograms, it is difficult to choose between the two. It is therefore premature to decide on a classification that indicates structure among the four taxa. For this reason and because of their phenetic distinctness, I term them all subfamilies. Even if one of the cladograms were known to represent the truth, I see no reason to unite two or three of the taxa in a single subfamily since all four are so different from one another.

There is, of course, considerable interest in the question of whether the highly social behavior of A and M is homologous or convergent. If either of the hypotheses indicated by Figures 1 or 3 is correct, as is likely, such behavior probably arose once. The other three cladograms (Figs. 2, 4, 5) suggest independent origin of highly social behavior in the two subfamilies, a view supported by Sakagami (1971), Winston and Michener (1977) and Kimsey (1984).

Unfortunately fossil Apidae as now known do not help in the solution of the problems discussed above. For most of them, anatomical details are not sufficiently well preserved or described. The fossil Apidae have been reviewed by Zeuner and Manning (1976) and in part by Wille (1977). Those with clear relations to existing subfamilies are discussed under the subfamilies, below. Taxa of greater interest, because they appear to represent extinct types that might shed light on the relationships of the subfamilies, are *Chalcobombus, Sophrobombus* (placed in Meliponinae by Zeuner and Manning) and *Electrapis* (with subgenera *Protobombus* and *Roussyana,* placed in the Apinae by Zeuner and Manning). All these are from the Eocene Baltic amber and none is so well preserved or studied that definitive placement is possible.

KEY TO THE SUBFAMILIES OF APIDAE

1. Posterior tibial spurs absent; arolia present; jugal lobe of posterior wing present; labrum three to four times as broad as long; marginal cell open or with veins narrow or evanescent distally or, if completely delimited by strong veins, reaching to within one-third or less of its length from wing tip 2

—Posterior tibial spurs present; arolia greatly reduced or absent; jugal lobe of posterior wing absent or much reduced; labrum at most twice as broad as long; apex of marginal cell completely delimited by strong veins, separated from wing tip by a distance equal to at least half length of cell. 3

2. Marginal cell open (or its veins weak) distally (Figs. 162-171), tapering from broad base; second recurrent vein absent; stigma of moderate to large size, extending well beyond base of vein r; claws of female simple; sting reduced, not exsertable. . . . . Meliponinae

—Marginal cell complete, parallel-sided for a large part of its length; second recurrent vein present; stigma minute, not tapering beyond base of vein r; claws cleft; sting well developed . . . . Apinae

3. Proboscis reaching at least to base of metasoma in repose; scutellum produced posteriorly to a margin overhanging metanotum and propodeum; posterior tibiae of male usually swollen, always with a deep hairy fossa on apical half of posterior margin . . . . Euglossinae

—Proboscis usually not reaching behind middle coxae; scutellum rounded posteriorly, overhanging metanotum but not propodeum; posterior tibiae of male neither swollen nor fossate . . . . Bombinae

SUBFAMILY MELIPONINAE

These are the stingless honey bees found in tropical and southern subtropical areas throughout the world (Roubik, 1989). They are the only highly social bees except the true honey bees, subfamily Apinae. There are several hundred species, an approximation to the real number being impossible because of the abundance of cryptic species, differing from their relatives only on the bases of seemingly trivial characters. Most genera in most areas have not been adequately analyzed for recognition of such forms; a good start for part of one genus *(Partamona)* is the fine work by Camargo (1980).

Description: Minute (1.8 mm long) to moderate sized (13.5 mm long), sparsely hairy or short haired to moderately hairy bees. Eyes usually bare. *Claws of female simple; arolia present; hind tibial spurs absent;* strigilis without prong on anterior side; hind basitarsus rather slender at base, without auricle; hind tibia of worker with penicillum. *Forewing with venation reduced* (Figs. 162-171); marginal cell often open apically, at least distal parts of its veins much narrower than veins of basal part near stigma; *stigma large to moderate sized,* vein r arising near middle; in *Melipona* stigma slender but in other genera stigma rather broad and margin within marginal cell convex; prestigma short, often almost absent; second recurrent vein absent; first recurrent vein, when present, short and strongly angled near anterior end; first and second submarginal cells, at most, weakly defined, third not defined, because of weakness or absence of transverse cubital veins. Hind wing with well developed jugal lobe one half to one third as long as vannal lobe. Clypeus flat, not protuberant. Maxillary palpus minute, one-segmented, sometimes less than twice as long as wide and extremely inconspicuous. Male S8 absent except for laterally compressed remnant of spiculum (largest in Fig. 145); S7 flat, weakly sclerotized and usually without large apodemes; S6 transverse, with lateral apodemes and usually with median apical process. Male gonobase absent or represented by narrow ribbon or weak lateral sclerites; gonostylus long, usually slender, simple (presumably this is the upper gonostylus, the lower one being absent); penis valve large with heavily sclerotized, slender, curved, tapering apex; spatha usually present; volsella absent. *Female with sting and associated structures greatly reduced* (Figs. 9-48).

A hitherto unrecorded apomorphy of Meliponinae, called to my attention by Ricardo Ayala, is the demarcation of the preaxilla. In most bees, including other subfamilies of Apidae and numerous groups of anthophorids, the preaxilla is separated from the dorsal surface of the mesoscutum by a strong supra-alar carina, immediately mesad to which is a groove that joins the scuto-scutellar suture posteriorly (Michener, 1944). In Meliponinae the supra-alar carina and adjacent groove are absent. The dorsal surface of the mesoscutum is either separated from the preaxilla by an angle (it could be called a weak carina but is not raised) or it rounds onto the preaxilla with only a change in sculpturing to indicate the upper margin of the preaxilla.

Camargo, Kerr, and Lopes (1967) give an excellent morphological account of *Melipona marginata* Lepeletier. Sakagami (1982), Wille (1983), and Roubik (1989) review biology of Meliponinae.

Larva: Without strong tubercles, but with small, conical, dark dorsolateral tubercles on first three to ten body segments. Mandible attenuate, apex blunt, concave on inner surface, margins and often apex denticulate but without large teeth.

Larvae are described and illustrated by Michener (1953) and Oliveira (1965).

Nest: The nests of most species occupy cavities that the bees find, and may limit by walling off unused areas, but the bees usually do little or no excavating. Some excavating is probably done by certain of the species that nest in the ground, and is done by some species that regularly establish their nests in nests of *Nasutitermes*. The cavities used vary from small, e.g., an abandoned cerambycid burrow, to large hollows in a tree trunk or cavity in the soil. Other species, however, do not occupy cavities but make exposed nests on tree branches or on cliff faces.

Nests are made of mixtures of wax secreted from the metasomal terga and resins and gums collected by the bees. A few species add mud, feces, or other materials to certain parts of the construct.

Cells are mass provisioned and either clustered or arranged in combs which are usually horizontal. The cells open upward (rarely horizontally) and are closed after an egg is laid on the provisions. Food is stored in pots, quite different from and larger than brood cells. Details of nest architecture are dealt with by Schwarz (1948); Michener (1961); Wille and Michener (1973); Fletcher and Crewe (1981); Sakagami, Yamane, and Hambali (1983); Sakagami, Inoue, Yamane, and Salmah (1983); Roubik (1979, 1983); and works cited therein. Reviews are by Sakagami (1982), Wille (1983), and Michener (1974).

Social behavior: This is one of the two groups of highly social bees, with "permanent" colonies and morphologically very different female castes (queens and workers). In contrast to the Apini, new nests are begun by workers going back and forth from an existing colony, carrying building materials and food. Ultimately a young queen goes to the new site, workers stay there, and independence from the old colony is gradually attained. Long distance dispersal by individual reproductives or by swarms is therefore impossible. Colony size ranges from a few dozen workers to thousands.

Distinctive aspects of meliponine social behavior include oviposition rituals and communication concerning resources. These are discussed further in the next section, on relationships among meliponine genera.

Distribution: This subfamily is found in the tropics of the world (except not east of the Solomon Islands in the Pacific). To the south it extends into temperate regions (about 35°S in Australia and South America, 28°S in Africa). To the north it extends little beyond the Tropic of Cancer (23.5°N).

Relationships among Meliponine Genera

History: The classification of stingless honey bees has been presented very differently by different authors (see review by Sakagami, 1982). Schwarz (1948) and Michener (1944) recognized only two principal genera, *Melipona* and *Trigona*. *Lestrimelitta* was often recognized as a distinct robber genus, lacking pollen collecting and carrying structures (e.g., by Schwarz, 1948) and *Meliponula* and *Dactylurina* often received generic status (e.g., by Wille and Michener, 1973). Wille (1979b) likewise recognized *Trigona* (with numerous subgenera) and *Melipona*, but in addition five small genera: *Cleptotrigona, Dactylurina, Lestrimelitta, Meliplebeia,* and *Meliponula*.

Moure (1951, 1961), however, elevated many of the subgenera to the genus level and described additional genera so that in 1961 he recognized 23 genera (no subgenera) from the Old World and 10 from the New World. In the New World, however, he recognized 27 supraspecific taxa (genera and subgenera). Moure (1971) elevated some of the subgenera (and by inference others) to the genus level, making his classification of New World Meliponinae more nearly comparable to that of the Old World. An additional genus was added subsequently (Camargo and Moure, 1983).

Sakagami (1975, 1982) presented an intermediate system, in some ways similar to that developed in the present study.

Many of Moure's genera (based on external characters of workers) seemed to me so similar that I saw no need to recognize them at the genus level, especially since some were justified largely on the basis of a single character. Nonetheless, the male genitalia of two of his externally similar genera, *Liotrigona* and *Hypotrigona,* turned out to be so different that I could not consider them congeneric (Brooks and Michener, 1988). Some details could not even be homologized. The sixth and seventh sterna were also very different, as were the gonostyli of the workers. These are all characters that can only be revealed by dissection. On the basis of external characters of workers, Brooks and Michener (1988) could not place certain species as to genus.

Analysis: In view of the situation described above, I reviewed all the supraspecific taxa, examining the worker gonostyli and sting, worker labial palpi (see Michener and Roubik, in press), as well as the male genitalia and hidden sterna when males were available. Originally the taxa had been based on external characters of workers.

Table 2 is a list of characters with synapomorphic character states. Autapomorphies were not included in the computer analysis and most of them are not listed in Table 2. They are often numerous, however, and contribute to the recognition of taxa but not to an understanding of their relationships.

Using a character matrix based on the characters 1-16 listed in Table 2 and the PAUP 2.4 computer program (Swofford, 1985), a preliminary cladistic analysis of supraspecific taxa was made. Six of the characters had either three or four states. PAUP options were as follows: Root = ancestor; addseg. = closest; swap = global. Some of the characters were polarized, as indicated within Table 2; others were not polarized for reasons stated in that Table. *Bombus* and *Manuelia* were used as outgroups, but the "ancestor" in the PAUP computer analysis was artificial, consisting of all the character states coded 0, i.e., plesiomorphic for the polarized characters.

Usually because of similarity to other taxa, but sometimes because of lack of material (males not known), certain taxa were omitted from the computer analysis. Of 52 supraspecific taxa recognized by one or more authors, 26 were included in the preliminary

TABLE 2. Characters used or considered in cladistic analyses of genera and subgenera of Meliponinae. Characters marked with asterisks were used in the generic analysis, after generic limits had been determined. (0) = the plesiomorphous character state; (1), (2), etc., indicate apomorphous alternatives in sequence such that (1) is thought to be derived from (0), (2) from (1), etc.

Character 1. Apical margin of mandible of worker (Fig. 172). (0) Most or at least lower half of mandibular margin edentate, usually one or two small teeth at upper end (or in the upper half) of margin. (1) With four or five teeth occupying entire margin. In other subfamilies of the Apidae the mandibular margin (at least of females) is partly edentate (Michener and Fraser, 1978) but in other bees with a broad mandibular margin (Xylocopinae, Megachilidae), it is usually dentate. This condition therefore could be plesiomorphic for the Meliponinae. This interpretation is supported by the fully toothed mandibular margin of the Cretaceous *Trigona prisca* Michener and Grimaldi (1988a, b). However, a toothed mandibular margin is found in only two recent taxa, *Trigona (Trigona)* and *Paratrigona,* quite unrelated groups neither of which is near the base of the dendrogram derived later. This distribution suggests that a fully dentate mandibular margin may be a derived feature. Moreover, the presence in Meliponinae of the oblique mandibular groove, not homologizable with grooves of other bees, suggests that such mandibular features are basic for Meliponinae, with teeth developed later, as apomorphies not homologous to teeth of xylocopine or other bees. In summary, the polarity of this character is in doubt but probably multiple teeth are a derived feature. This character was not used in the generic analysis (a) because of doubtful polarity; (b) because within *Trigona* multiple teeth characterize only one, derived subgenus (for cladistic analysis involving a variable feature, one should use the plesiomorphic condition since the objective is to clarify basal connections, not evolution within the taxon); and (c) because as a generic character state, multiple teeth characterize only *Paratrigona* and are thus in effect an autapomorphy.

Character 2. Mandible of male. (0) With apical acute point and preapical tooth on upper margin (Fig. 135), i.e., the apex of the pollex (see Michener and Fraser, 1978). This is the mandibular form of many bees, including *Manuelia* and *Anthophora.* (1) With apical point rounded, little exceeding pollex, the two separated by only a shallow emargination, or apex of mandible truncate, rounded, or rarely pointed (Fig. 136, 137). The supposedly plesiomorphic condition described above (0) is found among Meliponinae in *Hypotrigona.* Ths character was not used in the generic analysis since character state (1) is either a uniquely retained plesiomorphy or an autapomorphy of *Hypotrigona.*

**Character 3.* Scutellar fovea of worker. (0) Shining transverse depression on scutoscutellar line simple. (1) Depression on scutoscutellar line extending posteriorly into scutellum on midline, forming a V-shaped or U-shaped fovea in scutellum (Fig. 190). Character state (1) is not found outside of the Meliponinae and is therefore no doubt a derived feature. It characterizes *Nannotrigona* and *Scaptotrigona.*

**Character 4.* Keirotrichia of worker. (0) Keirotrichia uniformly distributed (as in other subfamilies of Apidae) over wide area from premedian longitudinal ridge of tibia nearly to posterior margin of tibia, leaving at most a narrow bare margin (as in *Plebeia* s. str., Fig. 184). (1) Keirotrichia leaving broad bare tibial margin (as in *Hypotrigona*). (2) Keirotrichia restricted to median longitudinal band on tibia (as in *Trigona,* Fig. 185). There is more or less a continuum between (0) and (2) but in nearly all cases there was no problem in assigning a species to one category or another, using the exemplars listed above. All other Apidae show state (0). Xylocopinae have a very different sort of tibia but lack bare zones comparable to those for states (1-2). The polarity indicated above can be questioned on the basis that the oldest fossil bee, the late Cretaceous *Trigona prisca* Michener and Grimaldi, has state (2). Moreover the Oligocene *Proplebeia dominicana* (Wille and Chandler) has state (1). These findings are hardly decisive, however.

**Character 5.* Hind tibial cross-section of worker. (0) Inner surface of hind tibia flat from premedian longitudinal ridge (most elevated part of inner surface) to posterior margin (with or without hairless margin) as in other Apidae. (Anthophoridae have no bare margin.) (1) Inner surface of hind tibia with narrow depressed zone along posterior margin (as in *Plebeia* s. str., Fig. 184). (2) Inner surface of hind tibia with broad depressed posterior zone (as in *Hypotrigona*). (3) Inner surface of hind tibia with broad raised median longitudinal zone with keirotrichia, behind which the depressed smooth zone is often as broad as the median ridge (as in *Trigona,* Fig. 185). This character is related to character 4 but provides additional information. For example there are forms having character state (0) of character 4 but state (1) of character 5. The polarity indicated above can be questioned on the basis of fossils as for character 4. There is evidence that state (1) has arisen more than once or has reverted to (0). Thus in *Plebeia (Scaura) timida* (Silvestri) the condition is intermediate between (0) and (1), although its relatives have state (1) and in the distantly related genus *Meliponula* intermediate conditions also exist.

Character 6. Fringe along posterior margin of hind tibia of worker. (0) Composed entirely of simple hairs (Figs. 184, 186, 187). (1) Including plumose hairs (Fig. 185). Polarization of this character remains uncertain, since plumose hairs are found in some other Apidae *(Bombus)* and on the equivalent tibial area of many Xylocopinae. However, the groups with such plumose hairs (*Dactylurina* and most *Trigona*) are not basal in the dendrograms developed later, a finding that supports the polarization indicated. (A few branched hairs are also found in *Plebeina* and some species of *Meliponula,* and in two species of *Plebeia.*) This character was not used in generic analysis because a plumose fringe is a generic character state only for *Dactylurina* and thus would appear as an autapomorphy. Although plumose hairs are prevalent in *Trigona,* the presumably plesiomorphic alternative also exists in that genus and would be used in analysis at the genus level. (See explanation for character 1.) (See also character 28.)

Character 7. Hairs on posterior apical angle (or curve) of hind tibia of worker. (0) Slender, often very long but similar in form and color to nearby hairs. (1) Robust bristles, thicker than nearby hairs and amber to blackish in color, forming the "posterior parapenicillum" of Wille (1979b). This character was not used in the generic analysis because all forms having state (1) are considered congeneric; the character state is therefore an autapomorphy of *Meliponula* at the genus level.

**Character 8.* Rastellum. (0) Of strong bristles, mostly ending somewhat bluntly. (1) Of soft hairs, with slender, tapering apices, suggesting tapering hairs of other bees. In *Dactylurina* and some others the bristles are strong but taper to slender points; they were coded as (1). Since the rastellum is absent in other families of bees, one would assume that in the Apidae a rastellum of ordinary hairs should be plesiomorphic relative to a rastellum of strong bristles. However, all subfamilies of Apidae other than Meliponinae have the rastellum strong in all nonparasitic, non-queen females. If, within the Meliponinae, the rastellum evolved from weak to strong, the same must have happened elsewhere in the Apidae, i.e., there must have been at least two origins of the strong rastellum. I prefer the view that it originated once, in primitive Apidae, and is reduced in some Meliponinae, such as *Meliponula.* The potential for reduction and loss is indicated by its loss in parasitic genera of Euglossinae and Bombinae, robber genera of Meliponinae, and in queens of all highly social forms. The polarity indicated above is in accordance with this view.

**Character 9.* Submarginal cells of forewing. (0) At least first submarginal cell defined by line representing first transverse cubital vein (Figs. 162-164). (1) Not defined because transverse cubital veins are entirely absent (Fig. 168). Generally associated with states (0) and (1) are all the differences in forewing venation enumerated in couplet 1 of the key to genera. Venational reduction evidently occurred independently in various taxa of minute Meliponinae; even in some relatively large ones, e.g., *Trigona (Papuatrigona),* the transverse cubital veins are essentially absent, being indicated by denser setae than on the adjacent wing membrane.

Character 10. Basal area of propodeum. (0) Bare, as in Xylocopinae and many other bees. (1) Hairy, as in other subfamilies of Apidae. Polarization of this character is in doubt on the basis of outgroups. Hairs crop up on the basal area of the propodeum of species widely scattered through the Meliponinae. At the genus level such hairs characterize four genera, *Cephalotrigona, Melipona, Meliponula,* and *Partamona,* but they occur also in *Plebeia (Schwarziana), P. (Plebeia) caerulea* (Friese), *Trigona (Tetragona) lurida* Smith, the *Trigona (Heterotrigona) planifrons* Smith group (part of *Platytrigona*), and *T. (H.) canifrons* Smith. Since polarity is not certain and hairs appear to have evolved sporadically (Figs. 82-129) even though they might be plesiomorphic in other cases, this character is omitted from the generic analysis.

**Character 11.* Gonostyli of worker. (0) Well separated at bases, usually parallel or converging apically (Figs. 9-33). (1) Adjacent or close together at bases, usually diverging apically (Figs. 40-48). In functional stings the bases of the gonostyli are well separated and the gonostyli converge to sheath the sting. It is therefore probable that even in the greatly reduced meliponine sting, separation of the stylar bases is the plesiomorphic condition. The bases are adjacent or nearly so in certain genera, and also in various species of diverse genera as an infrageneric apomorphy.

**Character 12.* Setae or bristles on gonostylus of worker. (0) abundant (unless gonostylus is reduced in size) and dispersed over nearly all parts of gonostylus (Figs. 9-39) (as in other bees). (1) Few and restricted to one edge or thickening on one side of gonostylus (Figs. 41-46). (2) Absent (Fig. 48). Characters 12 and 13 vary concordantly, states (1) and (2) of character 12 being correlated with state (1) of character 13. In theory a meliponine worker gonostylus with abundant setae as well as minute hairs should be possible. I know of no such gonostylus; possibly there is a developmental or physiological factor that prohibits such a combination.

**Character 13.* Minute, dense hairs on gonostylus of worker, usually much smaller than the smallest setae (Figs. 37-48). (0) Absent (Figs. 9-36). (1) Abundant. Minute hairs are scarce or absent in most related bees (other subfamilies of Apidae; Xylocopinae); *Apis* has an area of such hairs and numerous but small setae.

**Character 14.* Sting stylet of worker (Figs. 9-48). All Meliponinae have the entire sting apparatus greatly reduced. This character concerns the fused second valvulae or stylet. (0) Stylet distinct, sharp (thus most nearly like a functional sting) (Figs. 9, 41, 43-45). (1) Stylet with apex about right angular or with apex rounded, more often obtuse, broadly rounded, or reduced to a transverse band.

Character 15. Apical process of S6 of male. (0) Strongly sclerotized, directed posteriorly or downward. (1) Strongly sclerotized, reflexed and apex directed forward. Characters states (0) and (1) intergrade and in some cases coding was arbitrary. Outgroups lack the process. Polarity is based only on the belief that such a structure is more likely to have evolved flat, then become reflexed.

In scattered unrelated meliponine taxa, S6 is a broad, simple plate (Fig. 148) more or less like the preceding sterna and without or with only a small apical process. Such groups are *Lestrimelitta,* certain species of *Paratrigona, Trigona (Homotrigona), T. (Lepidotrigona)* and a subgroup of *T. (Heterotrigona),* i.e., the subgroup called *Odontotrigona = Tetrigona.* It is tempting to consider this the plesiomorphic (0) condition, because in many other groups of bees S6 is a simple plate. However, the appearance of this state in groups that show no other special signs of plesiomorphy suggests independent reversions from the usual meliponine condition. All bees must possess genes for producing ordinary sterna (S2-5); a developmental shift could no doubt cause such genes to function for S6. (Further discussions under several of the taxa listed above.)

Taxa lacking the apical process of S6 were coded 9 for the preliminary PAUP analysis, the hypothesis being that the process in some cases has been lost. Because of the dubious basis for polarity and because the states intergrade, this character was not used in the generic analysis.

**Character 16.* Gonobase. (0) Recognizable as separate band on each side. (1) A thin ribbon, or fused to gonocoxite, or absent.

**Character 17.* Base of male genital capsule. (0) Not curved ventrad and apicad. (1) Strongly produced ventrad and apicad (*Liotrigona* and *Cleptotrigona,* Figs. 153, 154). *Meliponula* s. str. has a slightly down-curved base of the genital capsule.

**Character 18.* Male genitalia (Figs. 130-161). (0) Rectigonal or amphigonal. (1) Seemingly permanently schizogonal. In most bees, including the Euglossinae and Bombinae, the genitalia are rectigonal. In most Meliponinae considered to exhibit state (0), the genitalia can probably take up the schizogonal conformation during the life of the individual, hence are termed amphigonal. *Lestrimelitta* and *Hypotrigona*, however, are probably permanently rectigonal and others may be. Character state (1), not found in other bees and hence clearly apomorphic, is found in *Melipona* and most of the African genera.

**Character 19.* Gonostylus of male. (0) Slender, not much flattened. (1) Broadly flattened beyond slender base (Fig. 161). (This character state varies between the two species of *Dactylurina.*)

Character 20. Attachment of gonostylus to gonocoxite of male. (0) At apex of gonocoxite, as in most Hymenoptera. (1) Preapical on gonocoxite. (2) Near middle of gonocoxite. (3) Near base of gonocoxite. The above coding of this character seemed appropriate for forms with elongate gonocoxites, but "apex" means something quite different for rectigonal and schizogonal gonocoxites. Moreover, in forms with short, transverse gonocoxites, the differences between the four states are negligible. (In *Trigona iridipennis* Smith and its close relations the gonostylus arises from the dorsum of the gonocoxite rather than from the side.) The character was ultimately abandoned for all cladistic analysis and was not used in the generic cladogram.

Character 21. Gonostylus of worker (Figs. 9-48). (0) Cylindrical or tuberculiform. (1) Flattened. Character state (0) most nearly resembles the form found in other bees. All degrees of flattening exist, and flattening is sometimes difficult to detect for these minute structures. There are already three characters (11-13) based on worker gonostyli. Moreover, flattening is largely concordant with minute, dense hairs (character 13, state 1). Character 21 was therefore abandoned as difficult to quantify and unlikely to provide additional information. It is listed here largely for historical reasons, because it was emphasized by Wille (1959a, 1979b).

**Character 22.* Sting lancet (first valvula) of worker (Figs. 9-48). (0) Long, free, apex more or less longitudinal and attaining at least bases of gonostyli. (1) Shorter, largely transverse, but apex free. (2) Short to absent, included in membrane. As for character 14, polarity is based on the degree of divergence from the structure found in functional stings. The three states intergrade so that some coding decisions were arbitrary.

**Character 23.* Scutellum. (0) Rounded and rather thick in lateral view. (1) Projecting as a thin shelf over metanotum and base of propodeum as seen in lateral view (*Nannotrigona, Paratrigona, Scaptotrigona,* Figs. 90-92). Character state (0) is suggestive of the condition in Bombinae, Apinae, and many other bees, and is therefore regarded as plesiomorphic.

**Character 24.* Vein M of forewing. (0) Bent at point where it meets (or would meet) first recurrent vein (Figs. 164, etc.). (1) Ending without such a bend (Figs. 168, 169). In other bees including the outgroups the vein bends and continues beyond the first recurrent vein. As is suggested by the first couplet of the key to genera, this character is highly correlated with character 9. It does provide some additional information, however, and is therefore included in the study.

**Character 25.* Submarginal angle in forewing. (0) Strongly acute (60°-70°). (1) Slightly acute to obtuse. A strongly acute angle is characteristic of most other bees, including the outgroups, and is therefore considered plesiomorphic.

Character 26. Setae on posterior surfaces of worker labial palpal segments one and two (Figs. 49-81). (0) Short, not or little longer than width of segments, and nearly straight. (1) Certain median (i.e., not marginal) setae much enlarged ("giants"), much longer than palpal width, straight or curved (hooked in terminology of Michener and Roubik, in press). (2) As in (1) but some or all giant setae sinuous (wavy). Character state (0) is plesiomorphic to judge by its occurrence in all other subfamilies of Apidae, and in other bees. States (1) and (2) are found in many Meliponinae. The problem with this character is that reversals occur, as in robber genera, necrophagous species, etc., that do not collect pollen from flowers (Michener and Roubik, in press). It is therefore impossible to know whether, in a given case, short setae are plesiomorphic or derived. If they are all plesiomorphic except for the robbers, necrophages, etc., then giant and sinuous setae arose repeatedly. For these reasons I have not used this character in the phylogenetic analysis.

Character 27. Hairs of outer surface and posterior margin of hind tibia of male. (0) All simple or some long hairs near posterior margin with short branches along one side. (1) With plumose hairs among longer simple hairs along posterior margin and sometimes also on outer surface. This is similar to character 6 (the equivalent character for workers) and is not used in analysis for the same reason. However, the distribution of the states is not the same as for workers. State (0) is found in all genera except *Dactylurina* and some subgenera of *Trigona*. This is true also for workers. Within the genus *Trigona,* state (0) is found in the subgenera *Tetragona, Tetragonisca, Lepidotrigona* and some *Heterotrigona* (some species but not all of the *Tetragonula* group, the *Platytrigona* group). Other *Heterotrigona* species and subgenera such as *Geotrigona, Frieseomelitta* and *Trigona* s. str. have state (1). Of the subgenera listed, only *Lepidotrigona* lacks equivalent plumose hairs in the worker. Illustrations of hind tibiae of some male melipones and discussion of assimilation of worker characteristics by males are given by Sakagami and Ito (1981). The outer surface of the hind tibia is usually convex but is concave and corbicula-like in some species having state (0) and in some with state (1).

computer analysis, as follows: *Apotrigona, Austroplebeia, Axestotrigona, Cephalotrigona, Cleptotrigona, Dactylurina, Hypotrigona, Lepidotrigona, Lestrimelitta, Liotrigona, Meliplebeia, Melipona, Meliponula, Nannotrigona, Nogueirapis, Oxytrigona, Paratrigona, Partamona, Plebeia, Plebeina, Scaptotrigona, Scaura, Schwarziana, Tetragona, Trigona* s. str., and *Trigonisca.* Except for *Trichotrigona, Lisotrigona,* and *Pariotrigona,* whose males are unknown, there is no confusion as to the relationships of the omitted taxa. Dissections were made and the omitted taxa were excluded from the cladistic analysis because of similarity to included taxa. That is, each omitted taxon (except for the three listed above) is similar to an included taxon, either being a sister group to the included taxon or to be incorporated into the included taxon. Most omitted taxa did not differ from corresponding included taxa in any of the characters used in this analysis and clearly, the included taxa cover the range of structural diversity in Meliponinae.

PAUP analyses were made using all 16 characters. Characters with three or four states were coded as ordered, but were also tried unordered. Analyses yielded numerous (>100) trees of which every tenth was printed. Consistency indices of shortest trees ranged from 0.41 to 0.47. Of course complete resolution was not achieved with so few characters. Inclusion of autapomorphies would have distinguished all taxa but would not have changed the topology of the cladogram as determined by the synapomorphies.

Informal (i.e., non-numerical) phenetic observations along with examination of these preliminary PAUP results led to my decisions as to 21 genera to be recognized and thus relegation of various taxa to subgeneric or synonym status. Study of character state distributions using McClade 2.1 (Maddison and Maddison, 1987) was useful in this process.

PAUP produces only the most parsimonious cladograms without regard to one's views as to the probability of reversals of particular characters. Some reversals that appeared in PAUP-generated cladograms were eliminated because they seem unlikely, e.g., reacquisition of lost wing veins as in 9(1) to 9(0) and redevelopment of an acute sting stylet as in 14(1) to 14(0). Such reversals were from state 1 to 0 for characters 9, 14, and 16.

For what is here called the "generic study" (as opposed to the "preliminary analysis"), characters 17 to 27 of Table 2 were considered for the analysis. They had not been recognized, or had not been appropriately coded, for the preliminary analysis. Several, however, cannot be reliably polarized, or are weak for various reasons, but are discussed in the table because others have used them. None of them led to changes in the taxa that were considered as genera. A new PAUP analysis, and a Hennig 86 analysis (the results were the same) was based on the 17 characters listed in Table 3 (marked by asterisks in Table 2) and the 21 taxa recognized as genera. The reasons for excluding the other characters are indicated below and in Table 2. The three genera whose males are not known were now included, male character states being recorded as unknown. Table 3 shows the states for the 17 characters, the characters and states being numbered as in Table 2. Certain genera are identical in the character states recorded in Table 3, as follows: genera 3 and 4; genera 6, 7, and 8; and genera 13 and 14. That is, complete resolution was impossible because some genera (recognizable by autapomorphies at the genus level) did not differ in strong, polarizable synapomorphies.

Some characters used in the preliminary analysis of 26 taxa were omitted in the generic study because they could not be polarized with any degree of confidence. Others were eliminated because they were not synapomorphic at the genus level. Character state 1(1), for example, occurs only in one (derived) subgenus of *Trigona* and in the distantly related genus *Paratrigona.* Thus at the genus level it does not characterize *Trigona* and becomes an autapomorphy for *Paratrigona.* Character state 7(1) became an autapomorphy at the genus level when the taxa possessing it fell together in the genus *Meliponula.* Other such cases are explained in Table 2.

As in the study of 26 taxa, numerous trees resulted from the PAUP analysis. Also as in that study, rather than developing a consen-

TABLE 3. Characters of the 21 genera of Meliponinae used in the generic analysis. All characters are polarized, with 0 as plesiomorphic, and the character states are ordered. The numbers of the characters correspond to those in Table 2.

Characters	3	4	5	8	9	11	12	13	14	16	17	18	19	22	23	24	25
1. Ancestor	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
2. *Melipona*	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0
3. *Hypotrigona*	0	1	1	1	1	0	0	0	1	1	0	0	0	2	0	1	1
4. *Pariotrigona*	0	1	1	1	1	0	0	0	1	?	?	?	?	2	0	1	1
5. *Lestrimelitta*	0	0	0	1	0	0	0	0	1	1	0	0	0	2	0	0	1
6. *Oxytrigona*	0	2	2	0	0	0	0	0	1	1	0	0	0	2	0	0	1
7. *Cephalotrigona*	0	2	2	0	0	0	0	0	1	1	0	0	0	2	0	0	1
8. *Trigona*	0	2	2	0	0	0	0	0	1	1	0	0	0	2	0	0	1
9. *Trichotrigona*	0	2	2	1	0	0	0	0	1	?	?	?	?	?	0	0	1
10. *Nannotrigona*	1	0	0	0	0	0	0	0	1	1	0	1	0	2	1	0	1
11. *Scaptotrigona*	1	0	0	0	0	0	0	0	1	1	0	0	0	2	1	0	1
12. *Paratrigona*	0	0	0	0	0	0	0	0	1	1	0	0	0	2	1	0	1
13. *Plebeia*	0	0	0	0	0	0	0	0	1	1	0	0	0	2	0	0	1
14. *Partamona*	0	0	0	0	0	0	0	0	1	1	0	0	0	2	0	0	1
15. *Trigonisca*	0	1	1	1	1	0	1	1	1	1	0	0	0	2	0	1	1
16. *Lisotrigona*	0	1	1	1	1	0	1	1	1	?	?	?	?	1	0	1	1
17. *Austroplebeia*	0	0	1	1	1	1	1	1	1	1	0	0	0	0	0	1	1
18. *Cleptotrigona*	0	0	0	1	1	1	1	1	0	1	1	1	0	0	0	1	1
19. *Liotrigona*	0	1	1	1	1	1	1	2	1	1	1	1	0	1	0	1	1
20. *Dactylurina*	0	2	2	1	1	1	1	2	1	1	0	1	1	2	0	0	1
21. *Plebeina*	0	1	1	1	1	1	1	2	1	0	0	1	1	1	0	0	1
22. *Meliponula*	0	1	0	1	0	1	1	1	0	0	0	0	0	0	0	0	1

sus tree, I have eliminated those that involve the most improbable reversals. The remaining trees resembled in topology Figures 6 and 7, differing only in trivial ways. For Figure 6, I modified the PAUP results only by rearranging character state 8(1). This state, the reduction of coarse, often blunt bristles of the rastellum to slender, tapering bristles or hairs, occurs not only in the genera above point A, but also in the robber or possibly parasitic genera *Lestrimelitta* and *Trichotrigona*. No doubt it evolved independently in these genera in connection with their loss of pollen manipulating behavior. I have therefore moved branches for those genera to show this character state as an independent apomorphy for each of these genera as well as on stem A. The fossil genus *Proplebeia* was added to Figure 6 by hand on the basis of features of the worker sting apparatus, some of them only vaguely seen.

For the part of the cladogram above point A, I have shown in Figure 7 an unmodified representation of the PAUP output. This parsimonious cladogram (26 character changes, not including autapomorphies) is improbable. The minute forms, *Pariotrigona* to *Liotrigona* on the tree (also *Cleptotrigona* and some *Austroplebeia*), constitute a group with greatly reduced wing venation, from which the African genera *Meliponula, Dactylurina,* and *Plebeina,* larger bees with fuller (ancestral) wing venation 9(0), 24(0), appear to have evolved. I believe that once lost, a vein is unlikely to reappear. Tinkering by differential weighting of characters is just as subjective as adjustments made, as in Figure 8, on the basis that the minute genera had independent origins and the larger African forms did not evolve from minute ones with reduced venation. I believe that parsimony programs are important aids in thinking about phylogeny but do not necessarily give the most probable cladistic hypotheses.

Figure 8 also is not without some improbable features. For example the sting stylet is shown as reverting to its acute pointed condition 14(0) in *Cleptotrigona* and *Meliponula.* The gonobase of the male is larger 16(0) in *Meliponula* and *Plebeina* than in

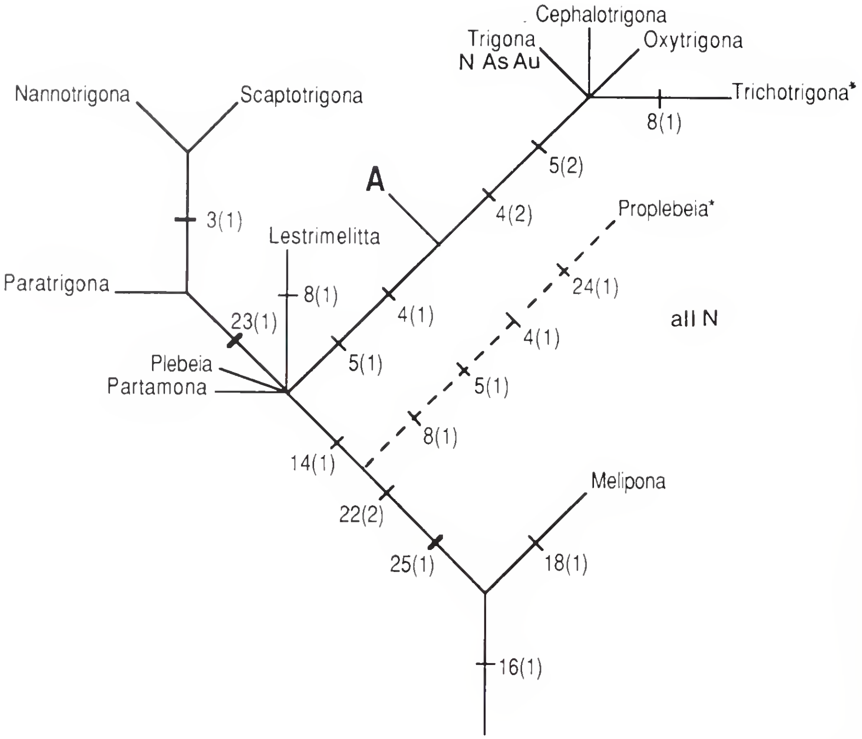


Figure 6. Dendrogram based on generic analysis of Meliponinae. A indicates continuation in Figures 7 and 8. The fossil *Proplebeia* was inserted by hand on the basis of few characters. Character numbers (and states in parentheses) are those used in Tables 2 and 3. Those marked with heavy cross lines are particularly strong. Males of genera marked by asterisks are unknown. All these genera are Neotropical (N); *Trigona* is also found from Asia (As) to Australia (Au).

any other Meliponinae. These would seem to be plesiomorphic features, but are reversals according to Figures 7 and 8.

Trigonisca is geographically isolated (in America) from other minute genera (all African or Asiatic). The relation with *Lisotrigona* shown in Figures 7 and 8 may be entirely wrong; when males of *Lisotrigona* are known they may indicate different relationships. The number of synapomorphies is so low that a few added characters could greatly change the cladogram. In the preliminary analysis (26 taxa) a sister-group relation was shown between *Austroplebeia* (Australia) and *Trigonisca*. Such a relationship is supported from an unexpected source. *Trigonisca* (along with *Hypotrigona*) and *Austroplebeia* have the last two metasomal ganglia completely fused, unlike other Meliponinae studied by Wille (1961). Thus the *Plebeia*-like *Austroplebeia* may indeed be the sister group of *Trigonisca*; alternatively, the fusion may be convergent.

The isolation of *Melipona* at the base of the cladogram (Fig. 6) is contrary to one of the relationships suggested previously, namely derivation of *Melipona* from *Plebeia*-like ancestors (Wille, 1979b). The acute sting (Fig. 9; character 14) and acute submarginal angle in the forewing (Fig. 162; character 25) are plesiomorphic features not shared by *Plebeia*, showing that *Melipona* could not have evolved from *Plebeia*. However, *Plebeia* and *Melipona* are in fact reasonably closely related; only four character changes separate them in Figure 6.

Wille (1979b) considered the flattened worker gonostyli of various African genera

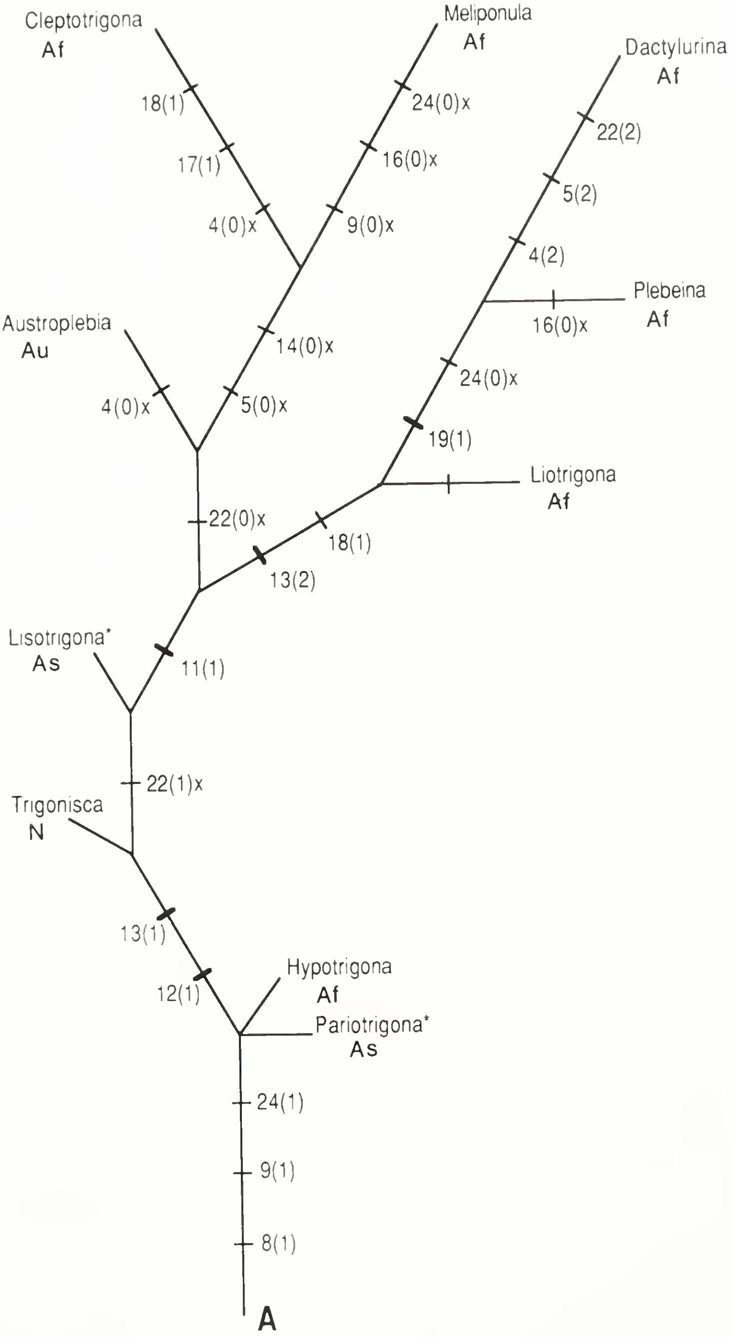


Figure 7. Continuation of Figure 6, showing results of PAUP analysis with character states of equal weight. Explanation as for Figure 6. Characters marked X represent reversals. N = Neotropical, Af = Africa, As = Asia, Au = Australia. Autapomorphies are omitted but provide additional characters for taxa without indication of characters or with reversals only.

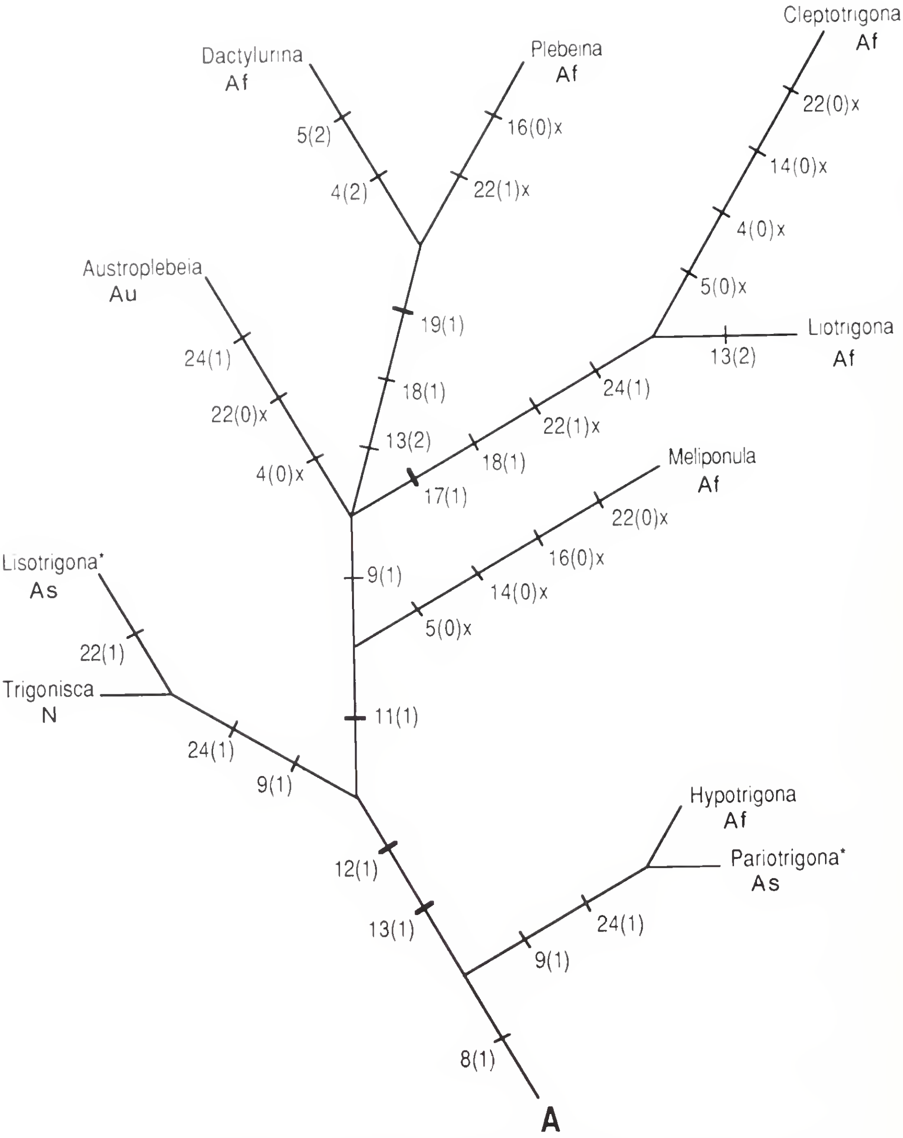
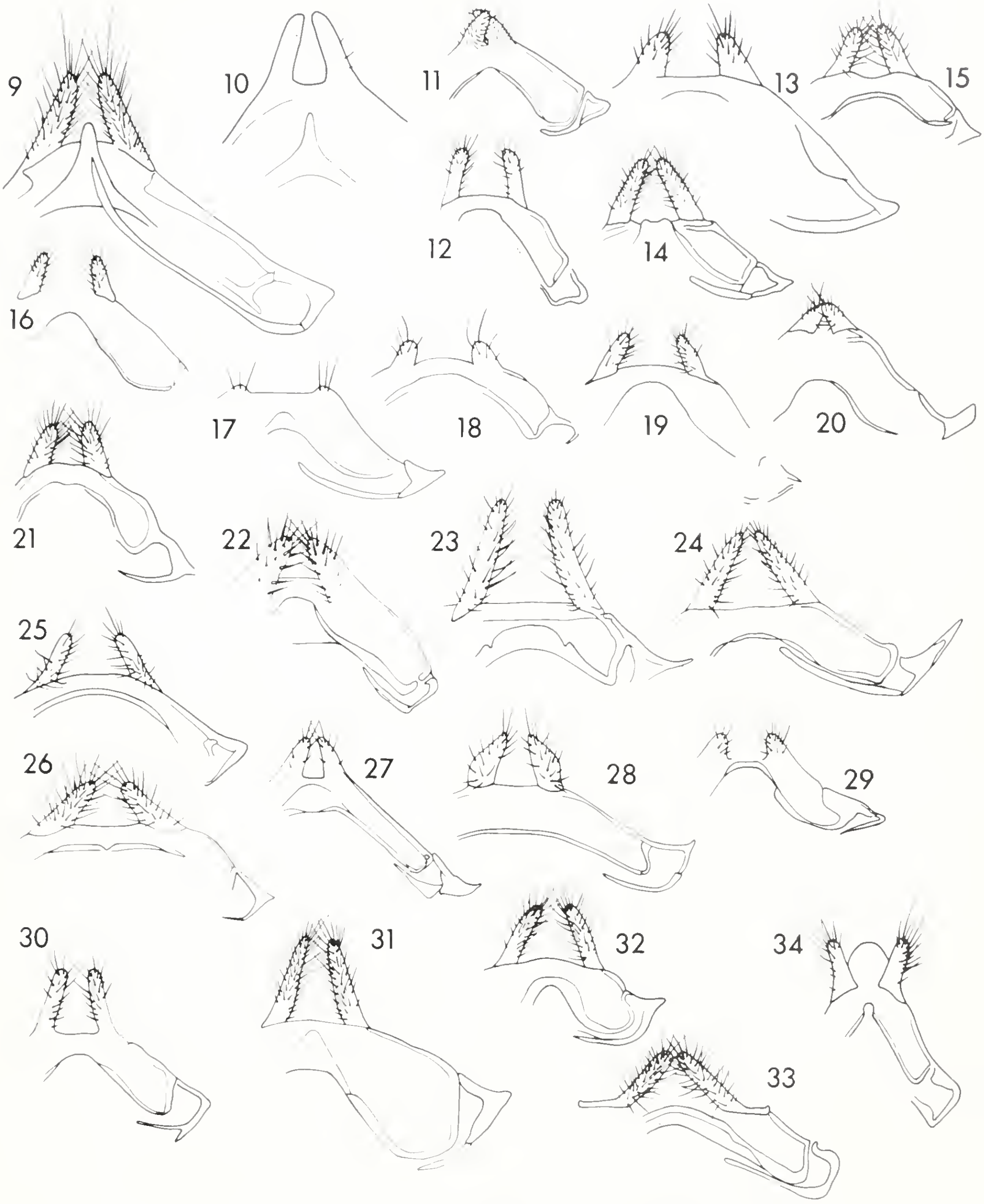


Figure 8. Continuation of Figure 6, showing modification of PAUP analysis. See text. Explanation as for Figures 6 and 7.

as ancestral, probably because in two of the genera (*Cleptotrigona* and *Meliponula*) this character state is associated with a pointed sting stylet. I consider the flattened gonostyli (Figs. 40-48; character 21, Table 2), presence of minute hairs on them (character 13), reduction of setae on them (character 12), and tendency of the gonostyli to diverge from proximate bases (character 11), to be derived character states, since they do not appear in other subfamilies of Apidae. I therefore do not follow Wille in regarding the African genera as an ancestral group from which other Meliponinae arose. Instead, the African, etc., group (Figs. 7, 8) appears to have evolved from a cluster of American genera (Fig. 6).

The genera appearing in Figure 6 have a distinctive combination of plesiomorphic and apomorphic character states. The for-



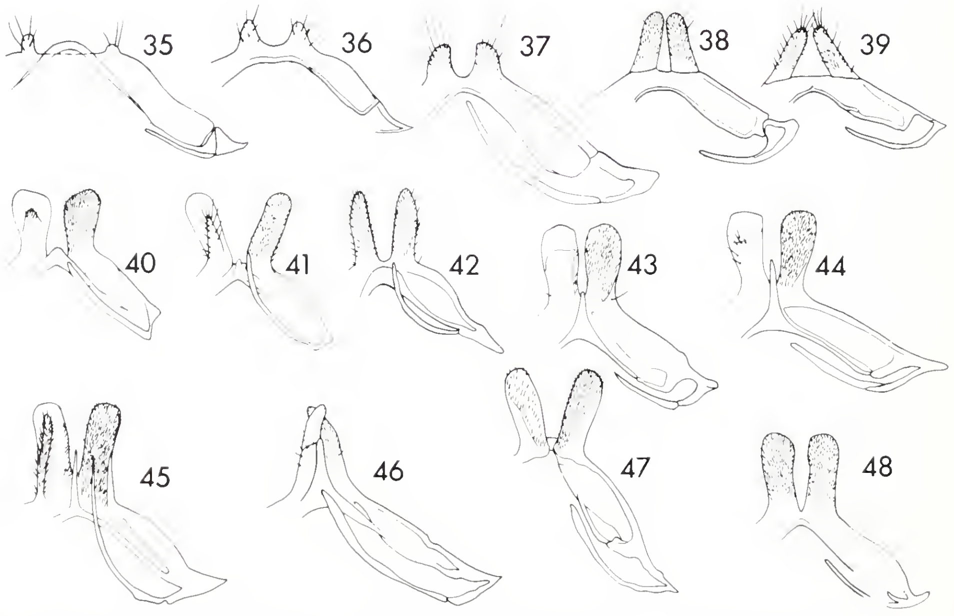
Figures 9-34. Sting rudiments of workers of Meliponinae. 9, *Melipona rufiventris* Lepeletier. 10, Fossil, *Proplebeia dominicana* (Wille and Chandler). 11, *Plebeia (Plebeia) frontalis* (Friese). 12, *Plebeia (Plebeia) caerulea* (Friese). 13, *Plebeia (Plebeia) schrottkyi* (Friese). 14, *Plebeia (Schwarziana) quadripunctata* (Lepeletier). 15, *Plebeia (Scaura) latitarsis* (Friese). 16, *Plebeia (Nogueirapis) mirandula* (Cockerell). 17, *Partamona* near *cupira* (Smith). 18, *Partamona zonata* (Smith). 19, *Paratrigona opaca* (Cockerell). 20, *Nannotrigona testaceicornis* (Lepeletier). 21, *Scaptotrigona mexicana* (Guérin). 22, *Lestrimelitta limao* (Smith). 23, *Oxytrigona mellicolor* (Packard). 24, *Cephalotrigona capitata* (Smith). 25, *Trigona (Lepidotrigona) terminata* Smith. 26, *Trigona (Papuatrigona) genalis* Friese. 27, *Trigona (Frieseomelitta) nigra* Cresson. 28, *Trigona (Geotrigona) mombuca* Smith. 29, *Trigona (Heterotrigona) carbonaria* Smith. 30, *Trigona (Tetragonisca) angustula* Latreille. 31, *Trigona (Tetragona) lurida* Smith. 32, *Trigona (Heterotrigona) apicalis* Smith. 33, *Trigona (Trigona) amalthea* (Olivier). 34, *Trigona (Trigona) cilipes* (Fabricius).

mer include cylindrical or papilliform, setose worker gonostyli (Figs. 9-34), commonly converging apically, with well separated bases and without minute hairs; the strong, usually blunt setae of the rastellum (Figs. 184, 185); and the posterior or downward directed midapical process of S6 of the male. Apomorphies include the obtuse or rounded sting remnant (except for *Melipona*) and reduced gonobase remnants.

The situation is in fact more complex. *Hypotrigona,* which agrees in various features with the genera in Figure 6, is restricted to Africa. In *Melipona,* a Neotropical genus, the sting is right angular to acute, in some species (e.g., *M. fulva* Lepeletier) as strong as in any African genus; the male gonocoxites are elongate and the genitalia schizogonal; and the gonobase is represented by a slender strip. Except that the gonobase remnant is quite different from the remnants in the African group, these character states are suggestive of that group. *Trigonisca,* a Neotropical genus, and *Austroplebeia,* an Australian genus, have worker gonostyli with minute hairs like those of the African group but in the other characters listed above they agree with the genera that appear in Figure 6.

The genera indicated by stars in Figures 6 to 8 are known only in the worker caste. Male genitalic characters are therefore unknown. *Trichotrigona* is possibly a robber or parasitic group derived from *Trigona (Frieseomelitta),* as suggested by the narrow ridge with keirotrichia on the inner surface of the hind tibia. *Lisotrigona* and *Pariotrigona* are minute forms superficially similar to *Hypotrigona, Liotrigona,* and *Trigonisca.* Their relationships remain uncertain until males are found (but see generic descriptions).

Biogeography: While cladograms, especially if based on relatively few characters, provide only hypotheses of relationships, they are strengthened if they make sense geographically or in terms of characters not used in



Figures 35-48. Sting rudiments of workers of Meliponinae. 35, *Hypotrigona braunsi* (Kohl). 36, *Pariotrigona pendleburyi* (Schwarz). 37, *Lisotrigona scintillans* (Cockerell). 38, *Trigonisca buyssoni* (Friese). 39, *Trigonisca longicornis* (Friese). 40, *Liotrigona mahafalya* Brooks and Michener. 41, *Cleptotrigona cubiceps* (Friese). 42, *Austroplebeia cassiae* (Cockerell). 43, *Meliponula (Meliplebeia) beccarii* (Gribodo). 44, *Meliponula (Axestotrigona) erythra* (Schletterer). 45, *Meliponula (Meliponula) bocandei* (Spinola). 46, *Meliponula (Meliplebeia) lendliana* (Friese). 47, *Plebeina denoiti* (Vachal). 48, *Dactylurina schmidti* (Stadelmann).

cladogram construction. Figures 6 and 8 do make reasonable geographic sense.

As indicated above, there is an African group of genera (Figs. 7, 8) with outliers, sharing some of its derived features, in Australia *(Austroplebeia)* and the Neotropics *(Trigonisca),* and a primarily Neotropical (also Indoaustralian because of *Trigona*) group (Fig. 6) with an outlier (or third group?), *Hypotrigona,* in Africa. *Melipona* (Neotropical) could be a member of this group but the evidence is weak. A biogeographical puzzle is how *Trigona* came to occur abundantly in the Neotropics and the Indoaustralian area while being absent from Africa. If male character states show *Lisotrigona* to be related to *Trigonisca,* they could constitute together a second genus having a distribution similar to that of *Trigona.*

No genus occurs both in Africa and South America. Therefore the meliponine faunas of these continents probably date from after the origin of the South Atlantic ocean in the late Cretaceous. The cladogram suggests that the Meliponinae arose in tropical America (which at that time extended far into North America). We know nothing of when the group moved between the American continents, but, as noted below, there is a late Cretaceous *Trigona* from New Jersey (Michener and Grimaldi, 1988a, b). The dissimilarity of the Neotropical and African faunas could suggest that meliponines reached South America from North America later, after considerable separation of South America from Africa.

Following the idea of Kerr and Maule (1964), the meliponines (including *Trigona*) may have spread through what is now the Holarctic region when it was warmer. The Eocene *Kelneriapis* from Baltic amber (see below) is evidence of meliponines in the Holarctic region. With climatic deterioration during the Tertiary, *Trigona* is now limited to southern Asia (south to Australia) and the Neotropical region.

The African fauna must have evolved when Africa was substantially isolated from American and Eurasian invasions (Michener, 1990).

Behavior: In view of the diverse types of recruitment to food sources found in Meliponinae (Kerr, 1969; Michener, 1974), it would seem that attributes of this system should be of phylogenetic significance. *Melipona* is quite different from the rest, in agreement with the cladogram. Otherwise, this system does not seem closely related to the branches shown in Figures 6 to 8. Rather, it seems that small forms (probably with small flight ranges) exhibit little recruitment ability while larger species have better recruitment. Scent trails, i.e., series of odor spots for recruiting, are known in *Cephalotrigona, Lestrimelitta, Oxytrigona, Scaptotrigona,* and *Trigona* (*Geotrigona* and *Trigona* s. str.). Kerr and Esch (1965, fig. 10) provide some details and exceptions [especially *Trigona (Duckeola) ghilianii* (Spinola), a large species not known to have scent trails].

Nest architecture, likewise, neither supports nor refutes the cladogram. The most striking variation in nest architecture is in brood cell arrangement. This feature has been emphasized by authors who wish to demonstrate that the subgenus *Frieseomelitta* is archaic or ancestral, having brood cells in clusters rather than combs.

It is not unreasonable to suppose that cells in a disorganized cluster is a plesiomorphy relative to cells arranged in combs. Most Meliponinae arrange cells in horizontal (sometimes spiral) combs. Cells in clusters, however, characterize not only all *Trigona (Frieseomelitta)* but also *T. (Heterotrigona) canifrons* Smith and most species of the *Tetragonula* group of *T. (Heterotrigona).* Moreover, cells are placed in clusters by all species of *Austroplebeia* [although layered, approaching combs, in *A. cincta* (Mocsary); Michener, 1961], *Cleptotrigona, Hypotrigona, Liotrigona, Trichotrigona,* and *Trigonisca,* and by some species of both *Plebeia (Plebeia)* and *Plebeia (Scaura).*

As suggested by Michener (1961), clustering may be the ancestral cell arrangement for Meliponinae (perhaps retained by *Austroplebeia*) while being derived for others. In particular, it is probably derived for species like *Trigona (Heterotrigona) fuscobalteata* Cameron that nest in small, irregular cavities where combs would be impractical. Indeed, most cluster-makers are small to minute bees. Michener (1961) contended that nearly spherical cells in clusters (as in *Austroplebeia*) are probably ancestral, that elongate cells resulted from packing cells into combs, and that therefore species that make elongate cells in clusters are derived from species that made combs. Unfortunately for this theory, spherical cells are almost unknown in other families of bees, so there is no good evidence for polarity of this character.

Dactylurina is unique among Meliponinae in that its combs, instead of being horizontal or nearly so with cells opening upward, are vertical with cells on both sides opening laterally, as in the combs of *Apis*.

Interesting aspects of social behavior of Meliponinae are the oviposition rituals and associated activities, much studied and described in a series of papers by Sakagami and others (reviewed by Sakagami, 1982; see also Sakagami, Yamane and Inoue, 1983, and Sakagami and Yamane, 1987). These rituals are often group-specific and often accompanied by laying of trophic eggs (usually queen food) by workers. The behavior of queens and workers during laying might produce characters of phylogenetic significance; some of the behavioral character states are indicated below in the comments on various genera and subgenera. It must be remembered, however, that these comments are based on few species and that sometimes closely related forms differ considerably in behavior. Therefore, generalizations as to a taxon's behavior may not always be applicable to all species. Polarization of most of these behaviors is dubious since there are no counterparts in outgroups. The following are some examples, selected from many possible characters.

New brood cell construction in most cases is unsynchronized (called successive), so that new cells at the advancing front (Michener, 1961) are in various stages of construction. This apparently unorganized construction of new cells is likely to be plesiomorphic. In a few taxa, while cell contruction starts successively, it becomes synchronized by the time that a number of cells are completed. Such taxa are *Trigona (Duckeola), T. (Lepidotrigona), Plebeia (Plebeia) minima* (Friese) and *schrottkyi* (Friese), and two groups of *Trigonisca,* namely *T. muelleri* (Friese) and *longicornis* (Friese), i.e., *Leurotrigona* and *Celetrigona,* respectively. Finally, in some taxa, a number of cells are constructed synchronously. Such taxa are *Plebeia (Plebeia)* except as indicated above, *Nannotrigona, Paratrigona, Trigona (Frieseomelitta) flavicornis* (Fabricius), and *T. (Heterotrigona) moorei* Schwarz. It should be noted that, in the successive group, there are the following close relatives of taxa listed above as partially or fully synchronous: *Plebeia (Schwarziana* and *Scaura), Trigona (Frieseomelitta)* of other species, *T. (Trigona* s. str., *Tetragona, Tetragonisca, Geotrigona,* and the *Tetragonula* group of *Heterotrigona),* and *Trigonisca* of other species. One can only conclude that if successive cell construction is plesiomorphic, synchronization has evolved independently in various groups.

Cell provisioning is in general parallel to cell construction, i.e., successive if cells are finished successively, synchronous if cells are constructed or finished synchronously.

Oviposition proper by the queen is less subject to brief summary than the features mentioned above, but egg laying by workers (in queenright colonies) is of interest. It is not confirmed in *Trigonisca muelleri* (Friese), *Trigona (Frieseomelitta)* and probably *T. (Duckeola).* Oviposition by workers occurs in queenright colonies of all other forms studied. In *Plebeia (Plebeia)* except *P. minima* Friese, in *Hypotrigona,* and in *Lestrimelitta,* the eggs are not laid in connection with the queen's oviposition process and are eaten by workers or the queen. In other taxa, worker laying is associated with queen oviposition, on or near a cell being provisioned, before provisioning starts in the case of *Trigona (Geotrigona),* but afterwards in all others. Such eggs are usually eaten by the queen. Usually the trophic egg is laid on the cell margin. [*Plebeia (Plebeia) minima* Friese is in this group.] It is much larger than the queen's egg in *Scaptotrigona* and *Plebeia (Schwarziana).* In certain taxa, however, it is laid on the food mass like the queen's egg. Such taxa are *Plebeia (Scaura), Paratrigona, Trigonisca longicornis* (Friese) *(Celetrigona), Melipona* and *Meliponula (Meliponula).* If, as seems likely, the last (laying on the food mass like the queen) is plesiomorphic, then modifications of that behavior must have occurred repeatedly and are not indicative of recognizable clades.

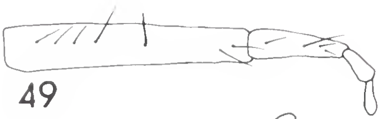
It is of interest that in all the characters listed above relevant to oviposition, *Melipona* has the presumably plesiomorphic behavior. This reinforces its position near the base of the cladogram rather than as a specialized derivitive group.

Labial palpi: The hairs of the posterior surfaces of the labial palpi of workers, character 26, provide character states that are of interest in connection with the cladograms (Figs. 49-81). Other subfamilies of Apidae, and various groups of Meliponinae, have these hairs short (little if any longer than palpal width) and straight. This is probably the plesiomorphic condition seen in *Melipona* and may also be plesiomorphic in such other taxa as *Cephalotrigona, Hypotrigona, Plebeia (Schwarziana* and *Scaura), Trigona (Geotrigona* and *Tetragona)* and even in *Meliponula (Meliplebeia).* If so, then giant curved and often wavy setae must have arisen repeatedly if Figures 6 to 8 mean anything. As indicated by Michener and Roubik (in press), the giant setae probably have to do with extracting pollen from anthers, minute flowers, etc. They appear to have been lost, i.e., replaced by short, straight setae, in bees that do not collect pollen from flowers, e.g., the robber genera *Lestrimelitta* and *Cleptotrigona,* the possibly parasitic *Trichotrigona,* and the species of the carrion-feeding group of *Trigona (Trigona) hypogea* Silvestri. When giant setae are lost, the condition is not visibly different from the plesiomorphic condition. These setae are therefore of little value in reinforcing or weakening the cladogram although their diversity as shown in Figures 49 to 81 suggests that they are important characters.

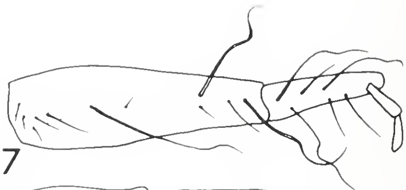
Wing venation: Characters 9, 24, and 25, Table 2, involve wing venation, but several additional features of wing venation vary widely among meliponine bees. In general they neither support nor refute the cladograms, but I deal with them at some length because they are conspicuous and have been used by others in the past. While of obvious interest, they sometimes vary within taxa, and some of them appear to vary with body size irrespective of phylogenetic relationship, along the lines indicated by Danforth (1989) for other groups of bees. For example, the basal vein is more transverse in small species, more longitudinal in large ones. The basal angle of the first submarginal cell (between first abscissa of Rs and Rs+M), i.e., the submarginal angle (character 25, Table 2), is acute in non-meliponine bees. It is also acute (60°-70°), no doubt plesiomorphic, in *Melipona* (Fig. 162). It is slightly acute in *Cleptotrigona, Plebeina,* most *Plebeia,* and some *Paratrigona.* It is right angular or approximately so (i.e., the first abscissa of Rs is more transverse) in most Meliponinae, grading to slightly obtuse in several groups such as *Scaptotrigona,* some *Partamona,* some *Paratrigona,* and *Meliponula (Axestotrigona).* It is very strongly obtuse, correlated with a short first abscissa of Rs (often only about one tenth as long as the basal vein (=first abscissa of M), in *Cephalotrigona, Dactylurina, Oxytrigona, Trichotrigona,* and some species of each of the following subgenera of *Trigona*: *Frieseomelitta, Tetragona, Trigona* s. str. (Figs. 166, 167). Other species of these subgenera as well as the subgenera *Geotrigona, Heterotrigona, Homotrigona, Lepidotrigona,* and *Tetragonisca,* have the angle weakly obtuse or right angular. Thus a strongly obtuse angle is found only in taxa with a narrow keirotrichiate ridge on the inner surface of the hind tibia, but has no doubt evolved independently in some such taxa (at least *Dactylurina* vs. the others). It is not clear whether the subgenera of *Trigona* like *Tetragonisca* retain an ancestral submarginal angle or have developed to a right angle along with their small body size. There are, however, rather large species of *Homotrigona* and *Heterotrigona* with the angle right angular.

The first abscissa of Rs is relatively long in related subfamilies and families of bees. Among Meliponinae it is about one fourth as long as the basal vein in *Melipona* as well as in *Lestrimelitta, Nannotrigona, Paratrigona,* and *Plebeina.* It is similarly rather long, one third to rarely one fifth (in *Cleptotrigona*) as long as the basal vein, in all the minute genera segregated in couplet 1 of the generic key, and in the minute *Plebeia (Plebeia) schrottkyi* (Friese). In *Cephalotrigona* and some species of *Trigona (Trigona* and *Tetragona)* it is only about one tenth as long as the basal vein, an obviously derived condition. All other Meliponinae have an intermediate Rs (first abscissa) length, one fifth to one eighth as long as the basal vein.

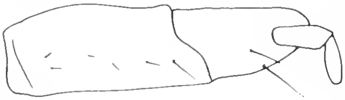
When the basal vein is relatively long, it is

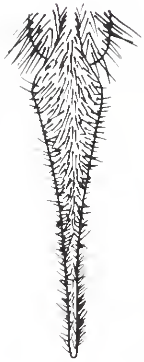

49

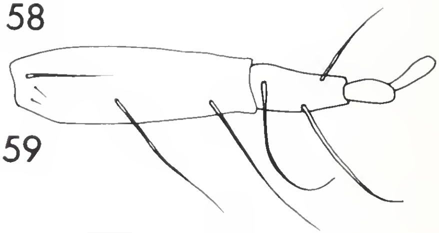

65

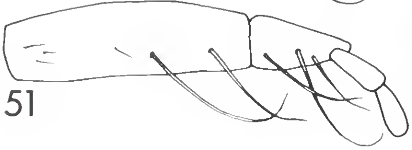

57

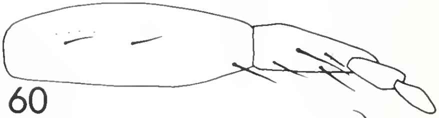

50

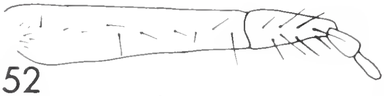

58

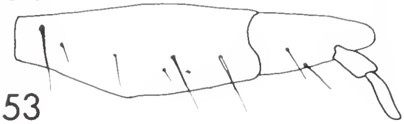

66

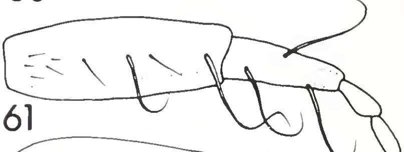

59

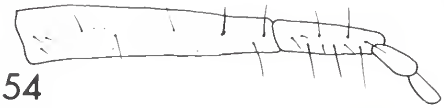

51

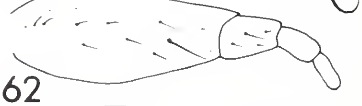

60

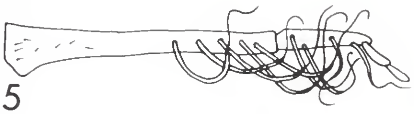

52

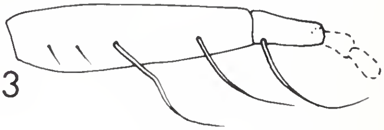

53

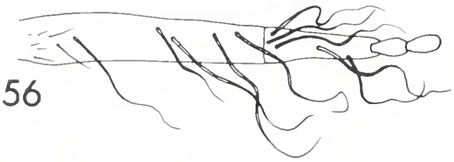

61

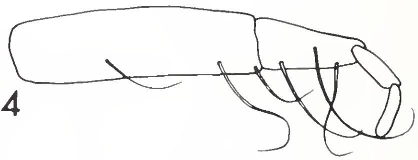

54


62


55

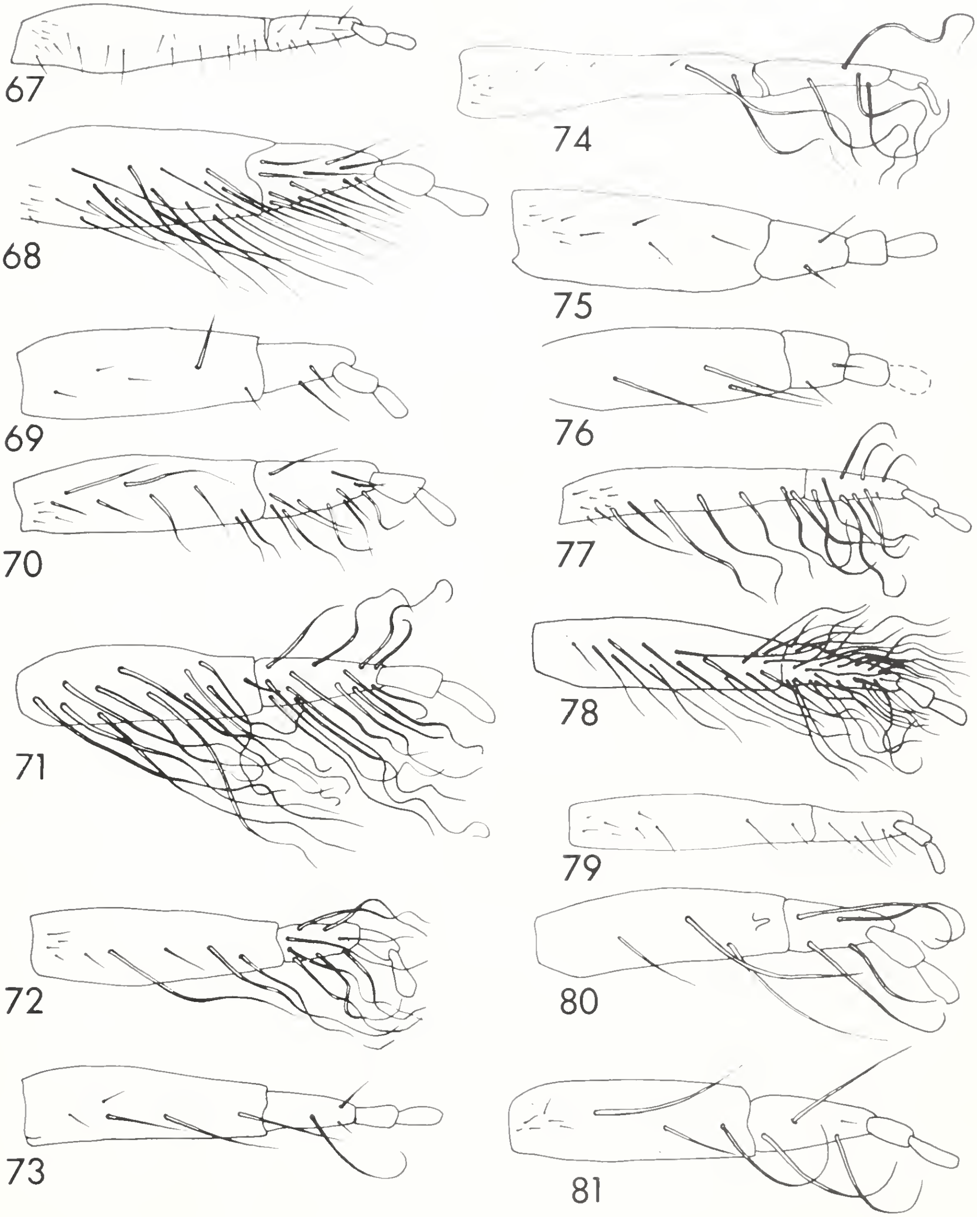

63


56


64

Figures 49-64 (modified from Michener and Roubik, in press). Posterior surfaces of labial palpi of workers. Marginal hairs and small hairs are omitted. Mesal margins are uppermost. The first and to some degree the second segments are sheath-like so that breadth varies with compression and should not be considered a useful character. 49, *Melipona fasciata* Latreille. 50, *Plebeia (Plebeia) frontalis* (Friese). 51, *Plebeia (Plebeia) schrottkyi* (Friese). 52, *Plebeia (Schwarziana) quadripunctata* (Lepeletier). 53, *Plebeia (Scaura) latitarsis* (Friese). 54, *Scaptotrigona pachysoma* (Cockerell). 55, *Paratrigona impunctata* (Ducke). 56, *Nannotrigona testaceicornis* (Lepeletier). 57, *Partamona* near *cupira* (Smith). 58, *Lestrimelitta limao* (Smith). 59, *Trigonisca buyssoni* (Friese). 60, *Hypotrigona braunsi* (Kohl). 61, *Liotrigona mahafalya* Brooks and Michener. 62, *Cleptotrigona cubiceps* (Friese). 63, *Pariotrigona pendleburyi* (Schwarz). 64, *Lisotrigona scintillans* (Cockerell).

Figures 65, 66. Flabellum of workers. 65, *Cephalotrigona capitata* (Smith). 66, *Trigona fulviventris* Guérin.



Figures 67-81 (modified from Michener and Roubik, in press). Posterior surfaces of labial palpi of workers. Explanation as for Figures 49-64. 67, *Cephalotrigona capitata* (Smith). 68, *Oxytrigona obscura* (Friese). 69, *Trigona (Tetragona) clavipes* (Fabricius). 70, *T. (Duckeola) ghilianii* Spinola. 71, *T. (Frieseomelitta) savannensis* Roubik. 72, *T. (Tetragonisca) angustula* Latreille. 73, *T. (Heterotrigona) carbonaria* Smith. 74, *T. (Trigona) pallens* (Fabricius). 75, *T. (Trigona)* species near *hypogea* Silvestri from Panama. 76, *Trichotrigona extranea* Camargo and Moure. 77, *Meliponula (Meliponula) bocandei* (Spinola). 78, *M. (Axestotrigona) erythra* (Schletterer). 79, *M. (Meliplebeia) beccarii* (Gribodo). 80, *Dactylurina staudingeri* (Gribodo). 81, *Austroplebeia cassiae* (Cockerell).

usually straight except near its basal end. This is the condition in most species of *Trigona* and its relatives with keirotrichia on a ridge *(Cephalotrigona, Trichotrigona, Oxytrigona)* as well as in *Dactylurina,* most *Meliponula, Plebeia (Schwarziana), Plebeina,* and *Scaptotrigona.* The basal vein is gently curved in all the other genera, although there are intermediates with very weak curvature such as *Partamona, Lestrimelitta,* some species of *Plebeia,* and some species of *Trigona (Heterotrigona).*

The basal vein is basal to cu-v in most species of *Trigona* and its relatives with a similar inner surface of the hind tibia *(Cephalotrigona, Dactylurina, Oxytrigona, Trichotrigona).* The same is true of *Scaptotrigona, Plebeina,* and some species of *Plebeia* and *Paratrigona.* The basal vein is distal to cu-v in the minute genera segregated in couplet 1 of the key to genera, and in the minute *Plebeia (Plebeia) schrottkyi* (Friese), also in *Lestrimelitta, Meliponula,* and some other species of *Plebeia.* The intermediate condition, the basal vein meeting cu v or nearly so, is found in the remaining groups including some species of *Plebeia* and *Trigona.*

Male genitalia: In the Meliponinae characters of males have been infrequently used hitherto for genus or subgenus recognition because of the scarcity of males in collections. It is risky to use male characters, as I have repeatedly done in keys and descriptions, when males remain unknown for many species. For various genera and subgenera for which males of only one species are known, I have indicated the male characters of the taxon on the basis of that one species. I hope that males of related species agree with my characterization, but they may not. As males of more species become known, any errors that I have introduced in this way will become evident.

A comment on schizogonal, rectigonal, and amphigonal genital capsules is appropriate here (see section on Terminology and Materials for explanation of these terms). I originally thought that these terms represented phylogenetically significant conditions, rectigonal being the plesiomorphic state and schizogonal derived. However, at least in various genera, this is clearly not the case, for specimens of the same species can be either rectigonal or schizogonal [see Fig. 134, based on two males of *Partamona* near *cupira* (Smith) from Costa Rica]. The genital capsule is so loosely put together that the gonocoxites are hinged on the median points where they meet and can fold basad to take the schizogonal position, so that sometimes the originally basal margins almost meet one another.

Commonly associated with this movement, the heavily sclerotized prong-like penis valves rotate and at the same time flex laterad. Note that in Figure 134, the shape of the prong of the penis valve in lateral view is the same as that shown in the dorsoventral drawing of a schizogonal specimen. Thus one has the same view of the penis valve in both cases because of its rotation.

Males often die with the penis valves directed laterally. It is not practical to return them to a more or less longitudinal position. Some illustrations show them directed laterad. Perhaps this is the position in copulation, with the penis valves hooking into the body of the queen so that the genitalia are pulled out of the male. Unfortunately lateral views of genitalia in this condition are not worth much and dorsoventral views look very different from those of the same species with the penis valves directed apicad.

Some of the conspicuous differences among genitalic preparations result from mobility of parts. Apparently the mobility varies; it is great in most meliponines, those that are amphigonal, but can apparently be slight in the permanently rectigonal and the permanently schizogonal forms.

Either by comparisons of different male specimens or of published drawings with specimens, it is clear that genitalia can appear either rectigonal or schizogonal (often with accompanying rotation of the penis valves) in the following species: *Austroplebeia essingtoni* (Cockerell), *Partamona cupira* (Smith), *Plebeia schrottkyi* (Friese), *Trigona amalthea* (Olivier), and *T. pallens* (Fabricius). There are numerous other taxa in which gonocoxal shape (about as long as broad) probably permits such change in genital appearance. These are *Austroplebeia, Nannotrigona, Oxytrigona, Paratrigona, Partamona, Plebeia, Scaptotrigona, Trigonisca,* and most subgenera of *Trigona.* Such forms are informally called amphigonal, to save explanatory space.

Nonetheless there are groups in which the genitalia appear to be permanently schizogonal, and in which this feature is therefore an apomorphic character state. These are the groups in which the gonocoxites are sufficiently elongate that they could hardly adopt a rectigonal conformation; in some such groups (especially *Melipona*) males of numerous species have been examined by me or illustrated by previous authors; all are schizogonal. Such taxa are *Cleptotrigona, Dactylurina, Liotrigona, Melipona, Meliponula, Plebeina,* and *Trigona (Geotrigona, Tetragonisca).* In at least some of these taxa the penis valves can flex laterad without great effect on gonocoxal positions. Figure 161 shows this for *Dactylurina.* In *Liotrigona* and *Cleptotrigona* the flexion is entirely different in that each penis valve flexes contralaterally, the penis valves crossing near their bases (Figs. 153, 154).

Finally there are taxa in which the genitalia are probably rigidly rectagonal: *Lestrimelitta* (Figs. 141-143) and probably *Hypotrigona* (Fig. 151). This condition should be ancestral to judge by Bombinae, Euglossinae, and other families of bees. Figures 6-8 do not support this view.

Poison glands: Kerr and Lello (1962) investigated remnants of the poison gland (and storage sacs) in meliponine workers. They found large sacs in *Meliponula bocandei* (Spinola) and in *Trigona (Frieseomelitta) freiremaiai* (Moure) and apparently assumed them to be plesiomorphic. In fact, they are much larger than in stinging bees *(Apis, Bombus)* and the large size must be a derived condition. In *Nannotrigona, Plebeia* [*schrottkyi* (Friese) and *droryana* (Friese)] and *Dactylurina* the glands are not large but are well developed; I suspect that this is the plesiomorphic condition. *Melipona* and *Trigona (Tetragonisca) angustula* (Latreille) have vestigial but recognizable sacs. In other genera examined the glands are vestigial or absent; such taxa are *Partamona, Trigona (Trigona), Cephalotrigona, Oxytrigona, Lestrimelitta,* and *Scaptotrigona.*

Chromosome numbers: Haploid chromosome numbers have been reported for numerous meliponine bees as well as other Apidae, etc., mostly by W. E. Kerr and his associates (see Mello and Kerr, 1984, and Kerr 1987, for summaries). Table 4 presents the data derived from these sources. These authors regard the ancestral chromosome number as 8, but since outgroups (other subfamilies of Apidea, Xylocopini) have 15 to 25 chromosomes, it seems likely that *Trigonisca muelleri* (Friese) (the *Leurotrigona* group of *Trigonisca*), with 8 chromosomes and *Melipona* with 9 or 10 chromosomes achieved these numbers by fusion rather than retention of ancestral numbers.

Unfortunately, bee chromosomes are minute and details that might clarify these matters are little known. Using numbers alone, no sensible pattern of phylogenetic importance is evident for the Meliponinae.

TABLE 4. Haploid chromosome numbers (largely based on Mello and Kerr, 1984, and Kerr, 1987).

Xylocopa	16
Melipona	9, 10, 18[1]
Plebeia	
Plebeia s. str. (including *"Friesella"*)	18
Schwarziana	16
Partamona	17
Paratrigona	18
Nannotrigona	17
Scaptotrigona	17
Lestrimelitta	14
Oxytrigona	17
Cephalotrigona	17
Trigona	
Geotrigona	17
Frieseomelitta	15
Duckeola	15
Trigona s. str.	14, 17
Hypotrigona	14[2]
Trigonisca	
"Leurotrigona"	8
"Celetrigona"	15
Cleptotrigona	18
Meliponula	
Axestotrigona	18
Meliplebeia	17
"Plebeiella"	18
Meliponula s. str.	18
Dactylurina	17
Euplusia	15
Eulaema	15
Bombus	18, 20
Psithyrus	25
Apis	16

---

[1] Based on Kerr (1972).

[2] Kerr (in litt.) indicated that this number is doubtful because of poor slides.

Convergence: Unless there has been convergence in such characters as worker gonostyli, there has been remarkable convergence in external features of workers of various meliponine bees. Wille (1979b) deals with this in some detail. The following paragraphs summarize the main points:

Melipona (Neotropical) and *Meliponula* s. str. (Africa). Robust, thorax and head densely hairy, integument dull, basal propodeal area hairy, dorsal vessel arched between longitudinal indirect muscles of flight. The arch of the dorsal vessel, characteristic of many large, fast-flying bees, may be related to the robust body and fast flight of *Melipona* and *Meliponula* s. str.; the form of the dorsal vessel is documented for various taxa by Wille (1958, 1963, 1979b).

Hypotrigona (Africa), *Liotrigona* (Africa), *Lisotrigona* (Asia), *Pariotrigona* (Asia) and *Trigonisca* (Neotropical). Minute, sparsely haired, pterostigma relatively large, wing venational characters as listed in first alternative of key to genera, below. All except possibly the two rare Asiatic taxa are attracted to perspiration. At least *Hypotrigona, Liotrigona, and Trigonisca* are quite unrelated to one another (Fig. 6) to judge by the sting and male genitalic character states, although superficially almost indistinguishable. *Cleptotrigona* (Africa) also falls in this group but has the special features of robbers.

Dactylurina (Africa), *Trigona* (Neotropical; Asia to Australia). Typically rather elongate and long-legged, although some American forms (like the subgenus *Geotrigona* and some species of *Trigona* s. str.) have the metasoma short and broad. Inner surface of hind tibia of worker with longitudinal band of keirotrichia on elevated ridge usually little if any wider than depressed, shining posterior zone of tibia. Posterior fringe of hind tibia of worker including plumose hairs except in some small subgenera of *Trigona.*

Austroplebeia (Australia), *Meliponula* (except s. str.) (Africa), *Nannotrigona, Paratrigona,* and *Plebeia* (Neotropical), *Plebeina* (Africa). Mostly small, robust bees of superficially similar aspect, often with restricted dull yellowish markings on head and thorax. Posterior margin of inner surface of hind tibia commonly shiny, often depressed, but sometimes with keirotrichia reaching margin.

Cleptotrigona (Africa), *Lestrimelitta* (Neotropical). Robber bees with shiny, sparsely haired bodies; vertex and genal areas broad; proboscidial fossa greatly narrowed posteriorly; eyes small; clypeus small; labrum concave between lateral prominences; corbicula absent, penicillum and rastellum reduced to tapering hairs. Wille (1979b) correctly showed that in spite of their similarities, these genera are not closely related.

Partamona, Scaptotrigona, and *Trigona* s. str. (*spinipes* group), *T. (Geotrigona)* (all Neotropical). Robust, often black bees with short metasomas, superficially similar in form and color.

Classificatory questions: Regardless of one's methods, decisions as to classificatory levels are subjective. There will be some reasonable disagreements with my decisions. Some would regard all genus-group names as genera. I believe that this obscures relationships that are useful to show in the classification. However, even if one accepts in a general way the classification presented below, there are decisions that I had to make arbitrarily and that could equally well have been different. Chief among these are the following:

Scaura could have been given generic status with *Schwarzula* as a monotypic subgenus if desired, instead of placement of *Scaura* as a subgenus of *Plebeia.*

Scaptotrigona could have been placed as a subgenus of *Nannotrigona.* They are sister groups whose relationship might well be indicated by the classification, but they are different in appearance, easily distinguished, and I hesitantly gave both generic status.

Cephalotrigona could have been considered a subgenus of *Trigona.*

Ptilotrigona could have been given subgeneric status in *Trigona*, instead of synonymizing it with the subgenus *Tetragona.*

Five groups of the subgenus *Heterotrigona* of *Trigona* could have been given subgeneric status, as suggested in the discussion of *Heterotrigona.* Subjectively these groups seem less distinct than the subgenera here recognized. No cladistic study of *Trigona* subgenera has been made.

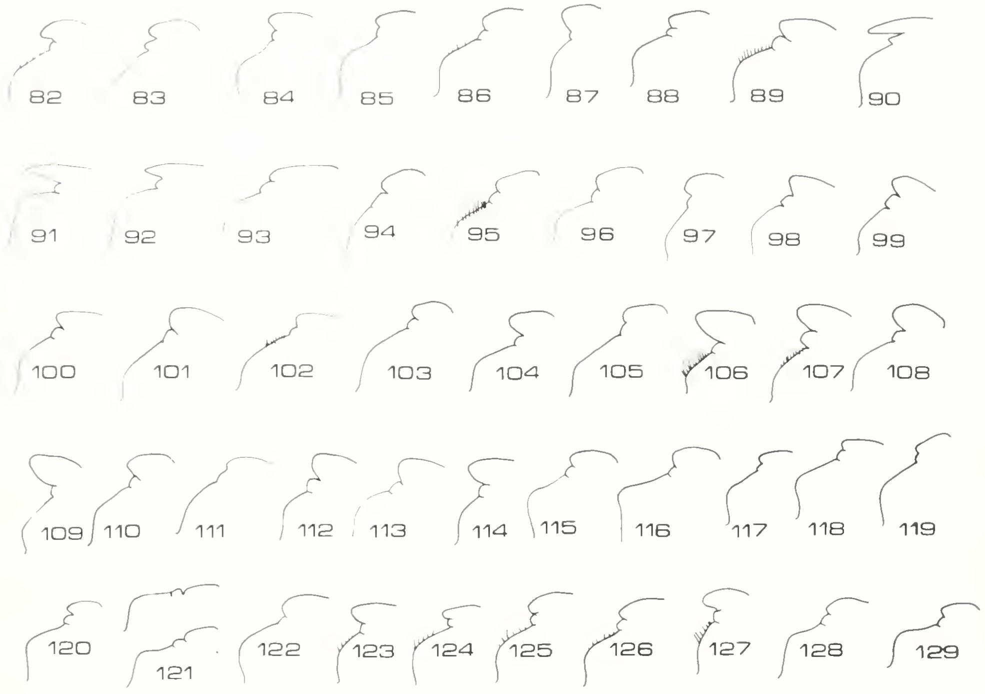
The four named groups of *Trigonisca* could have been given subgeneric status.

The three named groups of *Meliponula*

subgenus *Meliplebeia* could have been given subgeneric status.

Fossil Meliponinae

The best described fossil Meliponinae are *Plebeia (Nogueirapis) silacea* (Wille, 1959b) from the Miocene of southern Mexico, *Proplebeia dominicana* (Wille and Chandler, 1964) from the Oligocene of the Dominican Republic (see also Michener, 1982), and *Trigona prisca* Michener and Grimaldi (1988a, b) from the late Cretaceous of New Jersey.



Figures 82-129. Profile (head to the right) of posterior part of thorax and propodeum of workers (except as otherwise indicated) of Meliponinae. When hairs are present at or near the middle of the basal area of the propodeum, they are indicated. Otherwise hairs are omitted. 82, *Melipona favosa* (Fabricius). 83, *Proplebeia dominicana* (Wille and Chandler). 84, *Plebeia (Plebeia) frontalis* (Friese). 85, *Plebeia (Plebeia) caerulea* (Friese). 86, *Plebeia (Schwarziana) quadripunctata* (Lepeletier). 87, *Plebeia (Scaura) latitarsis* (Friese). 88, *Plebeia (Nogueirapis) mirandula* (Cockerell). 89, *Partamona* near *cupira* (Smith). 90, *Paratrigona opaca* (Cockerell). 91, *Nannotrigona testaceicornis* (Lepeletier). 92, *Scaptotrigona mexicana* (Guérin). 93, *Lestimelitta limao* (Smith). 94, *Oxytrigona mellicolor* (Packard). 95, *Cephalotrigona capitata* (Smith). 96, *Trigona (Lepidotrigona) terminata* Smith. 97, *Trigona (Papuatrigona) genalis* Friese. 98, *Trigona (Geotrigona) acapulconis* Strand. 99, *Trigona (Frieseomelitta) nigra paupera* Provancher. 100, *Trigona (Tetragonisca) angustula* Latreille. 101, *Trigona (Tetragona) clavipes* (Fabricius). 102, *Trigona (Tetragona) lurida* Smith. 103, *Trigona (Duckeola) ghilianii* Spinola. 104, *Trigona (Heterotrigona) apicalis* Smith. 105, *Trigona (Heterotrigona) itama* Cockerell. 106, *Trigona (Heterotrigona) canifrons* Smith. 107, *Trigona (Heterotrigona) planifrons* Smith. 108, *Trigona (Heterotrigona) fuscobalteata* Cresson. 109, *Trigona (Heterotrigona) atripes* Smith. 110, *Trigona (Homotrigona) fimbriata* Smith. 111, *Trigona (Heterotrigona) thoracica* Smith. 112, *Trigona (Trigona) cilipes* (Fabricius). 113, *Trigona (Trigona) fulviventris* Guérin. 114, *Trichotrigona extranaea* Camargo and Moure. 115, *Hypotrigona braunsi* (Kohl). 116, *Pariotrigona pendleburyi* (Schwarz). 117, *Lisotrigona scintillans* (Cockerell). 118, *Trigonisca buyssoni* (Friese). 119, *Trigonisca longicornis* (Friese). 120, *Liotrigona mahafalya* Brooks and Michener. 121, *Cleptotrigona cubiceps* (Friese), male below. 122, *Austroplebeia cassiae* (Cockerell). 123, *Meliponula (Meliplebeia) nebulata* (Smith). 124, *Meliponula (Meliplebeia) lendliana* (Friese). 125, *Meliponula (Meliplebeia) beccarii* (Gribodo). 126, *Meliponula (Axestotrigona) erythra* (Schletterer). 127, *Meliponula (Meliponula) bocandei* (Spinola). 128, *Plebeina denoiti* (Vachal). 129, *Dactylurina schmidti* (Stadelmann).

Information on less fully studied fossil stingless bees is summarized by Wille (1977) and Zeuner and Manning (1976).

P. silacea is no doubt correctly placed, since it is close at the species level to Recent species of *Plebeia (Nogueirapis)*. The other fossils are placed with little certainty because we now know that convergence in external features is rampant in Meliponinae. The gonostyli of workers are visible in at least one fossil of the Antillean *Proplebeia*, which is best regarded as a separate genus.

The true position of *T. prisca* must be viewed as dubious, even though it was originally described as a species of *Trigona* s. str. with which it agrees in toothed mandibles and other external characteristics except the probably simple hairs of the posterior margin of the hind tibia. In the latter feature it resembles the subgenus *Lepidotrigona* and perhaps *Papuatrigona*. There may have been a very few branched hairs, as in some *Trigona (Geotrigona)*. Thus there is nothing in its external characters to exclude it from the genus *Trigona* in spite of its great antiquity. The problem is that the same can be said of the African *Dactylurina*, yet the worker gonostyli and male genitalia show that *Dactylurina* is only distantly related to *Trigona*. The problem is accentuated by the realization that in the Cretaceous when *T. prisca* was living, its location (New Jersey) was not far from Africa, where *Dactylurina* now lives.

Three genus-group names have been based on fossils. The current status of our knowledge of each is indicated below.

Genus *Meliponorytes* Tosi

Meliponorytes Tosi, 1896:352. Type species: *Meliponorytes succini* Tosi, 1896, by designation of Sandhouse, 1943:570.

Two species were placed in this genus by Tosi (1896). Both were in Miocene Sicilian amber. The specimens have been destroyed (Wille, 1977). Schwarz (1948), Kerr and Maule (1964), and Zeuner and Manning (1976) give detailed interpretations of Tosi's descriptions and figures. Schwarz believed that Tosi's figures showed the inner surface of the hind tibia to be like that of *Melipona* while Zeuner and Manning interpreted the same figures to show a structure like that of *Trigona (Tetragona)*. Biogeographic considerations suggest a possible relationship to the African group, e.g., *Meliponula*. The relation to *Meliponula* was rejected by Wille (1977) but seems more reasonable in the context of the broad interpretation of that genus adopted here. More material will be necessary to place this genus.

Genus *Kelneriapis* Sakagami

Kelneriapis Sakagami, 1978 (June):232. Type species: *Trigona (Hypotrigona) eocenica* Kelner-Pillault, 1970, by monotypy.

Kelnermelia Moure and Camargo, 1978 (November 17):565. Type species: *Trigona (Hypotrigona) eocenica* Kelner-Pillault, 1970, by original designation.

This generic name is based on a species from the late Eocene Baltic amber. Many details of its structure are indicated by Kelner-Pillault (1970) and reworded by Moure and Camargo (1978). Unfortunately the inner surface of the hind tibia was not visible and the description and illustration do not even verify the existence of a corbicula on the outer surface. Lack of a corbicula (and apparently of a penicillum) suggests that the specimens were males. The antenna is illustrated and described as 13-segmented, further supporting the sex assignment. Nothing in the descriptions by Kelner-Pillault or by Moure and Camargo suggest realization that they may have been comparing male characters with the worker characters known for other genera.

The bee was minute (3 mm long) with wing venation more or less like that of modern minute species (couplet 1 of key to genera). Its relationships to modern genera remain unknown.

Re-examination of the type might partially clarify the situation. At the Institute of Geology and Paleontology, University of Göttingen, however, the type, which should have been there according to the original description, could not be found (inquiry in 1976); the late Dr. S. Kelner-Pillault wrote that she no longer had it in Paris at that time.

Genus *Proplebeia* Michener

Trigona (Proplebeia) Michener, 1982:44: Type species: *Trigona (Liotrigona) dominicana* Wille and Chandler, 1964, by original designation.

This species, from presumably Oligocene amber from the Dominican Republic, was illustrated and described in considerable detail by Wille and Chandler (1964), with additional characters described and illustrated by Michener (1982). It is a common fossil and hundreds of specimens are known, all workers. In the Snow Entomological Museum, University of Kansas, is one specimen (in an amber block containing many specimens) with the apex of the metasoma open, clearly showing the gonostyli and somewhat less clearly, the sting stylet (Fig. 10).

The gonostyli are separated by about 1.5 stylar widths at the bases and converge apically. They clearly have a few setae, visible along the outer margin of one gonostylus. Probable setal bases are visible on all parts of the gonostyli but against the pale background the setae themselves are not visible. There is no evidence of hairlike spicules but they would probably be invisible. It seems almost certain that the gonostyli are like those of most American genera; very clearly they are not like those of *Liotrigona* to which the species was originally attributed.

The sting stylet in some views is convincingly visible, dark in color, slender and acute. If this interpretation is correct, the sting stylet and gonostyli considered together resemble those of *Melipona,* but no other genus.

The placement of *Proplebeia* near *Plebeia* by Michener (1982) still seems reasonable. As noted at that time, the smooth posterior margin of the inner surface of the hind tibia is broader than in *Plebeia (Plebeia),* about as in *Hypotrigona* (illustrated by Michener, 1982). Moreover, the bristles of the rastellum, while strong, are pointed at the apices, not blunt as usual in *Plebeia.* The profile of the propodeum (Fig. 83) is more declivous, with less of a subhorizontal basal area, than in *Plebeia* and most other Meliponinae. If *Proplebeia* were Recent, there would be problems with couplet 1 of the key to genera, below. The first transverse cubital vein is indicated by a strong spur at the posterior (or basal) end, tapering to a weak line that completes the definition of the first submarginal cell. The veins outlining cell second Cu distally are weak but recognizable (see illustration by Wille and Chandler, 1964). But as in the genera of minute meliponines, vein M of the forewing ends abruptly without a bend (misstated as curved by Michener, 1982), and *Proplebeia* is minute. It must be noted that veins seem weaker in wings preserved in amber (or balsam) than in wings in the air. Except for the problem with vein M, *Proplebeia* runs reasonably well to *Plebeia* in the key to genera.

The principal differences of *Proplebeia* from *Plebeia* are the acute sting stylet and the broad smooth margin of the inner surface of the hind tibia, supplemented by the pointed rastellar bristles and the straight apex of vein M. *Proplebeia* seems best regarded as a distinct genus.

Taxonomic Account of Recent Genera of Meliponinae

The supraspecific taxa of Meliponinae have been described in detail and included in keys by Moure (1951, 1961) as well as by Wille (1959a). For this reason, although the classification is quite changed, no full descriptions are necessary here. Comments on each taxon are limited to interesting problems and character states, and structures not described by previous authors. Included species are listed for each genus and subgenus. Except for the smallest taxa, these lists are limited to a few well-known or for some reason important species, and will serve principally to facilitate the work of users of this paper whose collections were identified when most species of the subfamily were placed in the genus *Trigona.* More comprehensive lists of included species are found in the works cited, or in some cases are not available. Useful regional keys to supraspecific taxa and to species are included in the following works: Schwarz (1934), Panamá; Schwarz (1937), Borneo; Schwarz (1938), Guyana; Schwarz (1939a), Indomalayan region; Schwarz (1948), Neotropical region; Schwarz (1949), Mexico; Sakagami, Inoue, and Salmah (1985), Sumatra.

The following key will be most useful if attention is given to the geographical information provided. In certain cases *(Pariotrigona* and *Lisotrigona)* generic status is tentative, pending discovery of males, and geographic information is essential.

The key is based primarily on workers. Male characters have been added in various couplets. When "workers" are not specified, the character states given apply to males also but are often less well developed in males, so that identification of a male, not accompanied by workers, will often be difficult. Fortunately males are almost always found with workers. Queens have been available for only a few taxa and their characters have not been incorporated into the key or the descriptions.

Key to the Recent Genera of Meliponinae

1. Hind wing without closed cells, veins closing cells R and Cu, if visible at all, clear and unpigmented; forewing with transverse cubital veins almost always completely absent so that there are no indications of submarginal cells; at least distal part of cell second Cu of forewing undefined or defined by completely unpigmented vein traces; vein M of forewing

terminating without bend at about position of anterior end of first recurrent vein (1st m-cu) which, however, is absent (Fig. 168); minute, forewing length less, usually much less, than 4 mm (See comment at end of key.). 2

—Hind wing commonly with cells R and Cu closed by at least weakly brownish veins; forewing with one or two transverse cubital veins usually weakly indicated, first submarginal cell usually recognizable; cell second Cu of forewing completely indicated at least by faint veins; vein M of forewing except in some minute species of *Plebeia, Trigona (Heterotrigona),* etc. extending at least slightly beyond position of anterior end of first recurrent vein and angulate at end of that vein, which is usually at least faintly visible; forewing length commonly (but not always) over 4 mm (See comment at end of key.) 9

2. Outer surface of hind tibia of worker convex, corbicula and penicillum absent; clypeus much more than twice as wide as long (Africa) . . . . *Cleptotrigona*

—Distal part of outer surface of hind tibia of worker flat or concave, forming corbicula; penicillum present; clypeus twice as wide as long or less 3

3. Posterior apical part of hind tibia of worker forming distinct angle; gonostyli of worker adjacent or separated by one or two gonostylar widths 4

—Posterior apical part of hind tibia of worker rounded; gonostyli of worker minute, tuberculiform, separated by several diameters (Africa) . . . . *Hypotrigona*

4. Australia or New Guinea; scutellum and usually scutum and face with well developed yellow markings . . . . *Austroplebeia* (part)

—From other continents; scutellum, scutum, and face in some Neotropical species with white or yellow markings, otherwise without markings or scutellum and edges of scutum sometimes with straw-colored streaks 5

5. Southeast Asia (males unknown) 6

—Africa, Madagascar, and Neotropics. 7

6. Malar space almost one fifth as long as eye, much longer than flagellar diameter; gonostylus of worker with setae but without minute hairs . . . . *Pariotrigona*

—Malar space shorter than flagellar diameter; gonostylus of worker with many minute hairs (in addition to setae along outer and distal margins) . . . . *Lisotrigona*

7. Base of marginal cell broad, its basal angle (between stigmal margin and vein r, within marginal cell) slightly acute (about 68°) to nearly right angular; gonostylus of worker with a few setae in addition to minute hairs (Neotropical region). . . . . *Trigonisca*

—Base of marginal cell of usual shape, its basal angle strongly acute, not over 50°; gonostylus of worker with setae or minute hairs but not both 8

8. Gonostylus of worker with minute hairs but no setae (Africa and Madagascar). . . . . *Liotrigona*

—Gonostylus of worker with setae but no minute hairs (Neotropics). . . . . . *Plebeia* (part)

9. Inner surface of hind tibia with strongly depressed, shining, posterior marginal area which at least apically is usually about as broad as longitudinal median keirotrichiate ridge, and midway of tibial length is at least half as wide as keirotrichiate ridge (Fig. 185) 10

—Inner surface of hind tibia with depressed posterior marginal area narrow (much less than half as wide as area with keirotrichia) or absent, keirotrichia extending to or close to margin (Fig. 184). 14

10. Eyes hairy; rastellum reduced to tapering hairs (South America) . . . . . . *Trichotrigona*

—Eyes bare; rastellum strongly developed. 11

11. First metasomal segment longer than broad; gonostyli (third valvulae) of worker adjacent basally, flattened, with minute hairs but without setae; rastellum consisting of tapering bristles (Africa). . . . . *Dactylurina*

—First metasomal segment broader than long; gonostyli of worker usually separated at bases by at least width of a gonostylus, not flattened, with strong setae but no minute hairs;

rastellum with at least some bristles blunt (Neotropical and Indoaustralian regions). 12

12. Face short and broad, minimum distance between eyes much greater than length of eye; clypeus less than twice as broad as long; malar space almost twice as long as flagellar diameter; keirotrichiate zone on inner side of worker hind tibia nearly twice as wide as depressed marginal zone at midlength of tibia (Neotropical region) . . . . *Oxytrigona*

—Face of ordinary shape, minimum distance between eyes little more than to less than length of eye; clypeus usually more than twice as broad as long; malar space usually little over 1.5 times as long as flagellar diameter or usually much less; keirotrichiate zone on inner surface of worker hind tibia usually narrower, rarely over 1.5 times as wide as depressed marginal zone at midlength of tibia (Neotropical and Indoaustralian regions) 13

13. Preoccipital carina strong and shining across full width behind vertex; lower face and genal area shining and coarsely punctate in contrast to dull, densely, minutely punctate upper face, genal area and scutum . . . . *Cephalotrigona*

—Preoccipital carina absent; lower face and genal area finely sculptured like upper part of head and scutum . . . . *Trigona*

14. First flagellar segment of worker nearly as long as second plus third, of male nearly as long as second; outer surface of hind tibia convex, without corbicula, anterior margin convex like posterior margin; penicillum absent; rastellum consisting of tapering hairs (Neotropical region) . . . . *Lestrimelitta*

—First flagellar segment of worker shorter than second plus third together, of male much shorter than second; outer surface of hind tibia of worker (and some males) flat or concave at least distally, anterior margin gently convex to concave, unlike largely or wholly convex posterior margin; penicillum present; rastellum variable 15

15. Gonostylus of worker with setae having strong bases, without minute hairs; rastellum consisting of strong bristles, usually some of them with blunt apices (Neotropical region) 16

—Gonostylus of worker without or with few setae, with numerous minute hairs; rastellum usually consisting of weaker, flexible looking bristles or hairs that taper to attenuated apices and are sometimes plumose (Africa, Australia, New Guinea) 21

16. Hamuli 9-14 (rarely 8); wings extending little if any beyond apex of metasoma; stigma with margin within marginal cell straight or weakly concave (Fig. 162). (Body robust; basal propodeal area dull, hairy). . . . . *Melipona*

—Hamuli 5-7, rarely up to 9 or even 10; wings long, extending well beyond apex of metasoma; stigma with margin within marginal cell slightly convex (Figs. 163-171). 17

17. Anterior part of scutellum with longitudinal V- or U-shaped median shining depression opening anteriorly into scutoscutellar fossa (Fig. 190); preoccipital carina present, extending far down laterally on each side of foramen magnum 18

—Anterior part of scutellum without such a median, shining depression (Fig. 191); preoccipital carina absent or with transverse part only, behind vertex and weakly indicated 19

18. Head and thorax, or at least scutellum, with extremely coarse, cribriform punctation; posterior margin of scutellum notched or emarginate medially as seen from above; anterior margin of pronotal lobe with strong, transverse carina . . . . *Nannotrigona*

—Head and thorax with fine punctation; posterior margin of scutellum entire; anterior margin of pronotal lobe rounded . . . . *Scaptotrigona*

19. Mandible of worker with four apical teeth (lower two sometimes united by translucent septum but teeth still recognizable); scutellum seen in lateral view projecting posteriorly as thin shelf over median part of metanotum . . . . *Paratrigona*

—Mandible of worker with (rarely without) one or two denticles at upper end of apical margin, otherwise without teeth; scutellum in lateral view rather thick and rounded, not projecting as thin shelf over metanotum 20

20. Hind tibia of worker greatly broadened, spoon-shaped, about three times as wide as femur, outer surface largely occupied by corbicula (Fig. 187); basal area of propodeum densely hairy . . . . *Partamona*

—Hind tibia of worker triangular, not greatly broadened, much less than three times as wide as femur, corbicula extending but little if at all basad of middle of tibia (Fig. 184); basal area of propodeum usually hairless . . . . *Plebeia* (part)

21. Male genital capsule rectigonal, gonocoxite transverse, much wider than long; gonobase completely absent (Australia, New Guinea) . . . . *Austroplebeia* (part)

—Male genital capsule schizogonal, gonocoxite longer than broad; gonobase represented by fragment on each side (Africa) 22

22. Hind tibia of worker rather spoon-shaped, posterior apical angle rounded but with coarse, amber colored to blackish bristles (posterior parapenicillum); sting stylet of worker distinct, acute . . . . *Meliponula*

—Hind tibia of worker slender, triangular with distinct posterior apical angle which supports long hairs that are neither especially coarse nor amber colored; sting stylet of worker a mere rounded convexity . . . . *Plebeina*

Note on Couplet 1. This couplet conveniently separates some groups of minute species from the rest of the Meliponinae. Unfortunately, no one of the characters listed is completely reliable. For this reason *Plebeia* and *Austroplebeia* can be run both ways. Minute species exist among other genera [e.g., *Trigona (Heteroterigona) fuscobalteata* Cameron] and various such minute or merely small species possess some of the character states listed in the first alternative of couplet 1, yet should be run with the second alternative. Species such as *T. fuscobalteata* Cameron would run to 2 although cell second Cu is better defined than in most minute forms; it can easily be distinguished from all of the forms that should go to 2 by the characteristic *Trigona*-like inner surface and marginal fringe of the hind tibia. Many specimens of *Plebeia (Plebeia) schrottkyi* (Friese) lack the bend at the end of vein M shown in Figure 164, and would easily run to 2; this is why *Plebeia* can be run through either alternative. *P. schrottkyi* also lacks closed cells in the hind wing. The narrow depressed shining possterior margin of the inner surface of the hind tibia easily places this species in *Plebeia*. In *Austroplebeia cincta* (Mocsary) traces of a transverse cubital vein and of cell second Cu are evident, yet vein M ends without a bend. Some other species of the genus lack such traces and run easily to 2. I have placed this genus in the key twice to take care of this problem.

The following character states exclude small species from the first alternative and send them to 9 in the key:

(1) Hind tibia with plumose hairs among simple ones along posterior margin *(Trigona)*.

(2) Shining posterior margin of inner side of hind tibia absent or less than one third as wide as keirotrichiate zone at midlength of the tibia, except for *Cleptotrigona* and *Pariotrigona*. The forms that should go to 2 have the shining, marginal zone at least one third as wide as the keirotrichiate zone except for *Pariotrigona* (southeast Asia) and the African robber bee, *Cleptotrigona,* which lacks corbicula and penicillum.

(3) Rastellum consisting of strong, usually amber bristles, usually some of them blunt. In forms that should be run to 2 (except *Plebeia*), the rastellum consists of pallid, flexible, tapering hairs; such rastella also occur in some groups that run to 9, such as *Meliponula*.

Genus *Melipona* Illiger

(Figs. 9, 49, 82, 130, 162, 172, 176)

Melipona Illiger, 1806: 157. Type species: *Apis favosa* Fabricius, 1798, by designation of Latreille, 1810: 439.

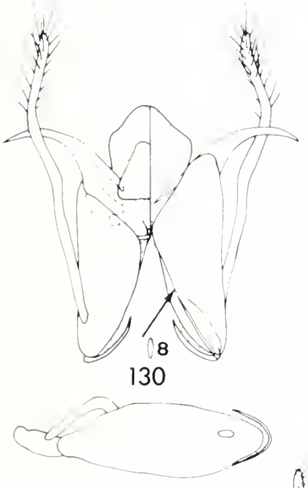
Melipona (Micheneria) Kerr, Pisani and Aily, 1967: 139 (not Orfila and Rossi, 1956). Type species: *Melipona scutellaris* Latreille, 1811, by original designation.

Melipona (Michmelia) Moure, 1975: 621. New name for *Micheneria* Kerr, Pisani and Aily. Type species: *Melipona scutellaris* Latreille, 1811 (autotypic) (new synonym).

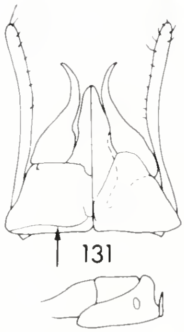
This is the most distinctive meliponine genus although it was not reliably distinguished from the others until well into the present century (see Schwarz, 1932). It consists of rather large (8-15 mm long) species, mostly somewhat more robust than workers of *Apis*. Wille (1979b) and Moure (1951, 1961) tabulated the most distinctive features (as the tribe Meliponini), which include wings that extend little if any beyond the apex of the metasoma, slender stigma that is not convex within the marginal cell, and 9 to 14 hamuli. The setae of the labial palpus are short and straight. The sting stylet of the worker is right angular or acute, sometimes (as in *M. fulva* Lepeletier, Fig. 9) as strong as in the African genus *Meliponula*, and the male genital capsule is schizogonal, the gonocoxites elongate, not transverse. Illustrations of male genitalia and hidden sterna can be found in Schwarz (1932), Snodgrass (1941), Camargo, Kerr and Lopes (1967), and Camargo, Moure and Roubik (1988). In the sting stylet and genital characters *Melipona* resembles the African group of genera. Unlike that group, however, the rastellum is strongly developed with many of the bristles blunt or abruptly narrowed at apices and the worker gonostyli are widely separated, setose and without minute hairs. It is the only Recent genus with such gonostyli and at the same time with an acute sting and long male gonocoxites. All three of these character states are plesiomorphies, as is the indication of a gonobase in males in the form of a slender sclerotic strip.

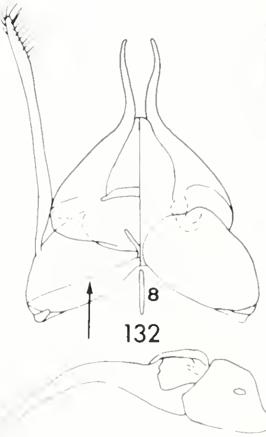
Melipona also differs from all other Meliponinae in having the third abdominal ganglion of workers and males (it innervates metasomal segment 2) in the thorax, the next one in the petiolar region and the last in metasomal segment 3 (Wille, 1961; Cruz-Landim et al., 1972). This cephalization is an apomorphy of the genus. Also, the digestive tract is relatively long (Cruz-Landim and Rodrigues, 1967).

In nesting biology, *Melipona* is unique among Meliponinae in rearing numerous small queens in cells that are identical to worker cells. In all other genera only a few large queens are pro-

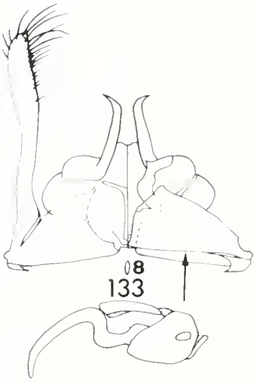


130


131



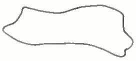
132

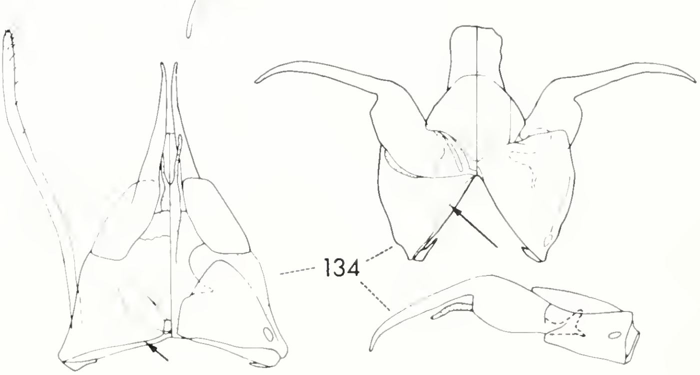


133


135


136


137


134

Figures 130-134. Male genitalia of Meliponinae, dorso-ventral views (dorsal at left) and lateral views with gonostylus and (for 130, 131) penis valve omitted or apex omitted. In this and other sets of figures of male genitalia, arrows indicate the basal opening of the gonocoxites into the metasomal cavity; 8 = probable relictual spiculum of S8. 130, *Melipona fulva* Lepeletier. 131, *Plebeia (Plebeia) frontalis* (Friese). 132, *Plebeia (Plebeia) schrottkyi* (Friese). 133, *Plebeia (Plebeia) caerulea* (Friese). 134, *Partamona* near *cupira* (Smith) rectigonal conformation at left, schizogonal conformation with gonostyli omitted at right.

Figures 135-137. Mandibles of male Meliponinae, apices at left. 135, *Hypotrigona braunsi* (Kohl). 136, *Liotrigona mahafalya* Brooks and Michener. 137, *Trigona (Trigona) fulviventris* Guérin.

duced in special large cells. Caste determination of *Melipona* is apparently partly genetic. The method of recruitment to resources is also different from that of other Meliponinae. See review by Michener (1974).

In view of its many autapomorphies, the recognition of a tribe Meliponini for *Melipona* can be justified on phenetic bases. Cladistic analysis does not strongly reinforce this tribal arrangement (Fig. 6) and tribal rank does not seem necessary for a single genus.

The division of the genus into two groups by Kerr, Pisani and Aily (1967) does not seem to me to necessitate subgeneric names. I have therefore included *Michmelia* as a synonym, but this is a matter of judgement.

Melipona ranges from Mexico to Argentina and contains about 40 species. The species were revised by Schwarz (1932) with an important review of the classification by Moure and Kerr (1950). Some well known species are *M. beecheii* Bennett, *fasciata* Latreille, *favosa* (Fabricius), *fulva* Lepeletier, *marginata* Lepeletier, *rufiventris* Lepeletier, and *seminigra* Friese.

Genus *Plebeia* Schwarz

This genus has shiny cephalic and thoracic integument with minute [somewhat larger in *P. (P.) caerulea* (Friese)], well separated punctures, varying to dull, densely and minutely punctate, in the subgenus *Schwarziana* and in *P. (P.) schrottkyi* (Friese). The scutellum is rounded in lateral view, not shelf-like, and often but not always overhangs and hides the median part of the metanotum as seen from above. The scutellum lacks a median depression in the anterior margin like that of *Nannotrigona* and *Scaptotrigona,* but in some species there is a weak indication of such a depression. The preoccipital carina is weak but present dorsally in the subgenus *Schwarziana* and some species of *Plebeia* s. str. but the lateral parts extending down toward the mandibles are always absent. The broad area with keirotrichia on the inner side of the hind tibia extends nearly to the posterior margin of the tibia but the margin is shiny, largely bare (Fig. 184), and abruptly depressed [except not depressed on distal third of tibia of *P. (Scaura) timida* (Silvestri) and not at all depressed in the subgenus *Nogueirapis*]; the area with keirotrichia may or may not reach the rastellum. The explanation of the inclusion of *Nogueirapis* as a subgenus in the genus *Plebeia* is given under the discussion of the subgenus.

A widely used character in Meliponinae is the presence or absence of plumose hairs on the posterior margin of the hind tibia of workers (character 6, Table 2). In *Plebeia* s. str. there are often one or two hairs with a branch or two near the apex of the posterior margin, and in *P. (Plebeia) caerulea* (Friese) and *P. (Schwarziana) quadripunctata* (Lepeletier) numerous hairs have short branches on one side. In *Plebeia* it is the long hairs that have such branches; in *Trigona* the long hairs are simple and intercalated shorter hairs are usually plumose.

The worker gonostyli are adjacent to widely separated, converging apically, overlapping apically when adjacent at bases, setose. The sting stylet is broad, rounded or irregular. The lancet is short; it is free at the apex only in the subgenus *Schwarziana*.

The male genitalia of *Plebeia* s. str. (Figs. 131-133 and Camargo and Moure, 1988) and *Schwarziana* (illustrated by Schwarz, 1948) are rather similar, rectigonal [in reality amphigonal at least in *P. (Plebeia) schrottkyi* (Friese), for which both rectigonal and schizogonal preparations are at hand (probably all species are amphigonal)]. Unlike most such forms, the gonocoxites are nearly as long as broad or longer. In *Scaura* (see Schwarz, 1948) the gonocoxites are short and transverse as in most rectigonal (amphigonal) Meliponinae and the same is probably true of *Nogueirapis* in view of Wille's (1964) comparison of the male genitalia of *P. (N.) mirandula* (Cockerell) with those of species of *Trigona* s. str. I have not seen males of the subgenus *Nogueirapis;* apparently males are not present in the collection at the Universidad de Costa Rica where Wille's material is preserved.

The forms listed above with dull cephalic and thoracic integument are not closely related to one another as judged by tibial and other characters. In *Trigona,* also, there is a subgenus with fine, dull thoracic integument *(Lepidotrigona),* a subgenus with a somewhat more shining and less closely punctate thoracic integument *(Papuatrigona),* in addition to the majority, which are shiny with well separated, minute punctures. Also in *Partamona* there are dull as well as shiny species. The idea that this is necessarily a generic or subgeneric character should be abandoned.

Brood cell construction is particularly variable in this genus. It is successive in the subgenera *Schwarziana* and *Scaura,* synchronous in most *Plebeia* s. str., and intermediate (starting successively but becoming synchronous) in *Plebeia (Plebeia) schrottkyi* (Friese) and *minima* (Friese).

Key to the Subgenera of *Plebeia*

1. Hind basitarsus thickened, nearly as broad as or broader than tibia. (Face without yellow markings.) . . . . *Scaura*

—Hind basitarsus flat, much narrower than tibia 2

2. Body (including metasomal terga) dull, minutely and closely punctured; forewing length about 6 mm; S3 of male with enormous procurved band of erect hooked hairs, behind which is a concave membranous area with erect hairs . . . . *Schwarziana*

—Body or at least metasoma shining; forewing length less than 5 mm, usually 4 mm or less; S3 of male unmodified 3

3. Hind tibia with posterior margin of inner surface narrowly depressed, shining, in sharp contrast to keirotrichiate area (Fig. 185) . . . . *Plebeia* s. str.

—Hind tibia with posterior margin of inner surface narrowly shining but not or scarcely depressed . . . . *Nogueirapis*

Subgenus *Plebeia* Schwarz, s. str.

(Figs. 11-13, 50, 51, 84, 85, 131-133, 163, 164, 184)

Trigona (Plebeia) Schwarz, 1938: 480. Type species: *Trigona mosquito* Smith, 1863, by original designation.
Mourella Schwarz, *in* Moure, 1946a: 442. Type species: *Melipona caerulea* Friese, 1900, by original designation.
Friesella Moure, 1946a: 441; 1946b: 611. Type species: *Melipona schrottkyi* Friese, 1900, by original designation.

This is a subgenus of small bees, mostly with whitish or yellow markings on the face and thorax. Unlike *Scaura*, which commonly has a more slender metasoma, that of *Plebeia* s. str. is as broad as the thorax. Except in *P. (P.) caerulea* (Friese), the labial palpi have five to nine large setae. At least one [in *P. (P.) franki* (Friese)] is curved and usually most are curved; in some species those on segment two are slightly sinuous.

Two unusual species have received genus-group names. *Mourella* was proposed for a rather large, robust species with the head and thorax dark blue-green (the only metallic meliponine), *P. caerulea* (Friese), with the mesoscutum a little more coarsely punctate than in other species, and with hairs on the basal area of the propodeum except medially. Unlike other *Plebeia* s. str., the scape of the worker is long, reaching to within one ocellar diameter of the median ocellus, and large setae are absent on the labial palpi, the hairs being short and straight. *Friesella* was proposed for a tiny species, *P. schrottkyi* (Friese). It has the mesoscutum dull with small close punctures and lacks yellow marks on the face; such marks on the thorax are absent in males, in workers there is commonly a weak pale line next to the tegula and sometimes a spot on the axilla. The wing venation is much reduced (see note after key to genera). While these two species are clearly quite different from ordinary species of *Plebeia*, I doubt if subgeneric names are needed for them. *Mourella* was described and illustrated by Schwarz (1948). Descriptions of *Plebeia* s. str. (and of the monotypic *Friesella* and *Mourella*, here synonymized) were given by Moure (1951).

Wille (1960) emphasized the intermediacy of *P. intermedia* (Wille) between *Plebeia* s. str. and *Schwarziana*. This species is large for a *Plebeia* s. str., with a rather closely punctured thoracic dorsum and with the scutellum not extending over the metanotum, features suggesting *Schwarziana*. However, the generally shiny surface, the shiny basal area of the propodeum, etc., are as in *Plebeia* s. str. and I suspect that when the male is found, it will not have the characteristics of *Schwarziana*.

Plebeia s. str. ranges from Mexico to Argentina. There are about 30 species; several occur in most areas. The unusual species, *P. (P.) schrottkyi* (Friese) and *caerulea* (Friese), occur in southern Brazil and adjacent countries; *P. (P.) intermedia* (Wille) is from Bolivia.

Familiar names are *Plebeia (Plebeia) caerulea* (Friese), *droryana* (Friese), *emerina* (Friese), *franki* (Friese), *frontalis* (Friese), *jatiformis* (Cockerell), *minima* (Friese), *mosquito* (Smith), *remota* (Holmberg), *schrottkyi* (Friese), and *tica* (Wille).

Subgenus *Schwarziana* Moure

(Figs. 14, 52, 86)

Trigona (Schwarziana) Moure, 1943: 147. Type species: *Melipona quadripunctata* Lepeletier, 1836, by original designation.

I have retained this name for a large species (body length 7 mm) that suggests in body form and pale markings a large *Plebeia* s. str. with a minutely punctate, dull body (including the metasomal terga). The dorsal propodeal area has a few hairs. The most remarkable features are those of the male sterna, which are highly modified as illustrated by Schwarz (1948); see also above key to the subgenera. The base of the propodeum is hairy, unlike other subgenera except for *P. (Plebeia) caerulea* (Friese). The scape is long, reaching nearly to the median ocellus, as in *P. (P.) caerulea.* The male genitalia are similar to those of *Plebeia* s. str. (see Schwarz, 1948; Camargo, 1974). The lack of large setae on the labial palpi (numerous short straight setae present) might be a plesiomorphic feature. Thus this could be the sister group to the subgenus *Plebeia* as here understood. Full descriptions were given by Moure (1951) and Camargo (1974).

The single species, *Plebeia (Schwarziana) quadripunctata* (Lepeletier), is found in Brazil (Goiaz and Minas Gerais southward), Paraguay, and northern Argentina.

Subgenus *Nogueirapis* Moure
(Figs. 16, 88)

Partamona (Nogueirapis) Moure, 1953: 247. Type species: *Trigona butteli* Friese, 1900, by original designation.

Nogueirapis has hitherto been placed either as a subgenus of *Partamona* (Moure, 1953, 1982) or as an independent genus. The association with *Partamona* is an error. It differs from that genus in the ordinary (not enlarged and spoon-shaped) hind tibia of the worker as well as small size, abundant yellow markings, the few and mostly curved (none sinuous) large setae of the labial palpi (as in various species of *Plebeia* s. str.), and the shining and hairless basal propodeal area as was indicated by Wille (1964). The detailed descriptions of *Plebeia* and *Nogueirapis* by Wille (1959) agree in all details except as follows: (1) *Nogueirapis* is said to have the posterior apical angle of the worker hind tibia rounded, *Plebeia* s. str., angular. Actually it is angular in both and some species of *Plebeia* s. str. have the tibia almost exactly as in *Nogueirapis*. (2) The inner surface of the hind tibia of *Nogueirapis* has a narrow, bare, shiny, but not depressed posterior margin whereas it is depressed in *Plebeia* s. str. This last character state has been the hallmark of *Plebeia* and would exclude *Nogueirapis* from *Plebeia*. No one character, however, should alone determine the classification, especially in a group so noted for convergence as the Meliponinae. Moreover, *P. (Scaura) timida* (Silvestri) is intermediate in this character, which is also variable within the genus *Meliponula*. In view of the many similarities between *Plebeia* s. str. and *Nogueirapis,* I regard them as congeneric.

Inclusion of *Nogueirapis* in the genus *Plebeia* results in a genus *(Plebeia)* with no known diagnostic apomorphies. The depressed posterior hind tibial margin is a probable synapomorphy for the rest of the genus. However, this character state is probably subject to reversals. A partial reversal is likely for *P. (Scaura) timida* (Silvestri) and polarization of this character is not at all convincing in the genus *Meliponula*. Thus the condition in *Nogueirapis* could be derived from that in other groups of *Plebeia* instead of the reverse. It is therefore best to place *Nogueirapis* on the basis of its close phenetic resemblance to *Plebeia* s. str., while hoping for the discovery of relevant synapomorphies.

This subgenus contains three species, *Plebeia (Nogueirapis) butteli* (Friese), *minor* (Moure and Camargo), and *mirandula* (Cockerell), and ranges from Costa Rica to Bolivia. In addition, it includes the Miocene fossil species *Plebeia (Nogueirapis) silacea* (Wille, 1959b) from southern Mexico.

Subgenus *Scaura* Schwarz
(Figs. 15, 53, 87)

Trigona (Scaura) Schwarz, 1938: 479. Type species: *Trigona latitarsis* Friese, 1900, by original designation.
Schwarzula Moure, 1946a: 439. Type species: *Trigona timida* Silvestri, 1902, by original designation.

This subgenus differs from other Meliponinae in the hind basitarsi which are nearly as broad as to broader than the tibia and convex on the outer surfaces, at least apically, as illustrated along with other character states (including those of male genitalia and sterna) of the *latitarsis* group by Schwarz (1948). These are small bees; *P. timida* (Silvestri) has the form of a *Plebeia* s. str., the others have variably more slender metasomas, very slender in *P. tenuis* (Ducke) and *longula* (Lepeletier). An interesting feature, best developed in *P. (S.) latitarsis* (Friese), is the series of flat, curved bristles on the posterior margins of S4 and S5 of the worker. The head and thorax are black, without the yellow markings characteristic of nearly all species of *Plebeia* s. str. The body surface is shining with small, scattered punctures like those of most *Plebeia* s. str. Unlike nearly all species of *Plebeia* s. str., the labial palpi lack large setae; the setae are rather short and straight. A full description of *Scaura* was given (as a genus) by Moure (1951).

The subgenus consists of two units that differ considerably. *P. (S.) timida* (Silvestri) has more plesiomorphies, as shown by the two denticles on the upper part of the apical mandibular margin and the less broad hind basitarsi which are only weakly convex on the outer surface. Unlike other species of the genus *Plebeia* (except *Nogueirapis*), the posterior margin of the inner surface of the hind tibia is not depressed in the apical third or fourth of the tibia. *P. timida* has been placed in a monotypic genus or subgenus *Schwarzula*. The other species of *Scaura* have untoothed mandibles (or the two denticles near the upper end of the apical margin are barely perceptible), broader and more convex hind basitarsi, and a fully depressed inner posterior margin of the hind tibia as in *Plebeia* s. str. *P. timida* appears to be the sister to all other species of *Scaura,* and I have elected to include it in *Scaura,* thus synonymizing *Schwarzula.*

Scaura ranges from southern Mexico to Brazil and Bolivia; there are four species, *Plebeia (Scaura) latitarsis* (Friese), *longula* (Lepeletier), *tenuis* (Ducke), and *timida* (Silvestri).

Genus *Partamona* Schwarz

(Figs. 17, 18, 57, 89, 134, 187, 191)

Trigona (Patera) Schwarz, 1938: 475 (not Lesson, 1837; not Albers, 1850). Type species: *Melipona testacea* Klug, 1807, by original designation.

Trigona (Partamona) Schwarz, 1939b: 23. Type species: *Melipona testacea* Klug, 1807 (autobasic and original designation). Replacement for *Patera* Schwarz, which is preoccupied.

Trigona (Parapartamona) Schwarz, 1948: 428. Type species: *Trigona zonata* Smith, 1854, by original designation.

This genus is composed of relatively robust forms superficially suggestive of *Scaptotrigona,* some species of *Trigona* s. str., etc. *Partamona* differs from such forms by having yellowish face marks (often restricted), by the rather dense covering of erect hair on the basal propodeal area, and by the hind tibial structure of workers. This tibia is greatly broadened, about three times as wide as the femur, spoon-shaped, the outer surface mostly occupied by the enormous corbicula (Fig. 187). There are two hairs, often about as long as the tibial width and often apically wavy, arising from the posterior part of the corbicula. The inner surface of the tibia has the broad keirotrichiate area extending nearly to the posterior margin, which is shining but not depressed. The worker gonostyli are mere rounded tubercles with a few setae or in *P. zonata* (Smith) about 1.5 times as long as broad. The sting stylet is rounded, the lancet is moderately long and the distal part free of the membrane, or almost absent in *P. zonata.* The male genital capsule is amphigonal [both conformations seen in *P. cupira* (Smith), Fig. 134]. It is illustrated here as well as by Snodgrass (1941). The large setae of the labial palpus are about 11 to 13 in number, mostly sinuous but some only curved.

In most species the cuticle is shining with minute, widely separated punctures. In *P. zonata,* the type species of *Parapartamona,* however, the cuticle is dull and exceedingly minutely punctate or roughened. Other species that have the extremely long wings of *Parapartamona* have intermediate cuticular structure, or even as in *P. grandipennis* (Schwarz), cuticle like that of typical *Partamona.* For these reasons I do not think that *Parapartamona* should be recognized as a subgenus. A full description of *Partamona* was given by Moure (1951) and of *Parapartamona* by Moure (1953).

Partamona has not been revised as a whole but the *Parapartamona* group was dealt with by Schwarz (1948) and the species with testaceous bodies by Camargo (1980).

The genus, with about 16 species, ranges from Mexico to central Brazil and Peru, but appears to be absent from southern Brazil and adjacent countries. Familiar species are *Partamona bilineata* (Say), *cupira* (Smith), *helleri* (Friese), *peckholti* (Friese), *testacea* (Klug), and *zonata* (Smith). Except as otherwise indicated, the references to and illustrations of *"Partamona* near *cupira"* are based on Mexican specimens that are probably *P. bilineata.*

Genus *Paratrigona* Schwarz

(Figs. 19, 55, 90)

Trigona (Paratrigona) Schwarz, 1938: 487. Type species: *Melipona prosopiformis* Gribodo, 1893.

Paratrigona (Aparatrigona) Moure, 1951: 60. Type species: *Melipona impunctata* Ducke, 1916.

This genus contains small species with the head and thorax (often also the abdomen) dull with extremely minute punctation and with conspicuous yellow to white markings on the thorax and usually on the face. As in *Nannotrigona* and *Scaptotrigona,* the scutellum is produced posteriorly as a thin shelf hiding the median part of the metanotum as seen from above. The scutellum, however, lacks the anteromedian depression characteristic of those genera. The proboscis is unusually long, the first segment of the labial palpus being about three times as long as the second which is about six times as long as wide. The eight or nine large setae of the labial palpi are strongly curved. The preoccipital carina is completely absent. The inner surface of the hind tibia has the broad keirotrichial area extending nearly to the posterior margin which is not depressed. There are two unusually long hairs (about as long as tibial width) arising from the posterior part of the corbicula; this is suggestive of *Partamona* but less conspicuous than in that genus because the tibia is narrower. The four-toothed mandibles of workers distinguish this genus from all Meliponinae except *Trigona (Trigona);* the two lower teeth may be united by a thin septum, however, so that the mandibular profile looks like that of an ordinary meliponine with the two denticles on the upper part of the apical margin unusually large. Full descriptions are given by Schwarz (1948) and Moure (1951), and Schwarz gives an illustrated account of the species, including figures of male genitalia and hidden sterna.

The worker gonostyli are widely separated, setose, convergent apically. The sting stylet is broad, rounded and the lancet, if present, is a mere strip in the membrane. The male genital capsule is rectigonal, but may well be really amphigonal. No specimens with the schizogonal conformation have been seen, however.

Moure (1951) separated two unusually robust species as a subgenus *Aparatrigona.* There is no doubt that they constitute a monophyletic unit that is the sister group to the rest of the genus.

They possess plesiomorphies relative to other species such as a partly smooth metasoma and relatively abundant hair (other species are nearly nude). I doubt that *Aparatrigona* is sufficiently different from *Paratrigona* s. str. to necessitate recognition of the subgenus for only two species.

It is noteworthy that in *P. opaca* (Cockerell) S6 of the male is a plate entirely without the apical process usual in meliponines and found in other species of *Paratrigona*. A somewhat intermediate condition exists in *P. prosopiformis* (Gribodo), in that S6 is broader than usual and the apical process triangular (see illustrations of Schwarz, 1948). These character states are not associated with other distinctive features and additional supraspecific taxa do not seem to be desirable for these species. In *Trigona (Heterotrigona)* also there is a species, *T. (H.) apicalis* Smith, with S6 similar to more anterior sterna; see also *Trigona (Homotrigona)*.

Paratrigona ranges from Mexico to Argentina. There are about a dozen species; see the revision by Schwarz (1948). Familiar names are *Paratrigona impunctata* (Ducke), *lineata* (Lepeletier), *opaca* (Cockerell), and *peltata* (Spinola).

Genus *Nannotrigona* Cockerell

(Figs. 20, 56, 91, 138)

Nannotrigona Cockerell, 1922: 9. Type species: *Melipona testaceicornis* Lepeletier, 1836.

This genus is characterized by the very strong, usually cribriform punctation of the head and thorax or at least the scutellum; the scutellum produced posteriorly as a thin shelf (side view) hiding the median part of the metanotum in dorsal view; the notched or emarginate apex of the scutellum (dorsal view); the presence of a shining, depressed V- or U-shaped median depression in the anterior margin of the scutellum (as in Fig. 190); the straight lateral clypeal margins (concave in most other Meliponinae); the distinct preoccipital carina, laterally extending down toward the mandibles, although weak dorsolaterally; the strong transverse carina across the anterior margin of the pronotal lobe; the distinct (although not carinate) angle between the anterior and lateral surfaces of the mesepisternum; and the broad area of keirotrichia on the inner side of the hind tibia, extending to or nearly to the posterior margin of the tibia which is not abruptly depressed, and extending apically to the bases of the rastellar bristles. The worker gonostyli are short, separated at the bases by less than a stylar width, strongly convergent and overlapping distally. The sting stylet is broad and rounded, the lancet absent. The male genital capsules examined are schizogonal, very thick, with the spatha nearly vertical; the schizogonal conformation may be permanent. The genitalia are strangely similar to those of *Trigona (Tetragonisca)*. The large setae of the worker labial palpi are few, about 10, sinuous. Full descriptions of the genus are given by Moure (1951) under his genus and subgenus *Nannotrigona*.

Nannotrigona looks like a deeply punctate, pitted *Plebeia* s. str. Thus it is quite different in appearance from the larger, robust *Scaptotrigona*. As emphasized by Schwarz (1938:483) and Wille (1959a, 1979b), however, *Nannotrigona* and *Scaptotrigona* share numerous character states and I do not doubt their close relationship.

Nannotrigona is so distinctive that Cockerell (1922), who was generally conservative in such matters, named it as a distinct genus while leaving other Meliponinae except *Melipona* in the genus *Trigona*. About nine species range from Mexico to southern Brazil and Paraguay. The most familiar is *Nannotrigona testaceicornis* Lepeletier.

Genus *Scaptotrigona* Moure

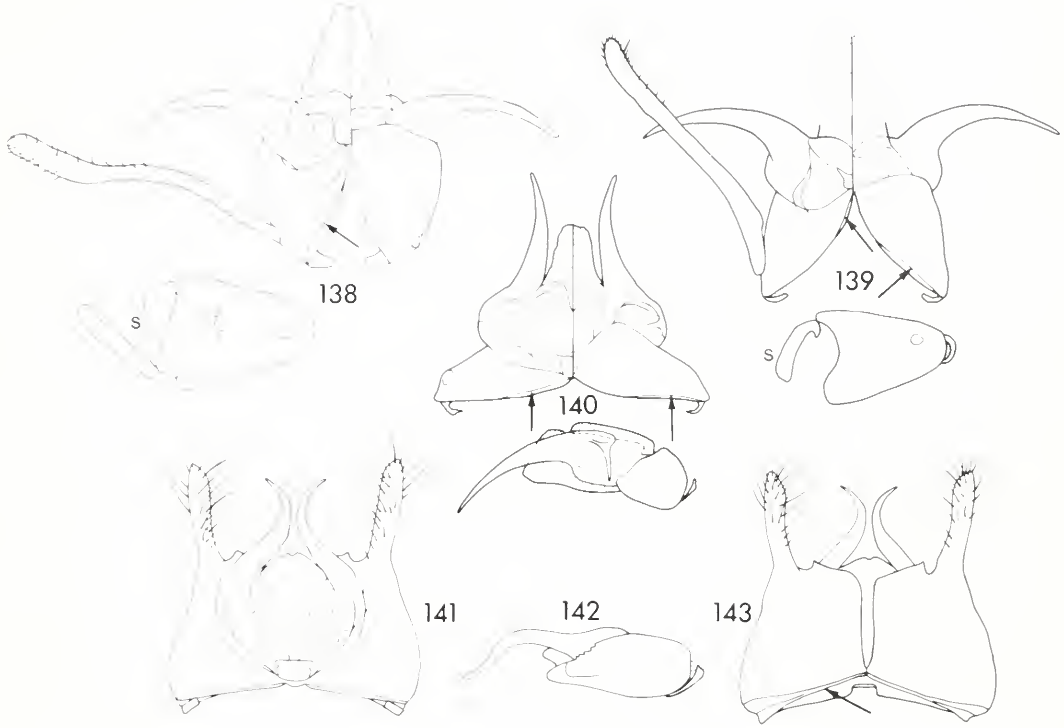
(Figs. 21, 54, 92, 139, 140, 190)

Trigona (Scaptotrigona) Moure, 1942: 315. Type species: *Trigona postica* Latreille, 1807, by original designation.

These are among the most robust of the Meliponinae. The head and thorax are rather strongly punctate, more coarsely so than in *Plebeia* and its relatives (although approached in coarseness by *Plebeia caerulea* Friese) and with shining ground between the punctures. As in *Nannotrigona* the scutellum is produced as a thin shelf (side view) hiding the median part of the metanotum from above. Also as in *Nannotrigona* there is a shining depressed V or U-shaped median depression on the anterior margin of the scutellum (Fig. 190) and the preoccipital carina and hind tibia are also as described for *Nannotrigona*. *Scaptotrigona* differs from *Nannotrigona* not only in form and punctation but also in the rounded apex of the scutellum (seen from above) and the rounded anterior margin of the pronotal lobe. A full description of the genus is given by Moure (1951) as a subgenus of *Nannotrigona*.

The worker gonostyli are setose, convergent apically. The sting stylet is broad and irregularly rounded and the lancet, if present at all, is short and fades into the membrane. The male genital capsule is schizogonal in specimens of *S. pectoralis* (Dalla Torre) and rectigonal in *S. mexicana* (Guérin). Probably it is really amphigonal in both. The setae of the labial palpus are short and straight.

Most character states of *Scaptotrigona* are plesiomorphic relative to *Nannotrigona* although the larger size and robust form may be derived



Figures 138-143. Male genitalia of Meliponinae, dorso-ventral views (dorsal at left), or separate dorsal and ventral views for *Lestrimelitta,* and lateral views with gonostyli omitted, penis valves also omitted in Figures 138 and 139. Arrows are explained with Figures 130-134; s = spatha. 138, *Nannotrigona testaceicornis* (Lepeletier), gonostylus omitted on ventral view. 139, *Scaptotrigona barrocoloradensis* (Schwarz), gonostylus omitted on ventral view, schizogonal conformation. 140, *Scaptotrigona mexicana* (Guérin), right gonostylus omitted, rectigonal conformation. 141-143. *Lestrimelitta limao* (Smith), dorsal, lateral (gonostylus omitted, attachment indicated by jagged line), and ventral views.

features. The genus is so distinct from the highly derived *Nannotrigona* that it is reasonable to recognize it at the genus level. Moreover, the worker-laid trophic eggs of *Scaptotrigona* are much larger than eggs of the queen, while in *Nannotrigona* they are not so large. This is no doubt an apomorphy of *Scaptotrigona,* supporting the view that the two are sister groups.

Scaptotrigona contains about two dozen species and ranges from Mexico to Argentina. Familiar species are *Scaptotrigona hellwegeri* (Friese), *mexicana* (Guérin), *pectoralis* (Dalla Torre), *postica* (Latreille), and *tubiba* (Smith).

Genus *Lestrimelitta* Friese

(Figs. 22, 58, 93, 141-143, 165)

Trigona (Lestrimelitta) Friese, 1903: 361. Type species: *Trigona limao* Smith, 1863 (monobasic).

Like *Cleptotrigona,* this is a robber genus. The workers do not forage except in nests of other Meliponinae, especially species of the genera *Plebeia* and *Nannotrigona,* more rarely *Melipona, Scaptotrigona* and *Trigona;* they even attack weak colonies of *Apis.* As in other forms that do not forage from flowers, there are only short, straight setae on the labial palpus.

Unlike nearly all other Meliponinae, S6 of the male lacks a median apical process and has instead a small notch. S7 has a broad, squarish body. Both S6 and S7 have long basolateral apodemes (see illustrations by Schwarz, 1948). These features seem ancestral (i.e., more like more basal sterna) relative to the specialized or reduced aspects of these sterna in other Meliponinae. However, it seems unlikely that a robber genus would preserve archaic structure, for its habits and the related features such as loss of the corbicula and rastellum are obviously derived. Another explanation is that since genes for ordinary sterna are obviously present, a developmental change could lead to their control of the more apical sterna as well as the preceding ones. The external generic character states were listed by Schwarz (1948), Moure (1951) and Wille (1979b).

The male genital capsule is probably permanently rectigonal; unlike other rectigonal and amphigonal Meliponinae except some *Plebeia,* the gonocoxites are about as long as broad, thus not strongly transverse. The male gonostyli are shorter than in most Meliponinae and broadly fused to the gonocoxites (Fig. 141 and Schwarz, 1948). The worker gonostyli are a little longer than broad, separated basally by a little more than a gonostylar width, convergent distally, and with setae (without minute hairs). The sting stylet is broad and blunt and the lancet, although short, has the apex free of membrane.

The hind tibia of the worker, on the inner surface, has only a narrow, slightly depressed, marginal zone without keirotrichia, suggesting *Plebeia (Plebeia).* This may be because the tibia is not flattened and expanded posteriorly as in forms with a corbicula. However the keirotrichiate area is broad; this combined with the narrowness of the marginal zone may indicate derivation from an ancestor of *Plebeia (Plebeia).* The rastellum is reduced to tapering hairs.

Lestrimelitta consists of possibly ten species (mostly unnamed), of which *L. limao* (Smith) is best known. The genus is widespread in the Neotropical region—Mexico to Argentina. Included species were described and illustrated by Schwarz (1948), Moure (1951), Wille (1979b), and Roubik (1980).

Genus *Oxytrigona* Cockerell

(Figs. 23, 68, 94)

Trigona (Oxytrigona) Cockerell, 1917a: 124. Type species: *Trigona flaveola mediorufa* Cockerell, 1913, by original designation.

This genus is closely related to *Trigona* and could be considered a subgenus of that genus. *Oxytrigona* has several striking character states of its own, however, and *Trigona* has at least one probable synapomorphy (the narrower, better defined keirotrichiate band) that usually distinguishes it from *Oxytrigona* and suggests that *Oxytrigona* is the sister genus of *Trigona* plus *Cephalotrigona.* When this character state fails in *Trigona,* the marginal depressed zone is nonetheless quite broad. In *Oxytrigona* it is narrower, suggestive of that of *Plebeia* although not so narrow as in that genus.

Noteworthy features of *Oxytrigona* include the following: the short, wide face (see key to genera); the small clypeus, widely separated from the eyes; the shining but distinctly punctate clypeus and lower paraocular areas; the long malar space of the worker (about one third as long as the eye); the convex genal area of the worker, providing space for the posterior ramus of the deeply bifid mandibular gland (Michener, 1974); the abundant, large, straight setae on the labial palpus of the worker, a feature unique in the Meliponinae; the simple hairs of the posterior margin of the hind tibia; the largely vertical propodeal profile (quite different from that of *Trigona*); and the worker gonostyli which are four or five times as long as wide, converging distad, separated at their bases by three or more stylar diameters, and bearing numerous setae. Unique among Meliponinae is the short second valvifer, shorter than the gonostylus (Fig. 23). The lancet of the sting is almost invisible, and may not be realistically illustrated in Fig. 23. As in many species of *Trigona,* the genital capsule is rectigonal but probably in reality amphigonal; the gonocoxites are strongly transverse. Schwarz (1948) listed the included species (as varieties) and provided detailed descriptions and illustrations of *Oxytrigona;* Camargo (1984) added species and raised some varieties to the species level. Moure (1951) described the genus comparatively.

An attribute of interest is the secretion of the mandibular glands which contain formic acid (Roubik, Smith and Carlson, 1987). Workers, in nest defense, bite this liquid into the skin of an intruder, causing painful and long-lasting lesions in human skin (Michener, 1974). The name "fire bee" is therefore in wide use for this insect.

Oxytrigona contains about eight closely related species ranging from Mexico to Bolivia and southern Brazil. *O. tataira* (Smith) is the best known of these species.

Genus *Cephalotrigona* Schwarz

(Figs. 24, 65, 67, 95, 166, 172)

Trigona (Cephalotrigona) Schwarz, 1940: 10. Type species: *Trigona capitata* Smith, 1854, by original designation.

This genus is closely related to *Trigona* and could be considered a subgenus of that genus. The body seems more strongly sclerotized than in *Trigona.* Unique features include (1) the strongly, coarsely punctate and shining clypeus, lower supraclypeal area, lower paraocular area, and lower genal area contrasting with the dull, reticulate frons, the dull, closely punctate vertex and scutum, and the extremely dull and minutely punctate upper genal area; (2) the distal margin of the mandible of the worker which has a single large tooth at the upper extremity, separated by a broad, shallow concavity from the rest of the margin which is edentate; and (3) the strong, shining preoccipital carina across the interocular width of the head. The large, broad mandibular tooth is more like the upper tooth of the mandible of *Trigona (Trigona)* than the one or two small or sharp teeth (denticles) on the mandibles of most Meliponinae. It may not be homologous to such denticles. Additional interesting features are the following: The keirotrichiate, median, elevated zone of the inner surface of the hind tibia is about as wide as the shining marginal zone and separated from it by a gentle slope, not an abrupt one; this slope fades away in the basal fifth of the tibia rather than continuing as a channel nearly to the tibial base. The propodeal triangle has conspicuous hair bases and, like the rest of the propodeum, abundant plumose hairs. S6 of the male has a short median process and lateral processes about as long as the median one (see illustrations in Schwarz, 1948). The male genitalia are rectigonal (probably amphigonal) with extremely short, broad gonocoxites. The labial palpus of workers and males has abundant short, straight setae and lacks large setae.

Cephalotrigona could be merely a specialized derivative of *Trigona,* in which case it probably should not receive generic status. However, the better defined keirotrichiate band of *Trigona* is probably an apomorphy suggesting that *Cephalotrigona* is the sister group of *Trigona.* S. F. Sakagami (in litt.) regards *Cephalotrigona* as a subgenus of *Trigona* because he considers its differences from *Trigona* to be no greater than differences among some subgenera of that genus. This was my opinion also early in the development of this work, but rather arbitrarily and for the reasons indicated above, I have decided to recognize it at the generic level. Sakagami notes that the oviposition behavior, with frequent "body insertions" by workers alternating with inspections by the queen of the cell in which she will oviposit, is similar in *Cephalotrigona* and *Trigona (Tetragona, Frieseomelitta* part, *Duckeola* and *Trigona* s. str.).

The characters of the genus are well illustrated by Schwarz (1940, 1948) and described comparatively by Moure (1951). The genus contains about three species (listed as varieties by Schwarz, 1948) and is found from Mexico to Argentina. *Cephalotrigona capitata* (Smith) is the best known species.

Genus *Trigona* Jurine

This is the largest and most widely distributed genus of Meliponinae. It is distinguished from all other genera except *Oxytrigona, Cephalotrigona,* and the superficially similar *Dactylurina* by the inner surface of the hind tibia of the worker which has a longitudinal elevation covered with keirotrichia, behind which is a depressed shining marginal zone without keirotrichia, usually about as wide as the elevated zone, at least toward the apex of the tibia (Fig. 185). In *Trigona* the slope separating the keirotrichiate ridge from the smooth zone behind it is abrupt (except in the subgenera *Lepidotrigona* and *Papuatrigona*) and extends basad as a shining channel nearly to the base of the tibia. The male genitalia and hidden sterna are similar in many members of the genus to those of *Oxytrigona,* as shown by illustrations of Schwarz (1939, 1948) and Figures 144 to 150; they are known to be amphigonal in some species and probably are in others. However, in the subgenera *Geotrigona, Tetragonisca,* and *Homotrigona* the genital capsule is probably permanently schizogonal and the gonocoxites about as long as broad or longer than broad (Figs. 145, 146). The gonostyli of the workers are setose, without minute hairs. They vary from about 1.5 to 6 or 7 times as long as broad. They vary even within species groups. Thus within the *iridipennis (Tetragonula)* group of the subgenus *Heterotrigona,* in *T. carbonaria* Smith they are less than 1.5 times as long as broad and separated by little more than one stylar length while in *T. fuscobalteata* Cameron they are about twice as long as broad and separated by about two stylar lengths. The gonostyli are typically separated by two or more stylar diameters basally and converge apically. In *T. (Frieseomelitta) nigra* Cresson and *T. (Trigona) cilipes* (Fabricius), however, the gonostyli are separated by one basal stylar diameter or less (Figs. 27, 34). In *T. cilipes* [but not in other species of *Trigona (Trigona),* e.g., *amalthea* (Olivier), *chanchamayoensis* Schwarz, and *fulviventris* Guérin], the gonostyli diverge apically (Figs. 33, 34).

The sting stylet is ordinarily a mere convexity but in *T. (Tetragona) lurida* Smith (Fig. 31) its lateral margins are at an acute angle to one another although the apex is broadly rounded and in *T. (Trigona) cilipes* (Fabricius) (Fig. 34) the sting stylet is only narrowly rounded at the apex. The stronger, longer stylet in the last two species and the diverging gonostyli in *T. cilipes* may be related to the elongate metasomas of these species, laterally compressed in *T. cilipes.*

The lancets of the sting are ordinarily much reduced and lie in the membrane, sometimes being transparent and almost invisible. In *T. (T.) amalthea* (Olivier) but not in *T. (T.) cilipes* (Fabricius), etc., the apices of the lancets are free of the membrane.

Trigona is found in the Neotropics from Mexico to Argentina and in the Indoaustralian region from India and Sri Lanka to Taiwan, east to the Caroline Islands (introduced?), the Solomon Islands, and south throughout Indonesia and New Guinea to about latitude 34°S in Australia.

In several subgenera of *Trigona* there is a well-defined sericeous area of short, dense, easily lost hairs (Fig. 184) on the base of the inner surface of the hind basitarsus. Such an area is present in workers, and in some subgenera, in males also. It is not a generic characteristic since it is altogether absent, the surface being uniformly setose, in some subgenera. Any bee with the sericeous area, however, belongs to the genus *Trigona*. Interestingly, the worker of *Dactylurina staudingeri* (Gribodo) but not *D. schmidti* (Stadelmann) has a weakly differentiated approach to such a sericeous area.

In the great majority of species of *Trigona* and in all those in the Americas, some of the hairs along the rear margin of the hind tibia are plumose (Fig. 184). No other Meliponinae except for the African genus *Dactylurina* have such hairs. (There are a few on the distal part of the margin in some species of *Meliponula* and *Plebeia.*) This characteristic is therefore useful in generic recognition of most species of the genus.

The subgenus with the hairs on the posterior margin of the hind tibia all simple, *Lepidotrigona,* has sometimes been given generic status. Because it is basically similar to the other subgenera, and because *Papuatrigona* has plumose hairs only on the apical sixth of the posterior tibial margin and is thus intermediate, I have chosen not to do so. As noted below, *Papuatrigona* is also intermediate between *Lepidotrigona* and the other subgenera in scutal sculpturing. *Lepidotrigona* and *Papuatrigona* differ from the remaining subgenera (and agree with the genus *Cephalotrigona*) in the less sharp distinction between the elevated keirotrichiate zone on the inner surface of the hind tibia and the shiny margin. In *Lepidotrigona* and *Papuatrigona* the area with keirotrichia is not *abruptly* elevated. In the genus *Cephalotrigona* the same is true. In the genus *Oxytrigona* it is more abruptly elevated but is unusually wide, so that at the middle of the tibia it is much wider than the depressed, shiny, marginal zone. A broad keirotrichiate zone is also found in some forms clearly placed in *Trigona* such as *T. (Heterotrigona) carbonaria* Smith and *planifrons* Smith, but in such species the zone is more elevated and its delimitation extends almost to the base of the tibia (see couplet 1, key to subgenera).

Workers of the genus *Oxytrigona* and of *Trigona (Lepidotrigona)* have unusually broad hind basitarsi, convex on the outer surfaces, thus suggesting *Plebeia (Scaura).* In *Oxytrigona* and in species of *Lepidotrigona* without greatly broadened tibiae, such as *T. (Lepidotrigona) terminata* Smith, the basitarsal width is about equal to the width of the tibia at midlength. In view of the dissimilarity of *Oxytrigona, Lepidotrigona,* and *Scaura,* I regard their large hind basitarsi as convergent rather than as a synapomorphy.

In most species of *Trigona* the scutum is shining with minute, widely separated punctures. In the subgenus *Lepidotrigona* it is dull with minute, dense punctures, as in the genus *Cephalotrigona. Papuatrigona* is intermediate with minute punctures separated by about a puncture width of shiny ground.

The two teeth of the upper part of the apical margin of the worker mandible are large and occupy about half of the mandibular margin in *T. (Homotrigona) fimbriata* Smith, but they are nearly as large in the *Heterotrigona* groups of *T. apicalis* Smith, *reepeni* Friese (the only member of the *Tetragonula* group with large teeth), and *canifrons* Smith. *T. (Tetragona) lurida (Ptilotrigona)* from the Neotropical region has similarly large teeth. There seem to be no other characters that associate these large-toothed species. *T. (Heterotrigona) itama* Cockerell and *erythrogastra* Cameron in southeast Asia have only one such tooth. As is well known, the species of *Trigona (Trigona)* have four or usually five mandibular teeth.

T. (Tetragona) lurida (Ptilotrigona) in the Neotropics and *T. (Heterotrigona) planifrons* Smith, *flaviventris* Friese, *keyensis* Friese *(Platytrigona)* and *canifrons* Smith *(Lophotrigona)* in southeast Asia are unusual in the hairy basal area of the propodeum, a feature that crops up several times in unrelated Meliponinae and does not even characterize all species of the *planifrons* group (i.e., *Platytrigona*). The American and Asiatic species show no other significant similarities and probably evolved the hairs independently; the Asiatic groups may also have evolved such hairs independently.

An architectural character that has received attention in classification of the genus *Trigona* is arrangement of the brood cells. Various species arrange the cells in combs. In the *iridipennis* group *(Tetragonula),* however, most species arrange cells in clusters although some (e.g., *T. carbonaria* Smith) make combs and others are intermediate (*T. hockingsi* Cockerell) (see Michener, 1961). *T. canifrons* Smith and the subgenus *Frieseomelitta* also arrange their cells in clusters. Probably the cluster arrangement within the genus *Trigona* is derived, presumably independently in the Indoaustralian and American taxa, the ancestral pattern being horizontal combs.

In most subgenera of *Trigona* brood cell construction is successive (Sakagami, 1982), a presumed plesiomorphic state, but in the subgenus *Lepidotrigona* and in *T. (Frieseomelitta) flavicornis* (Fabricius) but not other species of its subgenus, it is synchronous. It is intermediate, initially successive but becoming synchronous, in the subgenus *Duckeola*.

Key to the Subgenera of *Trigona*

1\. Hairs along posterior margin of hind tibia of workers and males all simple or some plumose only on apical fifth or sixth of margin; elevated, keirotrichiate median zone of inner surface of hind tibia separated from shining posterior marginal zone by gentle slope 2

—Hairs along posterior margin of hind tibia of workers and some males partly plumose (in some species of *Geotrigona* the few branched hairs may have only two or three branches so that plumosity is inconspicuous); elevated, keirotrichiate median zone of inner surface of hind tibia separated from shining marginal zone by abrupt slope. 3

2\. Head and thorax dull with minute close punctures; propodeal dorsum finely reticulate; posterior margin of hind tibia of worker without plumose hairs; scutum margined with whitish, densely plumose ("scalelike") hairs (Southeast Asia) . . . . *Lepidotrigona*

—Head and thorax shining although with minute, rather close punctures; propodeal dorsum smooth, shining; posterior margin of hind tibia of worker with plumose hairs among bristles on apical fifth or sixth of margin; scutum without conspicuous plumose hairs (New Guinea) . . . . *Papuatrigona*

3\. Mandible of worker with 4 or 5 teeth along distal margin; inner surface of hind basitarsus of males and workers with basal sericeous area (Neotropical region). . . . . *Trigona* s. str.

—Mandible of worker with lower half or two thirds of distal margin edentate, upper part of margin with one or usually two teeth; inner surface of hind basitarsus of male without basal sericeous area, of worker variable (Neotropical region; Asia to Australia). 4

4\. Metasoma short, dorsoventrally flattened, about as wide as thorax; posterior margin of hind tibia of worker usually with few plumose hairs, most of them with only two to six scattered branches not concentrated toward apices; yellow markings absent; vein M of forewing dark almost to wing margin (Neotropical region). . . . . *Geotrigona*

—Metasoma usually narrower than thorax, often noticeably elongate; posterior margin of hind tibia of worker with numerous strongly plumose hairs, usually with abundant branches toward apices; yellowish or reddish markings present on face of some Neotropical species; vein M of forewing usually fading away near widest part of wing (Neotropical region; Asia to Australia). 5

5\. Inner surface of hind basitarsus of worker with basal sericeous area covered with minute setae or sometimes lacking setae (Fig. 184) 6

—Inner surface of basitarsus of worker rather uniformly setose, without basal sericeous area 7

6\. S6 of male with median apical process very broad and long so sternum is much longer than broad (Neotropical region) . . . . *Tetragonisca*

—S6 of male much broader than long (Indoaustralian region) . . . . *Heterotrigona*

7\. S6 of male a broad sternum without apical process (Southeast Asia) . . . . *Homotrigona*

—S6 of male with median apical process of the usual slender, heavily sclerotized form (male of *Duckeola* unknown) (Neotropical region) 8

8\. Posterior margin of vertex elevated as strong, hairy ridge between summits of eyes; posterior distal angle of hind tibia of worker acute. . . . . *Duckeola*

—Posterior margin of vertex not elevated; posterior distal angle of hind tibia of worker broadly rounded 9

9\. Labial palpi with large, sinuous setae on first two segments . . . . *Frieseomelitta*

—Labial palpi with setae no longer than palpal width and straight or nearly so. . . . . *Tetragona*

Subgenus *Lepidotrigona* Schwarz

(Figs. 25, 96)

Trigona (Lepidotrigona) Schwarz, 1939a: 132. Type species: *Trigona nitidiventris* Smith, 1857, by original designation.

Schwarz (1939a) described and illustrated the main features of this subgenus; Moure (1961) described it comparatively and listed included species. These are delicate bees similar to many species of the subgenus *Heterotrigona,* but differing not only in the character states listed in the key but also in the mostly dull, minutely roughened integument and, in males, in the pair of long spines on S5 [but see *T. (Heterotrigona) itama* Cockerell]. S6 is more like an ordinary sternum than in most other males, having a moderately large disc with the median process short and triangular, as illustrated by both Schwarz (1939a) and Sakagami (1975). The genital capsule is rectigonal, probably actually amphigonal. The labial palpus of the worker has about 18 large, sinuous setae (or some merely curved); this is within the range of variation found in *Heterotrigona*. The hind tibia of the worker especially of *T. nitidiventris* Smith and *trochanterica* Cockerell, is slender, expanded apically, thus "racket-shaped," a convergence with some species of the New World subgenus *Frieseomelitta*.

This subgenus of about four species (plus color variants) occurs from India to the Philippines and Taiwan, south to Sumatra, Borneo and Java. Included species are *Trigona (Lepidotrigona) nitidiventris* Smith, *terminata* Smith, *trochanterica* Cockerell and *ventralis* Smith (list provided by S. F. Sakagami, in litt.).

Subgenus *Papuatrigona* Michener and Sakagami

(Figs. 26, 97, 195, 196, 198, 199, 201-205, 207, 208-210, 212-219)

Papuatrigona Michener and Sakagami, see Appendix. Type species: *Trigona genalis* Friese, 1908, by original designation.

This subgenus (which is fully described in the Appendix) at first seems to lack plumose hairs on the posterior margin of the hind tibia, but such hairs are present among simple hairs on the distal fifth or sixth of the tibial margin. The keirotrichiate ridge on the inner surface of the hind tibia is nearly twice as wide as the depressed marginal zone, and the slope from the ridge to the marginal zone is gentle, the ridge not being high; distally there is almost no slope, the ridge being undefined and scarcely higher than the zone behind it; proximally the slope is more distinct and extends well into the basal fourth of the tibia. The outer surface of the hind basitarsus has a posterior basal concavity behind a longitudinal, curved, hairy ridge (Figs 207, 210) as in *Lepidotrigona* and many species of *Heterotrigona*, suggesting a relationship with those subgenera, and also with *Homotrigona* which also has such a concavity. Such a basitarsal concavity also occurs in the American genus *Oxytrigona* which *Papuatrigona* resembles in certain features. The broad face, long malar space, and broad clypeocular space, so unusual and distinctive of *Oxytrigona*, are all approached in *Papuatrigona*. I presume this resemblance is a result of convergence; all these characteristics are apparently results of a single tendency in facial development. The unique vestiture of the labial palpus of *Oxytrigona* (abundant long, straight setae) is not shared by *Papuatrigona*, which has about eleven large, sinuous setae, thus falling within the range of variation of *Heterotrigona*. The worker gonostyli are setose, well separated, convergent; the second valvifer is not unusually short as it is in *Oxytrigona*. While the keirotrichiate ridge is similar in breadth in *Oxytrigona* and *Papuatrigona*, it is abruptly defined in the former, not in the latter.

Features distinguishing *Papuatrigona* from *Heterotrigona* and *Homotrigona* include the tibial character states listed above and also, for *Heterotrigona*, the lack of a sericeous area on the inner surface of the hind basitarsus. *Papuatrigona* is most similar to *Lepidotrigona*, which also lacks the sericeous basitarsal area. *Lepidotrigona* has the head and thorax dull with minute, dense punctation. The surface is less dull and the punctation less dense in *Papuatrigona*, which also lacks the areas of dense, highly plumose ("scalelike") hairs found in *Lepidotrigona*. *Lepidotrigona* has plumose hairs among simple hairs on the posterior apical angle of the hind tibia but not extending along the posterior margin. The inner surface of the hind tibia is alike, however, in the two subgenera. The longer malar area, wider face and interalveolar space, smaller mandibular teeth, smooth basal propodeal area, smaller corbicula, etc., as detailed in the Appendix, all differentiate *Papuatrigona* from *Lepidotrigona*.

This subgenus includes only one species, *Trigona (Papuatrigona) genalis* Friese. It is known only from New Guinea. Details of its character states are given in the Appendix.

Subgenus *Geotrigona* Moure

(Figs. 28, 98, 145)

Trigona (Geotrigona) Moure, 1943: 146. Type species: *Trigona mombuca* Smith, 1863.

This subgenus consists of robust black species, superficially resembling because of the short, broad metasoma some of the black species of *Partamona*, *Scaptotrigona*, and *Trigona (Trigona)*. The *Geotrigona* group was included in *Tetragona* by Wille (1979b) and others and it is closely related to that subgenus. In both, the hairs of the labial palpi are short and straight. *Geotrigona* differs, however, not only in the body form but in the relatively short legs (hind tibia much shorter than cell R of forewing) and the sparseness of branched hairs, and of the branches themselves, on the posterior margin of the hind tibia. The branches are scattered along the hairs, not concentrated toward the apices. These hairs are especially sparse and with few branches in *T. (G.) acapulconis* Strand, and are thus intermediate between the simple hairs of the preceding subgenera and the strongly plumose hairs of *Heterotrigona, Homotrigona, Tetragonisca, Tetrigona,* and *Trigona* s. str. The male genital capsule is schizogonal, probably permanently so, the gonocoxites being at least as long as broad (*T. mombuca* Smith examined). Moure (1951) described the external features of the subgenus comparatively.

This subgenus contains a few similar species and ranges from Mexico to Argentina (Santiago del Estero). Well known names in this subgenus include *Trigona (Geotrigona) acapulconis* Strand, *leucogastra* Cockerell, and *mombuca* (Smith).

Subgenus *Tetragonisca* Moure

(Figs. 30, 72, 100, 146)

Tetragonisca Moure, 1946: 438. Type species: *Trigona jaty* Smith, 1863 (= *Trigona angustula* Latreille, 1811).

This is one of a group of subgenera separated from *Tetragona* with some hesitation. It consists of small, slender species, and is the only Neotropical group other than *Trigona* s. str. with a sericeous area on the base of the inner side of the hind basitarsus of the worker (but not the male). The labial palpus differs from that of the subgenus *Tetragona* in having 12 to 15 large, sinuous setae; there are no large setae in *Tetragona*. In this respect *Tetragonisca* resembles *Frieseomelitta*. Males at least of *T. (Tetragonisca) angustula* Latreille differ from *Tetragona* in the probably permanently schizogonal genital capsule and from all other Meliponinae in the enormous (broad and long), not especially sclerotized, median apical process of S6, making the sternum much longer than broad, and in the elongate S7, reaching beyond the apex of S6. The male genitalia are unusual for *Trigona* (but interestingly similar to the very different genus *Nannotrigona*) in the great thickness of the genital capsule with the spatha almost vertical (Fig. 146). External characteristics are listed by Moure (1951).

The male metasomal character states are apomorphies that suggest that *Tetragonisca* is derived from *Tetragona,* leaving the latter paraphyletic. However, given the widespread occurrence of the sericeous area on the hind basitarsus *(Heterotrigona, Trigona* s. str., and *Tetragonisca),* it seems quite possible that it is lost in *Tetragona,* so that *Tetragonisca* and *Tetragona* could be sister groups. S. F. Sakagami (in litt.) notes that the oviposition behavior of *Tetragonisca* is very different from that of *Cephalotrigona* and *Trigona* [*Duckeola, Frieseomelitta* (part), *Tetragona* and *Trigona* s. str.]. Without knowledge as to the polarity of these characters, it is difficult to use them in classification.

Tetragonisca ranges from Mexico to Argentina and contains about four species, of which *Trigona (Tetragonisca) angustula* Latreille, *buchwaldi* Friese, and *pfeifferi* Friese are well known.

A characteristic of workers of *Tetragonisca* is the extremely small corbicula, the concavity being limited to the apical fifth of the tibia and not occupying the full tibial width. The same feature characterizes the subgenus *Frieseomelitta* which, however, lacks the sericeous area on the inner surface of the hind basitarsus. Species included in these two groups are listed by Wille (1962). The African genus *Dactylurina* has equally reduced corbiculae. This must be an independently derived feature in *Trigona* and *Dactylurina,* probably also independent in the *Trigona* subgenera *Tetragonisca* and *Frieseomelitta.* Intermediates between such small corbiculae and large ones occur in various groups of the subgenera *Tetragona* and *Heterotrigona.*

Subgenus *Tetragona* Lepeletier and Serville

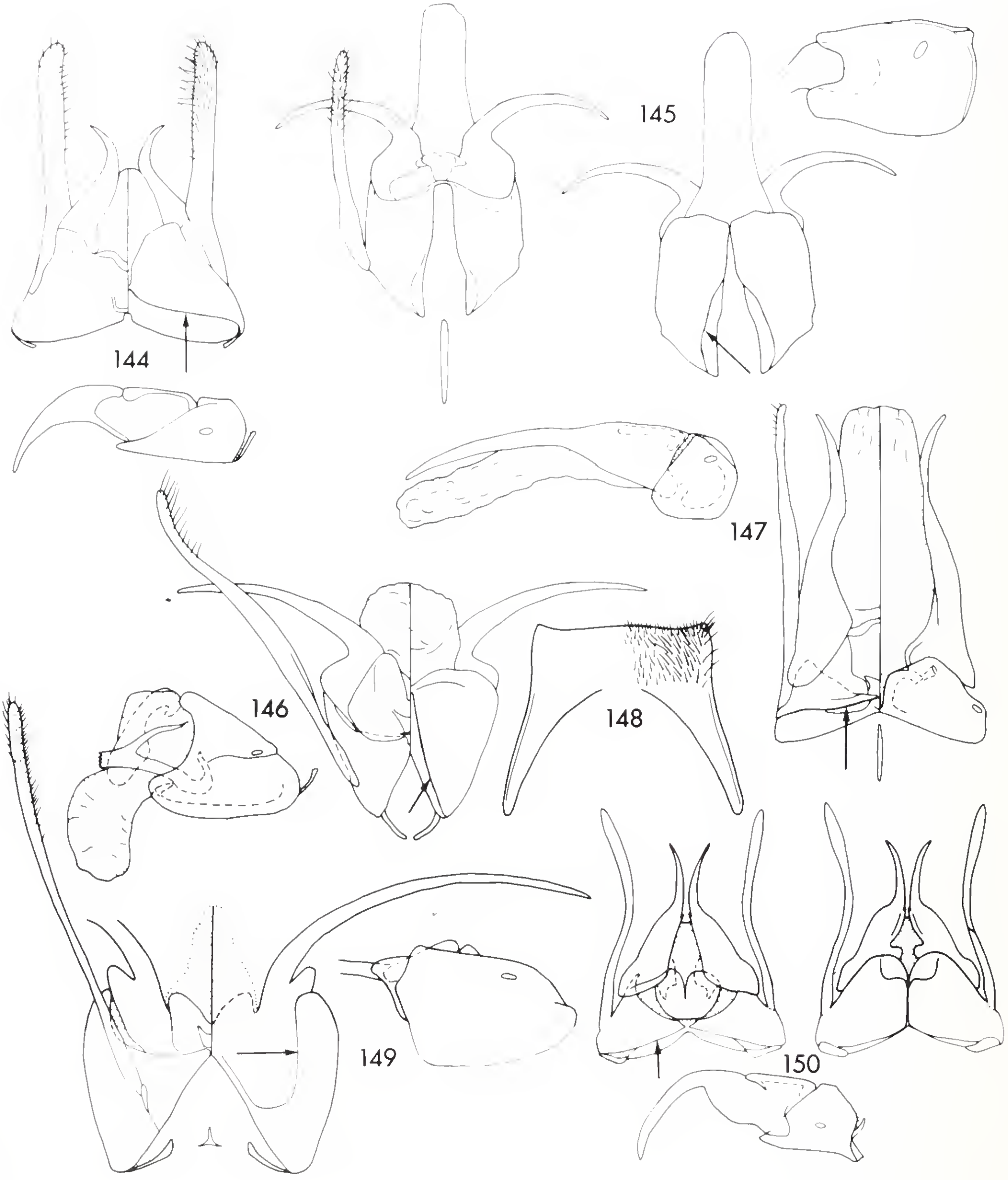
(Figs. 31, 69, 101, 102, 147, 149)

Trigona (Tetragona) Lepeletier and Serville, 1828: 710. Type species: *Trigona elongata* Lepeletier and Serville, 1828 (= *Centris clavipes* Fabricius, 1804) by original designation.

Trigona (Ptilotrigona) Moure, 1951: 47. Type species: *Trigona heideri* Friese, 1900 (= *Trigona lurida* Smith, 1854) by original designation.

This subgenus as here limited consists of long-legged bees, similar in form to *Tetragonisca* and *Frieseomelitta* but somewhat less delicate. The hind tibia is nearly as long as cell R of the forewing. *Ptilotrigona* is based on a distinctive species, differing from the rest of the subgenus in its large size, large mandibular teeth (two, on upper part of apical margin), and hairy propodeal triangle. The amount of difference is probably not enough to justify subgeneric rank for a single divergent species, but J. M. F. Camargo (in litt.) tells me of two undescribed species of *Ptilotrigona.* One could easily justify recognizing it as a subgenus. Comparative descriptions are provided by Moure (1951).

Tetragona differs from the Indoaustralian *Heterotrigona* in the uniformly setose inner surface of the hind basitarsus of the worker, and in lack of large setae on the labial palpi (palpal setae are short and straight). See also the discussion of *Heterotrigona.* Given the similarity of *Tetragona* and *Heterotrigona* it is necessary to compare the species groups of both of these subgenera, along with *Duckeola, Frieseomelitta, Geotrigona, Tetragonisca,* and *Homotrigona,* to see if some other classification makes more sense. The variation among the species groups is kaleidoscopic, each character seemingly distributed differently from the others. Moure's (1961) tabulation of character states of the Indoaustralian groups shows the lack of con-



Figures 144-150. Male genitalia of Meliponinae, dorso-ventral views (dorsal at left, dorsal and ventral for 145 and 150), gonostylus usually omitted from ventral views, lateral views with gonostyli omitted, apex of penis valve omitted in lateral 145, 146, 149. Arrows are explained with Figures 130-134. 144, *Trigona (Frieseomelitta) nigra paupera* Provancher. 145, *Trigona (Geotrigona) mombuca* Smith, gonostyli omitted from ventral view. 146, *Trigona (Tetragonisca) angustula* Latreille. 147, *Trigona (Tetragona) clavipes* (Fabricius). 148. S6 of *Trigona (Heterotrigona) apicalis melanoleuca* Cockerell. 149. *Trigona (Tetragona) lurida* Smith. 150. *Trigona (Trigona) fulviventris* Guérin.

cordance among characters. The same is observable with the American groups.

Male genitalia are rectigonal in *T. (Tetragona) clavipes* (Fabricius) and schizogonal in a male of *T. (T.) lurida* Smith; probably they are really amphigonal.

About 13 species of *Tetragona* are found from Mexico to Brazil. Well known species are *Trigona (Tetragona) clavipes* (Fabricius), *dorsalis* Smith, *lurida* Smith, and *perangulata* Cockerell.

Subgenus *Frieseomelitta* von Ihering

(Figs. 27, 71, 99, 144)

Frieseomelitta von Ihering, 1912: 5. Type species: *Trigona silvestrii* Friese, 1902 (monobasic).

This subgenus consists of slender, delicate-looking species that agree with *Tetragona* in subgeneric attributes except that the labial palpus of the worker possesses many (19-23 in species examined) large, sinuous setae. Such setae are absent in *Tetragona*, although present in *Tetragonisca*.

Frieseomelitta is further distinguished from all other American groups of the genus *Trigona* in the arrangement of the brood cells—in clusters rather than in combs. This architectural character does not separate subgenera among the Indoaustralian *Trigona* and in the genus *Plebeia*, but appears to do so in American *Trigona*. Another architectural character state of *Frieseomelitta* is the elongate storage pots. Elongate storage pots are also found in the genus *Trigonisca* and in some species of *Trigona (Heterotrigona)*.

The male genitalia are rectigonal in *T. (F.) nigra* Cresson and *silvestrii* Friese (see Camargo and Moure, 1988); probably in reality they are amphigonal.

Frieseomelitta contains about ten species and ranges from Mexico to Brazil. Well known species are *Trigona (Frieseomelitta) nigra* Cresson, *silvestrii* Friese, and *varia* Lepeletier.

Subgenus *Duckeola* Moure

(Figs. 70, 103)

Duckeola Moure, 1944a: 72. Type species: *Trigona huberi* Friese, 1901 (= *Trigona ghilianii* Spinola, 1853) by original designation.

This subgenus consists of a large, rather robust species, so different from other *Tetragona*-like bees that it must be placed in its own subgenus. It resembles *Tetragona* in lacking a sericeous area on the inner surface of the hind basitarsus of the worker. It differs from *Tetragona* and all other subgenera in the strong, hairy ridge on the posterior margin of the vertex between the summits of the eyes (this is different from the shiny, hairless carina in a similar position in the genus *Cephalotrigona*), in the rather slender hind tibia of the worker with the posterior apical angle strongly produced apicad and acute, and in the about 20 large setae of the labial palpi which are at most only about 1.5 times as long as the palpal width, yet are mostly curved or slightly sinuous. In other meliponines with curved or sinuous setae, these setae are much longer.

Two species, *Trigona (Duckeola) ghilianii* Spinola and *pavani* Moure, are found in Brazil. Males are unknown.

Subgenus *Homotrigona* Moure

(Fig. 110)

Homotrigona Moure, 1961: 200. Type species: *Trigona fimbriata* Smith, 1857, by original designation.

Like *Duckeola, Frieseomelitta, Geotrigona, Heterotrigona,* and *Tetragonisca,* this subgenus is separated from *Tetragona* with some hesitation. The male shows plesiomorphic features (especially S6) that suggest this as a possible outgroup for the rest of *Trigona*. It therefore seems reasonable to give it subgeneric status. Other phenetically distinctive groups, such as the group of *T. (Heterotrigona) itama* Cockerell, are distinguished by clearly derived, autapomorphic features and are not recognized here at the subgenus level.

Homotrigona consists of rather large, robust species with the metasoma short. The two mandibular teeth are large, occupying the upper half of the distal mandibular margin, and are along the mandibular axis so that a line between their apices is almost parallel to the long axis of the mandible. *Homotrigona* is the only Indoaustralian subgenus of *Trigona* except *Lepidotrigona* and *Papuatrigona* that lacks the sericeous area on the base of the inner side of the hind basitarsus; in this respect it resembles the American subgenera *Duckeola, Frieseomelitta,* and *Tetragona*. The most unusual feature is S6 of the male, which is a rather ordinary looking sternum, without traces of the heavily sclerotized median apical process usual in Meliponinae. *Lestrimelitta, Paratrigona opaca* Cockerell but not other species of the genus, *Trigona (Heterotrigona) apicalis* Smith and its relatives (i.e., the *Odontotrigona* = *Tetrigona* group of *Heterotrigona*) but not other species of that subgenus, and *Trigona (Lepidotrigona)* also have S6 broad although in the last it has a short, triangular median process. These forms do not seem closely related to one another. The shape and setal pattern of S6 are so similar, however, in males of *Homotrigona* and *T. (Heterotrigona) apicalis* Smith (Fig. 148) that they must indicate a common origin. To judge by bees in general, this condition should be plesiomorphic, but see comment on this character under *Lestrimelitta*. Prof. S. F. Sakagami has called my attention to the complete absence of a spatha in the male genitalia of

Homotrigona, a character state shared with the genus *Dactylurina* and with the *Tetragonula* and *Platytrigona* groups of *Heterotrigona.* The labial palpus of the worker has the large setae long and straight; in nearly all other Asiatic species of *Trigona* at least one or two are curved, and frequently they are sinuous.

The external character states of *Homotrigona* are given by Moure (1961) and those of the male by Sakagami (1963). Moure listed the included taxa, probably representing a single species, *Trigona (Homotrigona) fimbriata* Smith, that ranges from west Malaysia to Vietnam and south to Sumatra and Borneo.

Subgenus *Heterotrigona* Schwarz

(Figs. 29, 32, 73, 104-109, 111, 148, 184, 197, 200, 206, 209)

Trigona (Heterotrigona) Schwarz, 1939a: 96. Type species: *Trigona itama* Cockerell, 1918, by original designation.
Platytrigona Moure, 1961: 203. Type species: *Trigona planifrons* Smith, 1864, by original designation.
Lophotrigona Moure, 1961: 205. Type species: *Trigona canifrons* Smith, 1857, by original designation.
Tetragonula Moure, 1961: 206. Type species: *Trigona iridipennis* Smith, 1854, by original designation.
Tetragonilla Moure, 1961: 210. Type species: *Trigona atripes* Smith, 1857, by original designation.
Geniotrigona Moure, 1961: 212. Type species: *Trigona thoracica* Smith, 1857, by original designation.
Odontotrigona Moure, 1961: 213. Type species: *Trigona haematoptera* Cockerell, 1919, by original designation.
Tetrigona Moure, 1961: 215. Type species: *Trigona apicalis* Smith, 1857, by original designation.
Trigonella Sakagami and Moure, *in* Sakagami, 1975: 57. Type species: *Trigona moorei* Schwarz, 1939, by monotypy.

This subgenus contains minute to moderate-sized Indoaustralian bees with a sericeous area on the base of the inner side of the hind basitarsus of workers but not in males. The unity of *Heterotrigona* and *Homotrigona* is indicated, however, by the frequently concave surface of the posterobasal part of the hind basitarsus, this area being delimited anteriorly by a low ridge bearing a row of hairs (the "additional" row of hairs of the pollen press, Wille, 1979a; Figs. 206, 207, 209, 210). This structure is weakly developed or unrecognizable in small species. Contrary to Wille, I do not find it in any American species of *Trigona,* but it is present in *Oxytrigona.* Another character that is useful although not decisive in separating the Indoaustralian species from *Tetragona* is the setae of the labial palpus. In *Tetragona* there are no large setae. In *Heterotrigona* and *Homotrigona* there are large setae and at least one or two are curved; frequently most are curved or sinuous. All intergradations occur from about six with only one or two curved to about 35, mostly sinuous. Only in *T. (H.) canifrons* among Indoaustralian species are the setae straight and only moderately long. Except for these hind basitarsal and palpal characters, there are no other known group attributes that differentiate *Heterotrigona* from *Tetragona.* I hesitantly decided to recognize *Heterotrigona* because of these character states (only the first is entirely reliable) and because it occurs on the other side of the world from the neotropical *Tetragona.*

The genitalia are rectigonal in *T. (Heterotrigona) itama* Cockerell, *apicalis* Smith (*Tetrigona*), *atripes* Smith (*Tetragonilla*), *moorei* Schwarz (*Trigonella*), and various representatives of the *iridipennis* group (*Tetragonula*), varying to schizogonal among other species of the group (Sakagami, 1978; Sakagami and Inoue, 1985, 1987). Among all the above, the appearance of the genitalia suggests that each species is amphigonal, i.e., capable of either the rectigonal or schizogonal conformation.

Unfortunately the type species of *Heterotrigona, T. (H.) itama* Cockerell, is aberrant relative to nearly all of the rest of the species. Workers have only one denticle instead of two on the upper part of the apical mandibular margin. Males have a greatly enlarged and apically pointed hind tibia; much shortened small segments of the hind tarsus; long, thickened, and only briefly cleft hind claws; and long, fingerlike lateroapical processes on S5 (Schwarz, 1939a). These character states were the basis for *Heterotrigona,* a name which heretofore has been used only for *T. (H.) itama* and *erythrogastra* Cameron, along with various probable synonyms (Moure, 1961). Males of the group of *T. (H.) moorei* Schwarz (*Trigonella*) have hind legs and other features somewhat modified in the direction of *T. (H.) itama* as shown by Sakagami and Inoue (1987). The same is true for *T. thoracica* Smith (*Geniotrigona*), at least insofar as the hind tarsi are concerned (Sakagami and Inoue, 1989). These findings support the placement of other groups in the same subgenus as *T. itama.* Sakagami and Inoue (1989) have shown in greater detail the close relationship of what I call the *itama, moorei,* and *thoracica* species groups.

The males of *T. (H.) apicalis* Smith and *melanoleuca* Cockerell (*Tetrigona*), differ from other species of *Heterotrigona* in S6, which is an ordinary looking sternum with a large distal area of coarse hairs (Fig. 148); it is not short and heavily sclerotized with a median apical process as in other *Heterotrigona* and most other Meliponinae. In this respect they resemble *Homotrigona;* see comments on this character under that subgenus.

The name *Heterotrigona* is used here in a broad sense, as the oldest name for the various species groups listed in the above synonymy. Of these, several are monotypic or probably so; only the *iridipennis* group (*Tetragonula*) contains more than two or three species. The named taxa in the synonymy appear to represent natural groups or single distinctive species but do not seem different enough to recognize at the subgenus level. I have not seen males of all of them, however, and male characters might indicate recognition (at the subgenus level) of more of Moure's genera. Sakagami and Khoo (1987) have already united *Tetragonula* and *Tetragonilla*. Detailed descriptions of external features are provided by Moure (1961) and illustrations of genitalia and other structures by Schwarz (1939a), Sakagami (1978), and Sakagami and Inoue (1985, 1989).

Prof. S. F. Sakagami (in litt.) has kindly given me his opinions about the classification of the species of *Trigona* that I have placed in *Heterotrigona*. While I am not in full agreement with his view that five subgenera should be recognized instead of one, I recognize his groups and present his conclusions as follows:

Group 1. *Heterotrigona* (*T. itama* Cockerell, *erythrogaster* Cameron), *Trigonella* (*T. moorei* Schwarz, *lieftincki* Sakagami and Inoue), *Geniotrigona* (*T. thoracica* Smith). Similarity of these three subgroups are indicated in a paragraph above and by Sakagami and Inoue (1989).

Group 2. *Odontotrigona* and *Tetrigona* (*T. apicalis* Smith, *haematoptera* Cockerell, *melanoleuca* Cockerell and *peninsularis* Cockerell). There are no major differences among these species to justify two subgroups. See the comments above about S6 of the male.

Group 3. *Lophotrigona* (*T. canifrons* Smith). Like most species of *Tetragonula,* this species places its brood cells in clusters rather than combs.

Group 4. *Tetragonula* (numerous species) and *Tetragonilla* (four species). See Sakagami and Khoo, 1987. This group differs from others except number 3 by the exaggerated posterior displacement of the scutellum (Figs. 108, 109). Sakagami recognizes seven subgroups in *Tetragonula*.

Group 5. *Platytrigona*. Recognized by Moure (1961) on the basis of the medially hairy propodeal triangle but this character is variable. Sakagami recognizes three subgroups: a, *Platytrigona* sensu Moure (*T. planifrons* Smith, *flaviventris* Friese, *keyensis* Friese), recognized by the hairy propodeal triangle; b, *T. hobbyi* Schwarz with the middle of the propodeal triangle glabrous and without strong bristles on the vertex and scutellum; and c, *T. atricornis* Smith with a propodeum like that of *Papuatrigona,* i.e., hairless dorsally except for small lateral patches. Placement of *T. atricornis* is based on the male genitalia, which have a long neck joining the midbasal part of the penis valves with the median articulation of the gonocoxites. This is as in the *planifrons* subgroup (as well as *Lepidotrigona,* see Sakagami, 1975). Females of *T. atricornis* cannot be placed in *Platytrigona* with certainty; they could be in the *Trigonella* subgroup of *Heterotrigona*.

There are some 36 species in this subgenus. They were listed by Moure (1961) and Sakagami (1978). They are abundant in southeast Asia including Borneo and Sumatra. The number of species diminishes westward to only three in India, one of which reaches Sri Lanka; few species are found east and south to the Philippines, Solomon Islands, and Australia (south to about 34°S). The subgenus also occurs in the Caroline Islands, where it is likely to have been introduced. It apparently does not reach Taiwan. The species in marginal regions such as Sri Lanka, most of India, and Australia are all in the *iridipennis* group (*Tetragonula*). Familiar species of *Heterotrigona* are those listed above as type species of *Heterotrigona* and its synonyms, and those listed in the above account of five subgroups. To this list may be added *Trigona (Heterotrigona) carbonaria* Smith and *fuscobalteata* Cameron.

Species not included by Moure (1961) are *T. (Heterotrigona) keyensis* Friese, 1901, from Kai and New Guinea and *atricornis* Smith, 1864, from New Guinea. They are largely red, with coloration like that of *T. (Papuatrigona) genalis* Friese, but are members of the *planifrons* group of *Heterotrigona*. *T. keyensis* differs from members of that group listed by Moure and from his characterization of the group ("genus *Platytrigona*") in the wider interalveolar space; much shorter malar space (about two thirds of flagellar diameter); ocelloccipital distance about equal to ocellar diameter; scutellum not surpassing metanotum; bifurcation of veins M and Cu well beyond cu-v; etc. Thus it reduces the distinctness of *Platytrigona*. For identification of *T. keyensis* I am indebted to Prof. S. F. Sakagami. For information on *T. atricornis,* see Appendix.

Subgenus *Trigona* Jurine s. str.

(Figs. 33, 34, 66, 74, 75, 112, 113, 137, 150, 167, 172, 185)

Trigona Jurine, 1807: 245. Type species: *Apis amalthea* Olivier, 1789, by designation of Latreille, 1810: 439.

Amalthea Rafinesque, 1815: 123. Unnecessary replacement name for *Trigona* Jurine. Type species: *Apis amalthea* Olivier, 1789, autobasic.

The principal characteristics of this subgenus and the included species were well illustrated by Schwarz (1948) and Camargo and Moure (1988) and were listed comparatively by Moure (1951). The male genitalia and associated sterna of *T. cilipes* (Fabricius) were illustrated (as *T. compressa* Latreille) by Snodgrass (1941) and of this and other species by Schwarz (1948). The genitalia were shown in most cases as rectigonal, but for others as schizogonal. As noted above, both conformations are known for *T. (T.) amalthea* (Olivier) and *pallens* (Fabricius), and doubtless all species are in reality amphigonal. There are only two taxa of Meliponinae with the distal margin of the mandible of the worker toothed in its lower part (Fig. 172) and often for its full length—*Trigona* s. str. and *Paratrigona*. The teeth are best developed in the former, and are either four or five in number. Sometimes in *T. (T.) cilipes* (Fabricius) the distal teeth are united by a thin septum, but the dentate margin is still distinct from the convex margin with at most two denticles near its upper end, as in most Meliponinae (Fig. 172). The labrum differs from other Meliponinae in that the apex is produced to a distinct angle. Males and workers of *Trigona* s. str. have a basal sericeous area on the inner side of the hind basitarsus. Such an area occurs elsewhere only in workers of the subgenera *Tetragonisca, Tetrigona,* and *Heterotrigona*. The labial palpi of workers have six to about 38 large, mostly sinuous setae, except that in *T. hypogea* and its relatives there are only short, straight setae.

Trigona s. str. is found from Mexico to Argentina. It contains about 30 species, or more as sibling species are recognized. Well known species are *Trigona (Trigona) amalthea* (Olivier), *cilipes* (Fabricius), *corvina* Cockerell, *fulviventris* Guérin, *fuscipennis* Friese, *hyalinata* Lepeletier, *hypogea* Silvestri, *nigerrima* Cresson, *pallens* (Fabricius), *silvestriana* Vachal, and *williana* Friese. The subgenus was revised by Schwarz (1948).

Various species of this subgenus are attracted to carrion (Baumgartner and Roubik, 1989) and probably use it as a supplementary protein source as well as for nest construction. The group of *T. (T.) hypogea* Silvestri does not collect pollen, uses carrion as its protein source, lacks large palpal setae, has reduced corbiculae, and has relatively narrow hind tibiae (Schwarz, 1948; Roubik, 1982).

As noted previously, *Trigona prisca* Michener and Grimaldi (1988a, b) from the New Jersey Upper Cretaceous was placed in *Trigona* s. str. on the basis of the single known worker specimen. It has toothed mandibles similar to those of ordinary specimens of *T. (Trigona) cilipes* (Fabricius). The hairs on the posterior margin of the hind tibia are probably simple, unlike most *Trigona,* but there may be a few, sparsely plumose ones as in *Trigona (Geotrigona) acapulconis* Strand. The gonostyli are invisible in the fossil. In view of the impressive convergence of external characteristics in some Meliponinae, it could be that *T. prisca* is convergent with rather than closely related to *Trigona* s. str.

Genus *Trichotrigona* Camargo and Moure
(Figs. 76, 114)

Trichotrigona Camargo and Moure, 1983: 421. Type species: *Trichotrigona extranea* Camargo and Moure, 1983, by original designation.

This genus, known from a single nest collection in Amazonas, Brazil, was well described and illustrated by Camargo and Moure (1983). It has many features of *Trigona (Frieseomelitta)* including cluster rather than comb arrangement of its brood cells. The keirotrichiate ridge on the inner surface of the hind tibia is as in *Frieseomelitta* and most other subgenera of *Trigona,* with the shiny concave channel marking its posterior margin extending onto the basal fourth of the tibia. J. M. F. Camargo has kindly sent me a sketch of the sting rudiments and associated structures of *Trichotrigona*. The structure is similar to that illustrated here for *Trigona (Heterotrigona) carbonaria* Smith (Fig. 29) but with the gonostyli longer, as in *T. (Frieseomelitta) nigra* Cresson (Fig. 27).

Extraordinary features of *Trichotrigona* are (1) the hairy eyes and unusually hairy body and wings, with most of the hairs of the body coarse, almost bristle-like, not plumose; (2) the short, broad second segment of the labial palpus, about as broad as long and only somewhat over one fourth as long as the first segment [large setae on these segments few (about 5) and straight]; (3) the rudimentary penicillum and the replacement of the rastellar bristles with slender, tapering hairs; (4) the slender, parallel-sided, hind basitarsus of the worker (nearly four times as long as broad) with all its hairs directed apicad (i.e., without the posteriorly directed hairs and associated ridges near the base that contribute to the pollen press function in most Meliponinae; Wille, 1979a); (5) the lack of plumose hairs on the posterior margin of the hind tibia except at its apex where it rounds onto the convex apical margin of the tibia, which has numerous plumose hairs; (6) the presence of numerous, scattered, rather short hairs on the surface of the corbicula in addition to a few longer hairs; (7) the robust front tibia covered on the outer surface with coarse, weakly spatulate hairs; and (8) the flattened, pointed, bare projection suggestive of a pygidial plate on T6. Males of *Trichotrigona* are unknown.

The reduced rastellum and penicillum and lack of pollen press structures of the hind basitarsus, the presence of rather numerous hairs on the surface of the corbicula, and perhaps also the labial palpus as described above suggest that the only species, *Trichotrigona extranea* Camargo and Moure, is a robber bee like *Lestrimelitta* and *Cleptotrigona* or possibly the only known meliponine social parasite. The single known colony was found in the Amazon valley as a nest of *Trigona (Frieseomelitta) paranigra* Schwarz was being opened; the relation if any to the *paranigra* colony is unknown; no connection was observed. Three of the workers from the nest of *T. extranea* had pollen on the corbiculae and hind basitarsi according to J. M. F. Camargo (in litt.). Given the hind tibiotarsal structure, it is not clear how they would get pollen onto the corbicula using the usual apid movements (Michener, Winston and Jander, 1978). One could imagine, however, placement of sticky pollen from the host nest on the hind legs in the same way that meliponines manipulate and carry resin.

Probably *Trichotrigona* is a derivative of *Trigona (Frieseomelitta).* If so, its existence makes the latter and the genus *Trigona* paraphyletic taxa. *Trichotrigona* is so distinctive, however, that generic status for it is justified. Even those who do not tolerate paraphyletic taxa should hesitate until males of *Trichotrigona* are known and its cladistic position is clearly ascertained. J. M. F. Camargo (in litt.) is strongly of the opinion that *Trichotrigona* is a relictual type not closely related to *Frieseomelitta* in spite of common character states.

Genus *Hypotrigona* Cockerell

(Figs. 35, 60, 115, 135, 151)

Trigona (Hypotrigona) Cockerell, 1934: 47. Type species: *Trigona gribodoi* Magretti, 1884, by original designation.

This is one of the genera of minute stingless bees that exhibit (convergently) the character states listed in couplet 1 of the above key to genera. It is, however, a distinct and isolated genus (with the possible exception that *Pariotrigona,* unknown in the male, may be related). Character states unique within the Meliponinae include the apical process of S5 of the male (considered to be S6 by Brooks and Michener, 1988) which is not especially heavily sclerotized and lies horizontally in the concavity of S6 (S7 in 1988); the U-shaped S6 with strong basolateral apodemes like those of more anterior sterna; and the form of S7 (S8 in 1988) which is a transverse bar with a small, median, basal angle. The sternal characteristics were illustrated by Brooks and Michener (1988), who interpreted what I believe is the apical process of S5 as S6 fused to S5. The male genital capsule is illustrated by the same authors, and in Figure 151. It is rectigonal but unique among Meliponinae in the completely dorsal basal opening of the gonocoxites and the largely membranous basal bulb of the penis valves. The male gonostyli are freely articulated but do not break off easily. The gonostyli of workers are minute to papilliform, not flattened, separated by several times their lengths, with several setae (Fig. 35) but without minute hairs; those of all other African Meliponinae have minute hairs. The sting stylet is a mere convexity. The lancet is insignificant, in the membrane. A remarkable feature is the fusion of the second valvifer with the eighth hemitergite. The strongly bidentate male mandible (Fig. 135) is like that of many other families of bees but unlike that of other Meliponinae. The setae of the labial palpus are short and straight. The external generic character states were listed in detail by Moure (1961).

The mandibular and sternal characteristics of male *Hypotrigona* could be plesiomorphous. If so, then the alternative characters of other Meliponinae would be apomorphies showing that *Hypotrigona* is the sister group to all the other genera. However, the short, transverse male gonocoxites, the reduced wing venation, etc., are apomorphies shared by only part of the other meliponine genera. It therefore seems premature to place *Hypotrigona* as the first branch of the meliponine cladogram.

The mesoscutum is typically dull; in the worker the posterior apical angle of the hind tibia is absent, i.e., broadly rounded; and the scutellum is wholly dark. These are character states that usually distinguish *Hypotrigona* from other minute Meliponinae. Brooks and Michener (1988), however, were unable to distinguish certain workers from *Liotrigona* on the basis of these and other characters. Dissection of the workers shows that their Sp. 2 is a *Hypotrigona;* the gonostylar characteristics were not known to these authors in 1988.

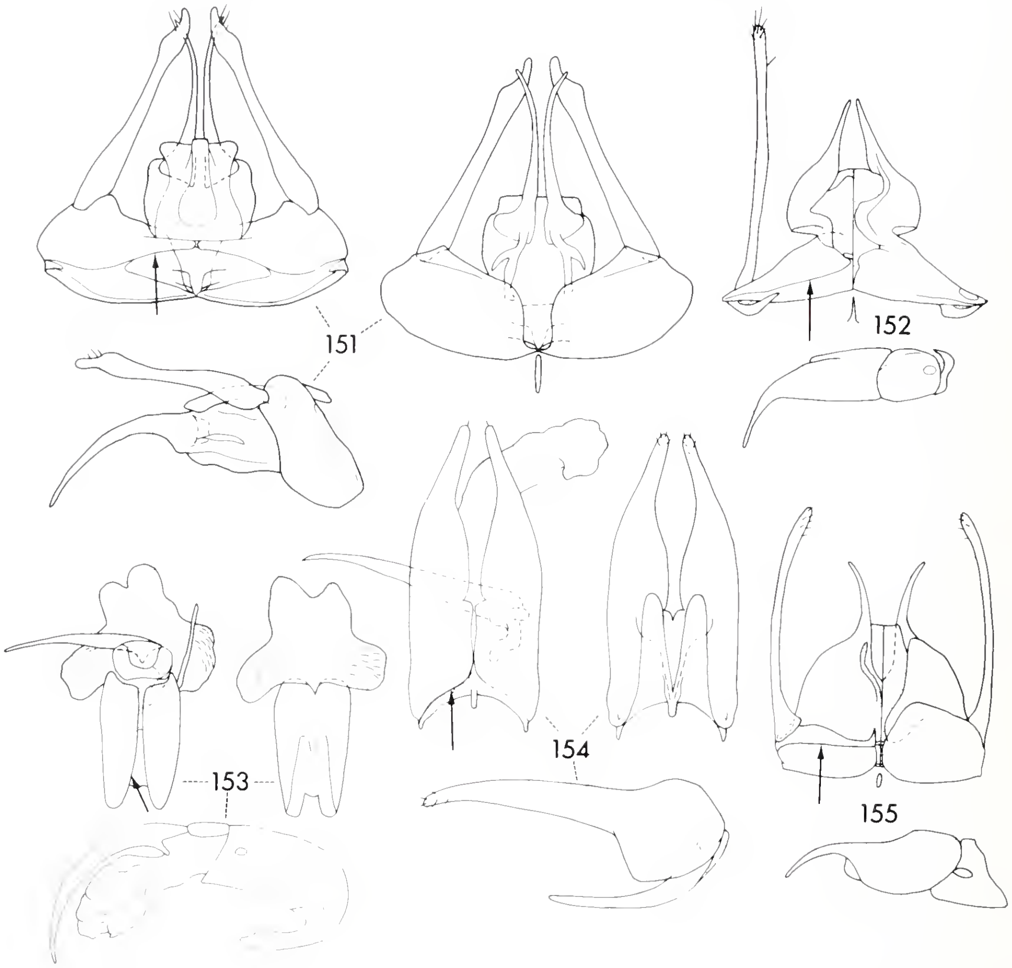
Hypotrigona is widespread and abundant in tropical Africa—Ghana to Kenya, south to Angola and Natal—although represented by only a few species. It does not occur in Madagascar. Included species were listed by Moure (1961), who, however, had not seen and did not place *Hypotrigona magrettii* (Friese, 1900) new combination. It is the smallest *Hypotrigona,* about 2 mm in body length. The type specimen (from Accra, Ghana) has a dull, closely punctate scutum, like that of typical *Hypotrigona;* the posterior apical angle of the hind tibia is rounded; there are no pale streaks on the scutellum; and I have not examined the worker gonostyli. Well known species are *Hypotrigona araujoi* (Michener), *braunsi* (Kohl) and *gribodoi* (Magretti).

Genus *Pariotrigona* Moure

(Figs. 36, 63, 116)

Pariotrigona Moure, 1961: 192. Type species: *Trigona pendleburyi* Schwarz, 1939, by original designation.

This is another genus of minute Meliponinae, sharing the character states listed in couplet 1 of the above key to genera. As it is known only from workers, its generic status and its position relative



Figures 151-155. Male genitalia of Meliponinae, dorsal (at left), ventral, and lateral views (dorsoventral for Figs. 152 and 155). Arrows are explained with Figures 130-134. 151, *Hypotrigona braunsi* (Kohl). 152, *Trigonisca buyssoni* (Friese), gonostylus on dorsal view only. 153, *Liotrigona mahafalya* Brooks and Michener, gonostylus only at right side of dorsal view, penis valve at right of dorsal view and on lateral view. 154, *Cleptotrigona cubiceps* (Friese), penis valve on right side of dorsal view only. 155, *Austroplebeia essingtoni* (Cockerell).

to other genera remain in doubt. The large setae of the worker labial palpus are few (two on segment 1, one on segment 2) and curved, as in *Lisotrigona*. The gonostyli of workers bear setae and lack minute hairs (Fig. 36). The only other minute genus with such gonostyli is *Hypotrigona*. However, those of *Pariotrigona* are quite different, being broadened at the bases and separated by little more than a stylar width. The sting lancet is absent, the stylet a broad convexity. The hind tibia has a distinct although rounded posterior apical angle in *Pariotrigona*, lacking in *Hypotrigona*. The long malar space of *Pariotrigona* suggests some species of the Neotropical genus *Trigonisca*, a similarity strengthened by the nearly right angular basal angle of the marginal cell and the transverse rows of hairs on the inner surface of the hind basitarsus. *Trigonisca*, however, has quite different worker gonostyli. The external generic characteristics were listed by Moure (1961).

Pariotrigona is known from two uncommon species found from the Malay Peninsula to Indochina, Borneo and Sumatra. I have dissected only *P. pendleburyi* (Schwarz) but *P. klossi* (Schwarz) appears certainly congeneric.

Genus *Lisotrigona* Moure

(Figs. 37, 64, 117)

Lisotrigona Moure, 1961: 194. Type species: *Melipona cacciae* Nurse, 1907, by original designation.

This genus of minute bees shares the character states listed in couplet 1 of the above key to genera. It is known only from workers; hence its position relative to other genera is in doubt. The gonostyli of workers are flat, separated by a median concavity about as wide as a gonostylus, and are covered with abundant minute hairs; on the outer and distal margin of each there are several long, delicate setae. Thus the gonostylar vestiture is similar to that of *Trigonisca*. The sting stylet is merely convex. The lancet, however, is long and free. The hind tibia has a much rounded posterior apical angle, the hairs on the inner side of the hind basitarsus are not in noticeable rows, and the base of the marginal cell is acute; in these features *Lisotrigona* differs from *Trigonisca*. It differs from the other minute Asiatic Meliponinae [ignoring small species of *Trigona* such as *T. (Heterotrigona) fuscobalteata* Cameron], i.e., the genus *Pariotrigona*, not only by the character states indicated in the key but by the acute base of the marginal cell and other features listed by Moure (1961) who described both groups in detail. The large hairs of the labial palpi, however, are essentially as in *Pariotrigona* and within the range of variation found in *Trigonisca*.

Lisotrigona contains two perhaps distinct, uncommon species known from Sri Lanka and Madhya Pradesh in India to Vietnam, Borneo and Sumatra. I have seen only *L. scintillans* (Cockerell) but Moure (1961) indicates its close similarity to *L. cacciae* (Nurse).

Genus *Trigonisca* Moure

(Figs. 38, 39, 59, 118, 119, 152, 168, 186)

Hypotrigona (Trigonisca) Moure, 1950a: 249. Type species: *Trigona duckei* Friese, 1900, by original designation.

Hypotrigona (Leurotrigona) Moure, 1950a: 244. Type species: *Trigona muelleri* Friese, 1900, by original designation.

Hypotrigona (Celetrigona) Moure, 1950a: 246. Type species: *Trigona longicornis* Friese, 1903, by original designation.

Hypotrigona (Dolichotrigona) Moure, 1950a: 248. Type species: *Trigona longitarsis* Ducke, 1916, by original designation.

Of the four simultaneously published names listed above, Wille (1979b) selected *Trigonisca* for the inclusive taxon (here recognized as a genus); several species resemble *T. duckei* and were included in *Trigonisca* by Moure while each of the other genus-group names was proposed for a single divergent species. A second species related to *Trigonisca muelleri* (Friese), i.e., of the *Leurotrigona* group, has recently been described, however (Moure, Camargo, and Garcia, 1988). (Unfortunately due to a lapsus the description is headed with the name *muelleri*, but the intended new name *pusilla* Moure and Camargo appears in the abstract, figure captions, etc., and is thus validated.) In the present classification it would be *Trigonisca pusilla* (Moure and Camargo) new combination.

Trigonisca is one of the minute, *Hypotrigona*-like genera segregated in couplet 1 of the key to genera. It is the only such genus found in the Western Hemisphere although a few minute American species exist in other genera, e.g., *Plebeia (Plebeia) schrottkyi* (Friese) and *P. (Nogueirapis) minor* (Moure and Camargo).

Trigonisca differs from all other American Meliponinae in the minute hairs which are widespread on the worker gonostyli. In addition there are setae, mostly or all along the outer margin of each gonostylus. The gonostyli are adjacent or separated by somewhat over one gonostylar width, and converge so that when adjacent at the bases, they overlap distally. The worker gonostyli of the Asiatic *Lisotrigona* are somewhat similar but are short, do not converge, and are separated by an emargination. The sting stylet of the worker is broadly rounded or very obtusely angulate. The lancet of the worker sting is short but its apex is free of the membrane. The male genital capsule is rectigonal in specimens that I have studied and as illustrated by Moure, Camargo, and Garcia (1988), although I categorize it as amphigonal because it can probably assume the schizogonal conformation, the gonocoxites being transverse, much broader than long or about as long as broad. The large setae of the worker labial palpus are few (5-7), straight or curved.

An unusual feature is the vestiture on the inner surface of the hind basitarsus of the worker; the hairs are in transverse rows, suggesting *Apis* and the Asiatic genus *Pariotrigona*. Also, some of the large hairs on the posterior margin of the hind tibia arise from tubercles (Fig. 186) which are particularly conspicuous in the species with the tibia slender. Thus the posterior edge of the tibia appears weakly nodulose to strongly tuberculate, instead of smooth as in other Meliponinae. The right angular or weakly obtuse basal angle of the marginal cell, associated with a broad base of this cell, as indicated in couplet 7 of the key to genera, is variable and requires some explanation. In *T. muelleri* (Friese) the marginal cell is much more as in other Meliponinae than is that of other *Trigonisca*. Nonetheless, in *T. muelleri* the basal angle of the cell (between the stigmal margin and vein r) is about 68° and the width of the marginal cell at the apex of the stigma is greater than the distance across the submarginal cell area from vein Rs to vein M. In other genera the basal angle is less than 50° and the width of the marginal cell at the apex of the stigma is not greater than the distance across the submarginal cell area. These characters, among others, show the relationship of the four groups listed in the generic synonymy.

The external character states of the genus are listed in detail by Moure (1951) and those of each group within the genus by Moure (1950); see also the above key to genera. Unlike most species which have two small denticles at the upper end of the apical mandibular margin, *T. longitarsis* (Ducke) and *schulthessi* (Friese) have only one. The former has a bituberculate labrum, suggesting *Lestrimelitta.* If more species of these groups are found, it will be reasonable to recognize the names in the above synonymy as subgenera. I think it is important, however, to indicate their close relationship (shown by the worker gonostyli, the broad base of the marginal cell, the tuberculate hind tibiae, etc.) to the rest of *Trigonisca.*

Within the genus there is considerable variation in brood cell construction and worker oviposition. In *Trigonisca* s. str. construction is successive but in *T. muelleri* (Friese) and *longicornis* (Friese) it starts successively but becomes synchronized by the time a number of cells are completed. Worker-laid eggs are unknown in *T. muelleri* but are deposited on the food mass like those of the queen in *T. longicornis* (Sakagami, 1982). The observations are fragmentary for these tiny bees but may support subgeneric status for the four names listed in the above synonymy.

These minute bees are attracted to perspiration and are sometimes pests from Mexico to Paraguay. There are about 17 species; familiar ones are *Trigonisca buyssoni* (Friese), *duckei* (Friese), *longicornis* (Friese), *longitarsis* (Ducke), and *muelleri* (Friese).

Genus *Liotrigona* Moure

(Figs. 40, 61, 120, 136, 153)

Liotrigona Moure, 1961: 223. Type species: *Trigona bottegoi* Magretti, 1895 (=? *Trigona madecassa* Saussure, 1891), by original designation.

This is one of the genera of minute bees segregated in couplet 1 of the above key to genera. Unlike the superficially similar *Hypotrigona, Liotrigona* is a member of the African group with flattened worker gonostyli bearing numerous minute hairs. The gonostylar bases are separated by less than the width of a gonostylus, and setae are absent. The gonostyli do not diverge as in most African Meliponinae. Each has a dorsal thickening, suggesting that of *Cleptotrigona,* but it bears minute hairs rather than coarse setae. The sting stylet is unsclerotized, blunt. The lancet is moderately long, free of the membrane.

The male genital capsule is elongate, permanently schizogonal, the gonocoxites much longer than broad and broadly fused ventrally, the bases (plus possibly the gonobase) curled under and directed apicad, fused to one another except distally. The gonostyli are slender, arising near the apices of the gonocoxites, easily detached from the gonocoxites during dissection. As in *Cleptotrigona,* the flexion of the penis valves is contralateral so that they cross one another when flexed. The genitalia and hidden sterna are illustrated by Brooks and Michener (1988). The sterna differ greatly from those of *Hypotrigona;* T6 has a midapical reflexed process that is much broader than in most Meliponinae. The large hairs of the labial palpus of the worker are few (5-6), mostly curved, unlike *Hypotrigona* which lacks such hairs. The external generic characteristics are listed in detail by Moure (1961).

Workers of *Liotrigona* can usually be distinguished without dissection from *Hypotrigona* by the shiny mesoscutum with only minute well separated punctures; the distinct posterior apical angle of the hind tibia, and the presence of pale or yellowish streaks on the preaxilla and posterior margin of the scutellum. As noted above in the discussion of *Hypotrigona,* these character states occasionally fail, and Brooks and Michener (1988) were unable to place certain undescribed species. Dissection of the worker gonostyli shows that their Sp. 1 is a *Liotrigona.*

Liotrigona is widespread but not very common in Africa—Ethiopia to Natal, Ghana to Angola—and is common in Madagascar. There are six or more species (Brooks and Michener, 1988; Michener, 1989) of which the most familiar names are *L. bottegoi* (Magretti), *madecassa* (Saussure), and *mahafalya* Brooks and Michener.

Genus *Cleptotrigona* Moure

(Figs. 41, 62, 121, 154)

Lestrimelitta (Cleptotrigona) Moure, 1961: 219. Type species: *Lestrimelitta cubiceps* Friese, 1912, by original designation.

Cleptotrigona forages in nests of *Hypotrigona* and probably *Liotrigona.* It is not known to visit flowers. This African robber genus is strongly convergent with the American robber, *Lestrimelitta,* so that Moure (1961) regarded them as congeneric. Wille (1979b), however, emphasized their distinctness and recognized their resemblances as convergent, although extending beyond loss of the pollen carrying and manipulating structures. Both authors listed many characters.

In *Cleptotrigona* workers the gonostyli are flat, divergent, the bases separate by about half a gonostylar width; they bear many minute hairs in addition to several setae along the edges of a dorsal thickening. The sting stylet is slender, acute, and little sclerotized, especially basally. The lancet is long and largely free of membrane. The male gonocoxites are longer than broad, broadly fused apically to gonostyli that are broad and flattened at the bases and tapering apically. Such gonostyli are unique in the Meliponinae and strikingly different from the extremely slender, easily deciduous gonostyli of *Liotrigona*. The genitalia appear to be permanently schizogonal although the base of the genital capsule is perhaps secondarily rectigonal, curled under the rest of the genitalia and extends apicad as far as the bases of the gonostyli as two slender lobes. This suggests the structure of *Liotrigona* in which, however, the lobes are fused to one another except apically. The sixth and seventh sterna are quite ordinary for Meliponinae, not platelike as in *Lestrimelitta*, the sixth with a midapical reflexed process.

Cleptotrigona is one of the genera of minute Meliponinae segregated in couplet 1 of the above key. The short, straight setae of the worker labial palpus suggest *Hypotrigona* but probably reflect loss of large setae associated with the robbing way of life (Michener and Roubik, in press). *Cleptotrigona* appears to be the sister group of *Liotrigona*, as indicated especially by the curled-under base of the genital capsule. Moreover, in both genera the penis valves, when extended laterad, cross at their bases, so that the left hand penis valve is directed to the right, and the right hand one to the left (Fig. 153). This is unlike other Meliponinae and is a probable synapomorphy supporting the relationship shown in Figure 8. *Liotrigona* has apomorphies not shared by *Cleptotrigona* (smaller, less slender sting stylet of workers; fused ventral lobes of the genital capsule of males), indicating that *Cleptotrigona* was not derived from *Liotrigona*. Both have the rastellum reduced to tapering hairs.

The rather flat scutellum, not at all overhanging the metanotum and elevated but little above the level of the dorsal surface of the propodeum (Fig. 121) is unique in the Apidae. Among bees as a whole this feature is a plesiomorphy but within the Apidae it must be an apomorphy, i.e., a reversion to the condition found in many non-apid bees.

Cleptotrigona consists of two species, *C. cubiceps* (Friese) and *curriei* (Cockerell) known from Liberia to Tanzania, Angola and South Africa. The species are listed by Moure (1961). *Trigona magrettii* Friese (1900), considered as a possible *Cleptotrigona* by Moure, is a *Hypotrigona*.

Genus *Austroplebeia* Moure
(Figs. 42, 81, 122, 155, 169)

Austroplebeia Moure, 1961: 195. Type species: *Trigona cassiae* Cockerell, 1910, by original designation.

This genus includes bees that superficially closely resemble species of the Neotropical group *Plebeia (Plebeia)* as well as the African *Plebeina*. *Austroplebeia* species are rather robust with distinct yellow areas on the scutellum and axillae, usually also on the lateral margins of the scutum and on the face. It differs from *Plebeia* in the abundant, minute hairs and few small setae on the worker gonostyli and the slender and pointed bristles of the rastellum. The worker gonostyli are slightly divergent, separated at the bases by about a gonostylar width. The sting stylet is rounded. The lancet is quite long, mostly free of the membrane. The five to about seven large setae of the labial palpus are curved to weakly sinuous. *Austroplebeia* differs from the *Plebeia*-like African genera *Plebeina* and *Meliponula* by the well separated worker gonostyli which are not noticeably flattened; the not or scarcely depressed posterior margin of the inner surface of the hind tibia (variable in *Meliponula*); the short, transverse, amphigonal male gonocoxites [both conformations seen in *A. essingtoni* (Cockerell)]; and lack of the male spatha and gonobase.

In the reduced wing venation, especially the lack of a bend near the end of vein M of the forewing and lack [except in *A. cincta* (Mocsary)] of vestiges of the first transverse cubital vein, *Austroplebeia* resembles the minute genera segregated in the first couplet of the key to genera (see Note after that key). Although small, *Austroplebeia*'s robust form does not resemble that of the other minute genera. Unlike those genera, the inner side of the hind tibia has the keirotrichiate area closely approaching the posterior margin of the tibia, leaving a narrow shiny margin as in *Plebeia* s. str. but less depressed or even not depressed.

Because of its male genitalic character states this genus does not appear related to African genera, but rather to American ones. The hairlike spicules of the worker gonostyli are shared only with *Trigonisca* in America, *Lisotrigona* in Asia, and most African genera. Discovery of males of *Lisotrigona* might expose a relationship between it and *Austroplebeia*. External features of *Austroplebeia* were described by Moure (1961).

This genus contains several species found in the northern half of Australia and in New Guinea. The specific names involved were listed by Michener (1965, as *Plebeia*) and by Moure (1961). Well known specific names are *Austroplebeia australis* (Friese), *cassiae* (Cockerell), *cincta* (Mocsary) and *essingtoni* (Cockerell).

Genus *Meliponula* Cockerell

This generic name is used in a new sense to include not only the type species, *M. bocandei* (Spinola), but also a series of smaller African forms placed in other genera (see subgenera, below) by Moure (1961) and Wille (1979b). Some of the latter, such as *M. beccarii* (Gribodo) and *erythra* (Schletterer), are almost as robust and *Melipona*-like as *M. bocandei*. *Meliponula* shares with most other African Meliponinae the flattened worker gonostyli with many minute hairs (sometimes also with a few setae), the presence of a conspicuous remnant of the gonobase attached to the male gonocoxite lateroventrally, the schizogonal (presumably permanently) male genital capsule with the gonocoxites longer than broad, at least in ventral view, and the strongly reflexed median apical process of S6 of the male.

Meliponula resembles *Cleptotrigona* and the American genus *Melipona* in having the sting stylet of workers distinct and acute. *Meliponula* differs from *Plebeina* in the reduction of the rastellum to slender hairs, no coarser than those of similar length on adjacent parts of the tibial apex; the rounded or very obtuse posterior apical angle of the worker hind tibia so that the tibia is rather spoon-shaped; the presence of coarse, amber or blackish bristles arising from or near this angle forming what Wille (1979b) calls the posterior parapenicillum in *M. bocandei* (Spinola); the presence of hairs, at least laterally, on the basal area of the propodeum, and the acute worker sting stylet. Like *Plebeina* and unlike other African genera, *Meliponula* has a broad area of keirotrichia on the inner surface of the worker hind tibia; the posterior margin may be depressed and shining, almost as in *Plebeia* s. str., only slightly depressed (e.g., in *Meliponula* s. str.), or poorly defined and not at all depressed (subgenus *Axestotrigona*). The smaller species of *Meliponula* resemble the larger species of *Plebeia* s. str. superficially, but differ from most *Plebeia* not only in character states indicated in the above discussion but in the dense punctation at least of the mesoscutum.

The reduction of the rastellum to slender hairs is not found among other moderate-sized, pollen-collecting Meliponinae, although it is seen in some minute genera. Given the function of the comblike rastellum in other Apidae (Michener, Winston, and Jander, 1978), a study of the pollen manipulating movements in *Meliponula* would be interesting.

Key to the Subgenera of *Meliponula*

1. Propodeal profile largely vertical; corbicula occupying less than distal half of hind tibia; apical reflexed process of S6 of male short and rounded; metasomal terga dull, minutely sculptured . . . . *Meliponula* s. str.
—Propodeal profile with slanting dorsal portion rounding onto vertical portion; corbicula occupying more than distal half of hind tibia; apical reflexed process of S6 of male longer than body of sternum; metasomal terga at least partly shining 2
2. Head and thorax without yellow markings; inner surface of worker hind tibia without well defined shining, depressed posterior margin, although keirotrichiate area does not reach margin at least distally . . . . *Axestotrigona*
—Head and thorax with yellow markings; inner surface of worker hind tibia with shining posterior margin at least slightly depressed . . . . *Meliplebeia*

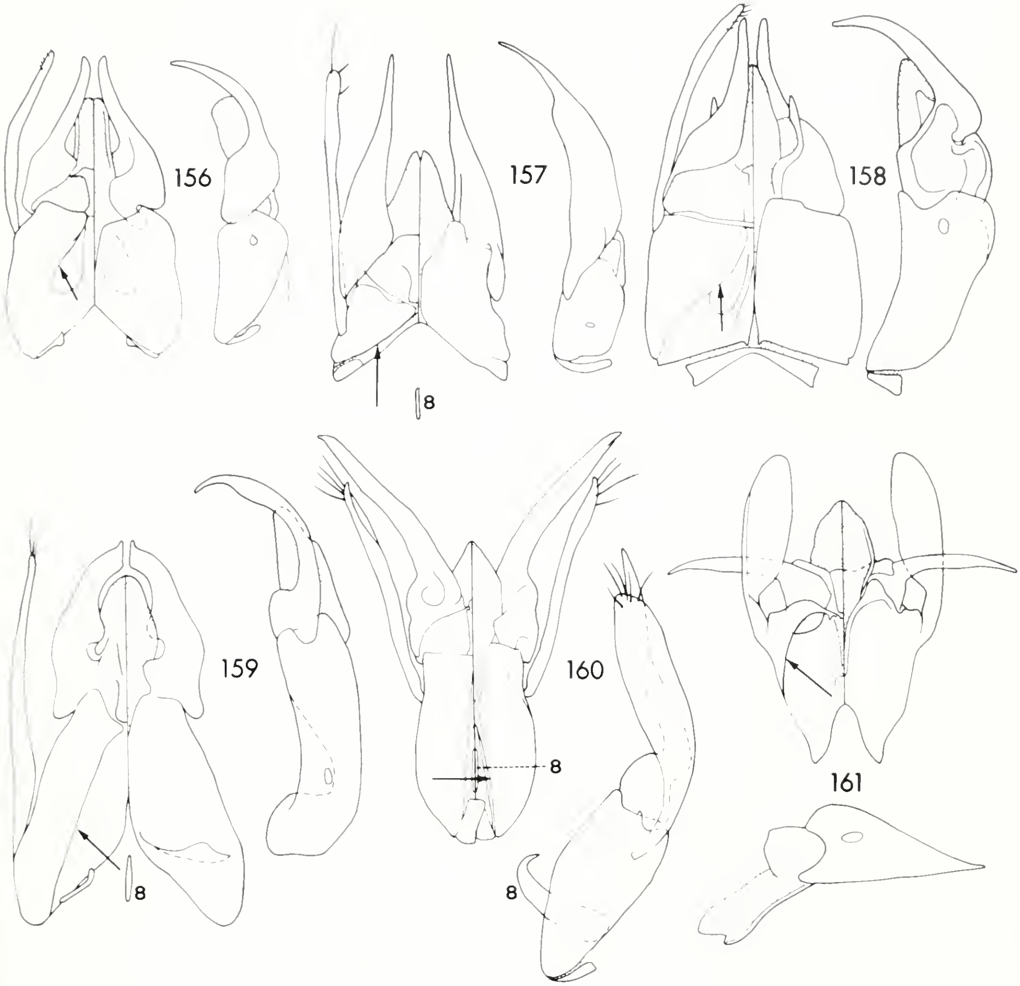
Subgenus *Axestotrigona* Moure

(Figs. 44, 78, 126, 158)

Axestotrigona Moure, 1961: 237. Type species: *Melipona ferruginea* Lepeletier, 1836, by original designation.

This subgenus contains moderate-sized robust species. There are delicate plumed hairs among the marginal bristles at the posterior apical angle of the worker hind tibia and across the apex of the tibia. The sting stylet of the worker is long and slender, almost as in *Meliponula* s. str., but the lancet is weak and in the membrane. The about 24 large hairs of the worker labial palpus are mostly curved on segment one, sinuous on segment two. The male gonostylus arises near the apex of the gonocoxite. I regard the genitalia (Fig. 158) as permanently schizogonal, as in the other subgenera. However, this is only evident in dorsal view, for ventrally the gonocoxites are broadly expanded so that they are secondarily rectigonal. The principal characteristics are indicated in the above key and in the description by Moure (1961).

There are several species; their names are indicated by Moure (1961). The most common species is *Meliponula (Axestotrigona) erythra* (Schlet-



Figures 156-161. Male genitalia of Meliponinae, dorso-ventral views (dorsal at left) and lateral views, gonostyli omitted from most lateral and ventral views. Arrows and "8" are explained with Figures 130-134. 156, *Meliponula (Meliplebeia) beccarii* (Gribodo). 157, *Meliponula (Meliplebeia) lendliana* (Friese). 158, *Meliponula (Axestotrigona) erythra* (Schletterer). 159, *Meliponula (Meliponula) bocandei* (Spinola). 160, *Plebeina denoiti* (Vachal). 161, *Dactylurina schmidti* (Stadelmann).

terer) which may be a form of *ferruginea* (Lepeletier). The subgenus ranges from Gambia to Kenya, south to Angola and the Transvaal.

Subgenus *Meliplebeia* Moure

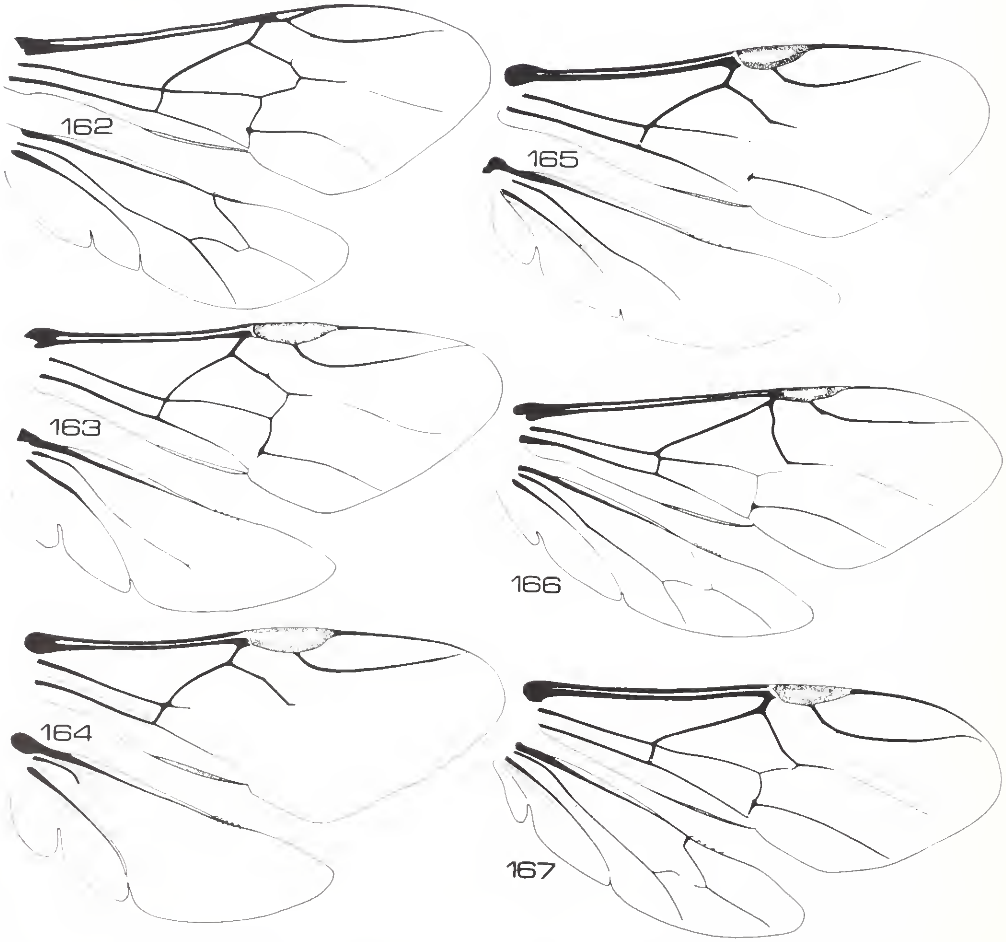
(Figs. 43, 46, 79, 123-125, 156, 157)

Meliplebeia Moure, 1961: 229. Type species: *Trigona beccarii* Gribodo, 1879, by original designation.
Plebeiella Moure, 1961: 226. Type species: *Trigona lendliana* Friese, 1900, by original designation.
Apotrigona Moure, 1961: 233. Type species: *Trigona nebulata* Smith, 1854, by original designation.

Wille (1979b) selected the name *Meliplebeia* for this group, rather than either of the other names proposed at the same time. The three groups named by Moure are distinctly different from one another. The subgenus contains moderate-sized [e.g., *M. beccarii* (Gribodo)] to small [*M. lendliana* (Friese)] species. In *Meliponula (Meliplebeia) beccarii* there are delicate plumed hairs among the bristles near the posterior apical angle of the worker hind tibia, as in the subgenus *Axestotrigona*. Such hairs are absent in the other groups of *Meliplebeia*. The lancet of the worker sting is weak and in membrane in *M. (M.) beccarii* but quite long and apically free, although transparent, in *M. (M.) lendliana* (Friese) and *nebulata* (Smith). The hairs of the first two segments of the labial palpus of workers in *M. (M.) beccarii* are short and straight, while in both *M. nebulata* and *lendliana* there are large setae, hooked and slightly sinuous.

In view of the characters listed above, it is tempting to recognize two subgenera *Meliplebeia* and *Plebeiella*, with *Apotrigona* as a synonym of *Plebeiella*. The differences between the groups of *Meliplebeia* are accentuated by S6 of males. In *M. (M.) beccarii* (Gribodo) S6 is a transverse band not greatly different from that of *Axestotrigona*, and the reflexed median apical process, although long, ends in a rounded apex. In *M. (M.) lendliana* (Friese) S6 is enlarged, dorsoventrally thickened laterally, and the reflexed apical process is bifid near the base, one prong above the other, both long and slender, the upper one extending toward the base of the metasoma (broken off in the one available specimen). Unfortunately the male of *M. (M.) nebulata* (Smith) is unknown to me. Until its character states are known, I have decided that the best classification is one that shows the close relationship of the three groups given generic names by Moure, especially in view of the small number of species involved.

Meliplebeia contains several species (representatives listed above) and ranges from Senegal to Ethiopia, south to Namibia and Natal. The species names and external character states are listed by Moure (1961) under his three generic names (see above synonymy). The emphasis that Moure places on mesoscutal sculpturing (punctate in *Apotrigona*, tessellate in the others) seems to me misplaced. It is dull, finely and closely punctate, finest in *M. lendliana* (Friese).



Figures 162-167. Wings of Meliponinae. 162, *Melipona fasciata* Latreille. 163, *Plebeia (Plebeia) frontalis* (Friese). 164, *Plebeia (Plebeia) schrottkyi* (Friese). 165, *Lestrimelitta limao* (Smith). 166, *Cephalotrigona capitata* (Smith). 167, *Trigona (Trigona) chanchamayoensis* Schwarz.

Subgenus *Meliponula* Cockerell s. str.

(Figs. 45, 77, 127, 159, 170, 172)

Trigona (Meliponula) Cockerell, 1934: 47. Type species: *Melipona bocandei* Spinola, 1851, by original designation.

This subgenus contains the largest and most *Melipona*-like species of the genus. It is robust, compact in form, and lacks yellow markings although it has yellowish brown areas, for example, the scutellum and axillae. On the posterior and distal margins of the hind tibia there are bristles, no plumose hairs. The inner surface of the worker hind tibia has a well defined but rather dull, slightly depressed posterior margin. The worker sting stylet is unusually long and slender and the lancet is long and largely free. The about 15 large setae of the worker labial palpus are curved to slightly sinuous. The male gonostylus arises near the base of the gonocoxite. Other character states are indicated in the above key and in Moure's (1961) comparative description, and especially in Wille (1963). An interesting feature emphasized by Wille is the arch of the aorta between the longitudinal muscles of the thorax. This is as in *Melipona*, but unlike other stingless bees [including *Meliponula (Meliplebeia) beccarii* (Gribodo), see Wille, 1958]. It is, however, a feature of many moderate-sized and large, fast flying bees and is doubtless a convergence in *Melipona* and *Meliponula* s. str., not an indication of close relationship.

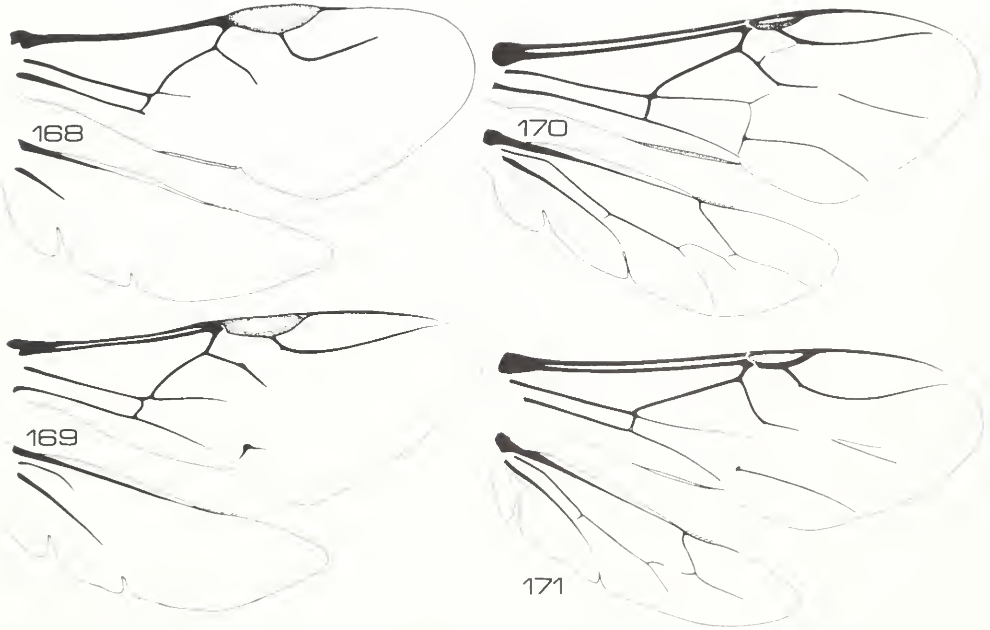
The single species, *Meliponula (Meliponula) bocandei* (Spinola), ranges from Liberia, the Central African Republic, and Uganda south to Angola.

Genus *Plebeina* Moure

(Figs. 47, 128, 160)

Plebeina Moure, 1961: 228. Type species: *Melipona (Trigona) denoiti* Vachal, 1903, by original designation.

This African genus is similar to the Neotropical *Plebeia (Plebeia)* in body form, presence of limited yellowish marks at least on the face, and the narrow, depressed, shining posterior margin of the inner surface of the worker hind tibia. It differs in having the worker gonostyli diverging apically, flattened, without setae and with numerous minute hairs; the sting lancet moderately long and largely free of membrane, the male gonocoxites schizogonal (probably permanently) and much longer than wide; and the gonobase remnants rather large. These features are as in most African Meliponinae. In spite of its appearance, this genus is evidently not closely related to *Plebeia*. Another character state that distinguishes it from most *Plebeia* is the presence of branched hairs at the posterior distal angle of the worker hind tibia and a few on the distal fourth of the



Figures 168-171. Wings of Meliponinae. 168, *Trigonisca buyssoni* (Friese). 169, *Austroplebeia australis* (Friese). 170, *Meliponula (Meliponula) bocandei* (Spinola). 171, *Dactylurina schmidti* (Stadelmann).

posterior margin of the tibia. This is as in some species of *Meliponula,* a genus to which *Plebeina* is closely related. In two species of *Plebeia, P. (Plebeia) caerulea* (Friese) and *P. (Schwarziana) quadrimaculata* (Lepeletier), there are branches on one side of numerous hairs. *Plebeina* differs from *Meliponula* in the about right angular posterior apical angle of the worker hind tibia, this angle bearing long, slender whitish hairs; in the strong although pointed bristles of the rastellum; in the hairless basal area of the propodeum; and especially in the sting stylet of the worker which is merely a rounded, membranous prominence. The about 15 large setae on the worker labial palpus are curved to weakly sinuous. A full description of external characteristics is given by Moure (1961).

This genus contains one variable species, *Plebeina denoiti* (Vachal), or a few closely related species. Moure (1961) omitted presumably inadvertently the name of a form considered in the last paragraph of his discussion of the genus. It was *Plebeina denoiti katangensis* (Cockerell). The genus ranges from Kenya and Uganda to eastern Zaire, Botswana, northern Transval and Natal. It may be absent from West Africa.

Genus *Dactylurina* Cockerell

(Figs. 48, 80, 129, 161, 171)

Dactylurina Cockerell, 1934: 47. Type species: *Trigona staudingeri* Gribodo, 1893, by original designation.

This is the only African group that has the long legs, slender body, plumose hairs on the posterior margin of the hind tibia, and narrow keirotrichiate ridge on the inner surface of the hind tibia, as in *Trigona;* the resemblance is closest to some species of the subgenera *Heterotrigona* and *Frieseomelitta.* A further similarity to some *Trigona* is found on the inner surface of the hind basitarsus of workers of *D. staudingeri* (Gribodo), but not *D. schmidti* (Stadelmann). In the former, in the basal area where many *Trigona* species have a well-defined sericeous area covered with short, dense, fine and sometimes deciduous hairs, there is an ill-defined somewhat sericeous area where the bristle-like setae are sparse. In *D. schmidti* the bristle-like setae are uniformly distributed as in most Meliponinae.

Dactylurina has sometimes been given generic status in the past because of its nest architecture (see introductory section on this topic). Its male genitalia and worker gonostyli show that it is only distantly related to *Trigona* in spite of its resemblance to species of that genus. Unusual features include the slender, fingerlike metasoma and the presence of only one denticle on the upper part of the apical mandibular margin.

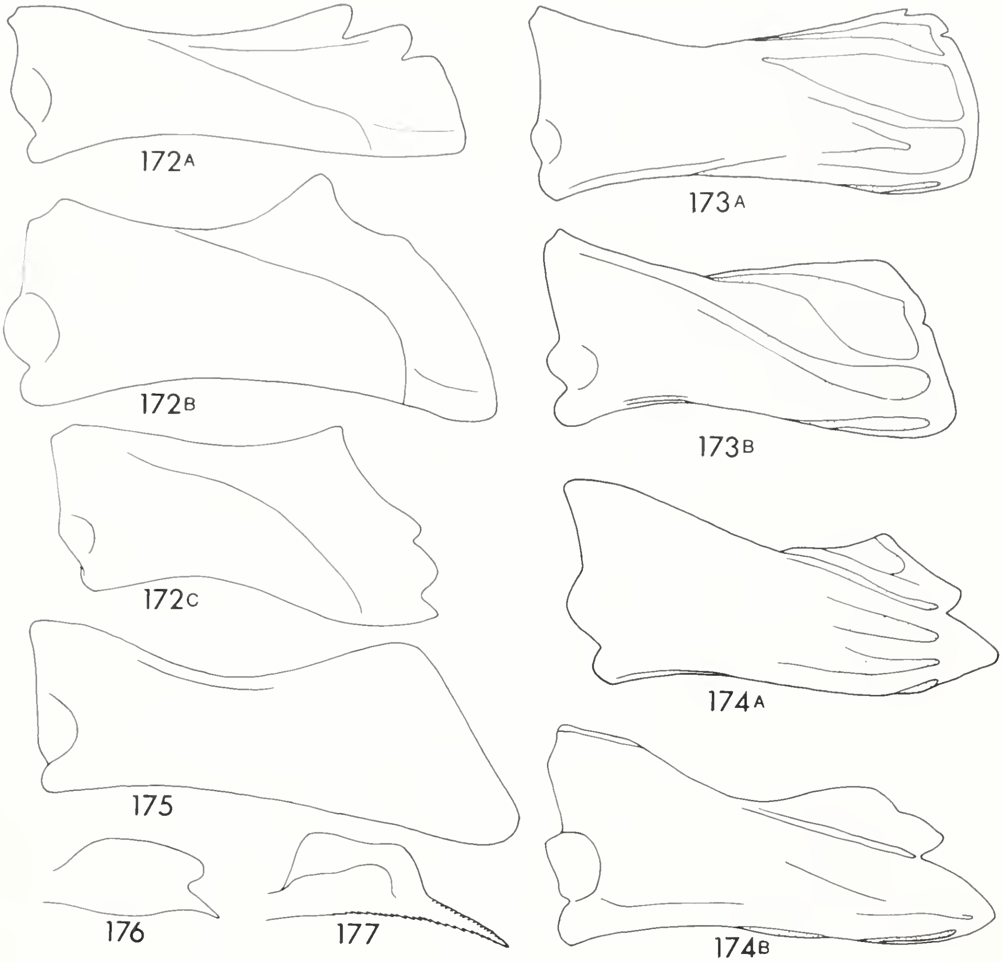
The worker gonostyli are adjacent to one another basally, slightly divergent apically, covered with minute hairs, and without setae. The sting stylet is a mere convexity. The lancet is short and in the membrane, unlike that of most African Meliponinae. The male genital capsule is schizogonal (probably permanently), the gonocoxites longer than broad. The gonobase appears to be absent. The male gonostyli are hairless, firmly attached to the gonocoxites and, although slender in *D. staudingeri* (Gribodo), are broad and flattened in *D. schmidti* (Stadelmann). The gonocoxites are wide open on the ventral side. The labial palpi of the worker have about six large, curved setae; an unusual feature is that segments three and four together are much longer than segment two. The worker gonostyli and male gonocoxites show the relationship of this genus to other African genera. As shown in Figure 6 it appears to be the much modified sister group of *Plebeina.*

There are two species, *Dactylurina staudingeri* (Gribodo) from west Africa and *schmidti* (Stadelmann) from east Africa. Considered together they are widespread in tropical Africa—Kenya and Tanzania to Zaire and Liberia.

SUBFAMILY APINAE

These are the true honey bees. More has been written about *Apis mellifera* Linnaeus than any other insect. Probably because of the familiarity and importance of that species, there has been considerable proliferation of names, considering that *Apis* is a small and morphologically and behaviorally unified group. Maa (1953) made a careful revision of the subfamily, recognizing four genus-group names and many species. His work has often been ignored because of the widespread belief that there are only four species. While he clearly split more than necessary at both the genus-group and species levels, more and more of his conclusions are turning out to be correct. His work is the basic one for a study of apine systematics. Many more recent papers have been reviewed by Ruttner (1987), whose morphometric studies are important at the infraspecific level. A phylogenetic treatment is provided by Alexander (in press).

Description: Small (7 mm long) to large (19 mm long), moderately hairy, rather elongate bees. *Eyes hairy.* Claws of female cleft; arolia present; *hind tibial spurs absent;* strigilis with prong on anterior side; hind basitarsus of worker almost as broad at base as at middle, with posterior basal projection or auricle; hind tibia without penicillum. Forewing with complete, strong vena-



Figures 172-175. Mandibles of females (workers in social species) of Apidae. 172, Meliponinae; a, *Meliponula bocandei* (Spinola), b, *Cephalotrigona capitata* (Smith), c, *Trigona (Trigona) cilipes* (Fabricius). 173, Bombinae; a, *Bombus pennsylvanicua* (Degeer), b, *Psithyrus variabilis* (Cresson). 174, Euglossinae; a, *Eufriesea violacea* (Blanchard), b, *Exaerete smaragdina* (Guérin). 175, Apinae; *Apis mellifera* Linnaeus.

Figures 176-177. Strigilis of worker, inner surface. 176, *Melipona rufiventris* Lepeletier. 177, *Bombus pennsylvanicus* (Degeer).

tion, marginal cell about four times as long as distance from its apex to wing tip; stigma small and slender, scarcely recognizable in large species, vein r arising near middle, margin within marginal cell straight to concave; prestigma almost as long as stigma; second and third transverse cubital veins directed posterodistad and forming acute angles with vein M. Hind wing with jugal lobe little more than half to nearly two thirds as long as vannal lobe (measured from wing base); *jugal and vannal incisions shallow* (Fig. 182). Clypeus gently convex but scarcely protuberant. Maxillary palpus minute, two segmented. Male S8 reduced to a transverse bar, without a spiculum; S7 hidden by S6, transverse, sometimes attenuate medially, with strong lateral apodeme. *Male genitalia of other Hymenoptera largely replaced by huge and elaborate endophallus;* gonobase absent; gonocoxite represented by plate bearing a minute, hairy, apical projection, broader than long, presumably the gonostylus; gonocoxites sometimes widely separated by membrane; penis valves thick, blunt, hairy (incorrectly identified as gonostyli by Smith, 1970); spatha and volsella absent (Fig. 183).

Larva: Without small conical tubercles but with transverse dorsolateral elevations on segments 1 to 4, strongest on 1 and progressively weaker to the rear. Mandible scarcely sclerotized, bluntly pointed, edentate or with fringe of small teeth at apex, without concavity on inner surface.

Larvae are described and illustrated by Michener (1953), Torchio and Torchio (1975), and others.

Nest: Nests are exposed or in cavities such as hives or hollow trees, sometimes in cavities in the ground. The nests are made primarily of wax secreted by the sternal wax glands of workers.

Cells are subhorizontal, forming vertical combs of two layers of cells opening in opposite directions, their bases constituting a median vertical wax sheet. Food for larvae is provided progressively; cells are not closed until the larva has finished feeding. A nest may consist of a single exposed comb or of multiple combs, usually in a cavity. Brood cells for workers and storage cells for honey or pollen are hexagonal, similar in diameter; brood cells for males are similar but larger. Queen-producing cells are not in combs and tend to hang from brood combs of worker cells.

Social behavior: This is the only group of highly social bees (i.e., bees with "permanent" colonies and morphologically very different castes) other than the Meliponinae. New colonies are formed by fission, the old queen and a swarm of workers leaving to find a new site. Colony sizes range from a few thousand to 60,000 or more workers. Accounts of behavior can be found in Michener (1974) and Ruttner (1987), and in innumerable books on the honey bee (*Apis mellifera* Linnaeus); an excellent recent one with numerous references to others is by Winston (1987).

There are no parasitic or obligate robber species.

Distribution: This subfamily is primarily tropical, and was restricted to the Old World until *Apis mellifera* was introduced worldwide. Unlike the Meliponinae, the Apinae spread primarily northward from the tropics, *Apis mellifera* probably being native as far north as southern Norway and *A. cerana* as far as northern China and the Pacific maritime provinces of the U.S.S.R. Only in Africa does the original range of *Apis* extend into the south temperate zone, to the southernmost part of the continent. In the tropical asiatic islands, *Apis* ranges south to Java and east to Timor and the Philippines, but did not reach New Guinea, Australia, etc., before *A. mellifera* was introduced.

Taxonomic Account of Apinae

There is only one genus, *Apis,* in the subfamily Apinae. The relatively few species are so impressively similar that there is no need to recognize multiple genera; it is important instead to emphasize the similarity among the species.

Ruttner (1987) followed tradition in recognizing only four "or at most five" modern species of *Apis* although Maa (1953) had recognized many more. Recent work has demonstrated that a few more of Maa's species are valid, but the total number is small. The two genus-group names based on fossils both have the highly characteristic *Apis* wing venation and have no character states that separate them at a genus level from *Apis*. *Synapis* is from the Oligocene, *Hauffapis* from the upper Miocene, both from Germany.

Genus *Apis* Linnaeus

(Figs. 175, 182, 183)

Apis Linnaeus, 1758: 343, 574. Type species: *Apis mellifica* Linnaeus, 1761 = *A. mellifera* Linnaeus, 1758, designation of Latreille, 1810: 439.

Apicula Rafinesque, 1814: 29 (unnecessary replacement for *Apis* Linnaeus; type automatically the same as for *Apis*).

Apiarus Rafinesque, 1815: 123 (unnecessary replacement for *Apis* Linnaeus; type automatically the same as for *Apis*).

Megapis Ashmead, 1904: 120. Type species: *Apis dorsata* Fabricius, 1793, by original designation.

Micrapis Ashmead, 1904: 122. Type species: *Apis florea* Fabricius, 1787, by original designation.

Apis (Synapis) Cockerell, 1907: 229. Type species: *Apis (Synapis) henshawi* Cockerell, 1907 (fossil), by monotypy.

Hauffapis Armbruster, 1938: 37. Type species: *Hauffapis scheuthlei* Armbruster, 1938 = *Apis armbrusteri* Zeuner, 1931 (fossil), designation of Zeuner and Manning, 1976: 243. *Hauffapis* is not a valid name. It was proposed to include several species. No type species was designated by Armbruster; original type designation is required for genus-group names proposed after 1930 (Internat. Code Zool. Nomen., article 13c). The subsequent type designation by Zeuner and Manning was in the synonymy of *Apis* and thus does not validate the name as *Hauffapis* Zeuner and Manning (I.C.Z.N., art. 11c).

Apis (Sigmatapis) Maa, 1953: 556. Type species: *Apis cerana* Fabricius, 1793, by original designation.

As noted by Ruttner (1987), various authors have regarded *A. florea* Fabricius (or its group) as the first branch of a dendrogram of *Apis* species. Information from various sources has led to this conclusion, but one of the formerly most convincing works concerns geotaxis (Jander and Jander, 1970), which is similar (progeotactic) in diverse families of bees (Colletidae to *Apis florea*) but is different (metageotactic) in *Apis dorsata* Fabricius, *cerana* Fabricius, and *mellifera* Linnaeus. (The Janders' study, in Malaysia, was doubtless based on *A. andreniformis* Smith, not on *florea,* which is rare or absent there.) Horn (1975), however, has shown that the progeotaxis of *A. florea* is different from that of *Bombus* and presumably other bees, so that the Janders' conclusion may not have the phylogenetic significance originally attributed to it. But it has been widely overlooked that morphological data on males of the sort regularly used by systematists, published by Snodgrass (1941), show that in certain characters *A. florea* is plesiomorphic relative to *A. cerana* and *mellifera*.

Some plesiomorphies of the *A. florea* group (recognized because they are more like other bees, e.g., anthophorids, as well as other apids such as *Bombus*) are listed below, followed by the corresponding apomorphies of *A. cerana* and *mellifera* in parenthesis:

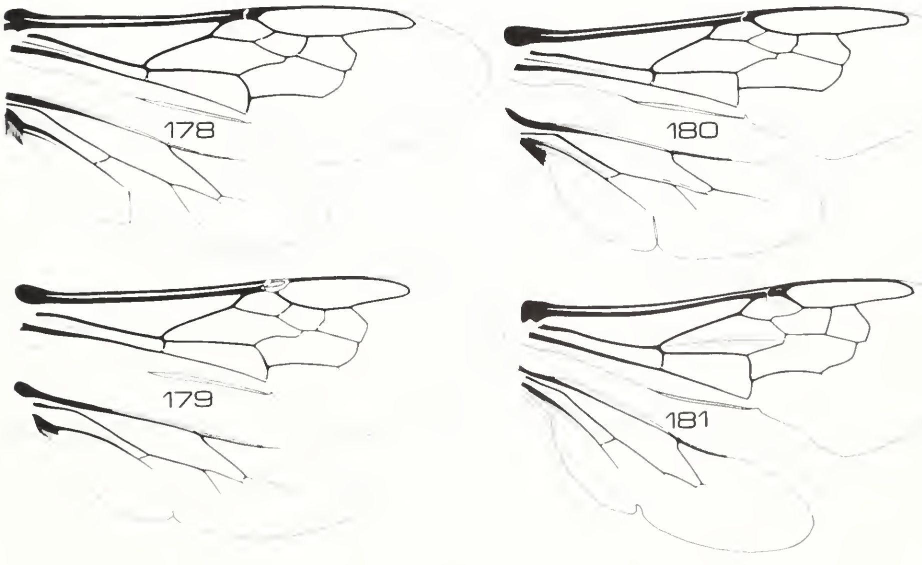
Gonocoxites large and almost meeting (small and widely separated).
S7 and S8 separated by suture (fused medially).
Area behind S8 membranous (a sclerotized, sternum-like region).

Of the remaining species (i.e., other than the *florea* group), *A. cerana* and *mellifera* are obviously close relatives, so that the *dorsata* group must constitute the second branch of a phylogenetic tree, after divergence of *florea*. This viewpoint is supported by the male sternal and genitalic characteristics of *A. dorsata*, which, according to Alexander (in press), are similar to those of *A. mellifera*, but with some features such as gonocoxite size differing in the direction of *A. florea*.

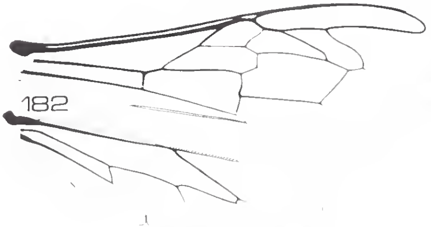
The following is a list of the species that are probably distinct, annotated to explain or give references to accounts justifying specific rank for forms not considered specifically distinct by Ruttner (1987):

florea Fabricius, 1787.
andreniformis Smith, 1858. Sympatric with *florea* in southern China and parts of southeast Asia (Wu and Kuang, 1986, 1987).
dorsata Fabricius, 1793.
binghami Cockerell, 1906. (This is an allopatric insular form from Sulawesi (Celebes). It seems distinctive enough to justify specific separation from *dorsata*, but this is a subjective decision.)
breviligula Maa, 1953. (A Philippine form; comments the same as for *B. binghami*.)
laboriosa Smith, 1871. A Himalayan species probably parapatric with *dorsata* although the two are sometimes found at the same place (Sakagami, Matsumura, and Ito, 1980; Roubik, Sakagami and Kudo, 1985; McEvoy and Underwood, 1988).
cerana Fabricius, 1793.
koschevnikovi Buttel-Reepen, 1906. (This = *vechti* Maa, 1953, and is sympatric with its closest relative, *A. cerana*, in Borneo; Tingek et al., 1988.)
mellifera Linnaeus, 1758.

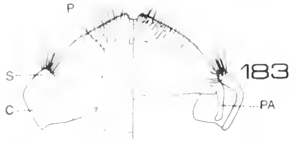
Additional species of the *cerana* and *mellifera* groups may eventually be recognized.



Figures 178-181. Wings of Euglossinae and Bombinae. 178, *Exaerete smaragdina* (Guérin). 179, *Eufriesea violacea* (Blanchard). 180, *Eulaema cingulata* (Fabricius). 181, *Bombus pennsylvanicus* (Degeer).



182



Figures 182, 183. 182, Wings of *Apis mellifera* Linnaeus. 183, Genitalia of male of *Apis mellifera* Linnaeus, endophallus omitted; dorsal view at left, ventral at right. P = penis valve, PA = penis valve apodeme, S = gonostylus (#), C = gonocoxite.

SUBFAMILY EUGLOSSINAE

These are the orchid bees of the American tropics, so called because the males are pollinators of the larger orchids of that region. The name is also appropriate because of the large size and gaudy coloration of many of the bees themselves.

Males are attracted to various aromatic compounds (Dodson et al., 1969; Dressler, 1982a). For this reason they have been much collected in recent years. A list of species was given by Kimsey and Dressler (1986).

Description: Moderate-sized (8.5 mm long) to very large (29 mm long), moderately to densely hairy, usually robust bees. Claws of female with basal tooth, of male similar or cleft; *arolia absent;* hind tibial spurs present; strigilis with prong on anterior side; hind basitarsus of nonparasitic females broadest at base, with posterior basal angle or auricle; hind tibia of nonparasitic females greatly expanded with immense corbicula, without penicillum; *hind tibia of males with large hairy slit on upper margin distally,* male hind tibia greatly swollen in nonparasitic genera. Forewing with complete, strong venation, marginal cell less than twice as long as distance from apex to wing tip; stigma minute, vein r arising near middle, margin within marginal cell straight or concave; prestigma shorter than to longer than stigma. *Hind wing without jugal lobe, with comb of bristles in its place* (Figs. 178-180). Clypeus strongly protuberant; labrum much less than twice as wide as long, thus longer than in other apids, sometimes longer than broad. Maxillary palpus two-segmented. Male S8 large, strongly sclerotic, longer than broad, with strong, usually pointed apical process and short, posterolaterally directed apodemes; S7 with apically hairy, sometimes bifid disc and long lateral apodemes (see illustrations in Sakagami and Michener, 1987). Male genitalia strongly sclerotized with distinct gonobase (narrow but almost continuous ventrally); large gonocoxite; small to moderate-sized, sometimes bifid, hairy upper gonostylus; minute to large, hairy, lower gonostylus; and rather small, minutely hairy volsella (Fig. 192).

Larva: With small, pointed dorsolateral tubercles on thoracic segments and at least sometimes on first abdominal segment and a pair of similar tubercles on vertex. Mandible heavily sclerotized, blunt, with large apical concavity on inner surface.

Larvae of *Eufriesea* were described by Michener (1953), of *Euglossa* by Roberts and Dodson (1967).

Nest: Nests are exposed (some species of *Euglossa*) or in cavities in banks, tree trunks, logs, old buildings, etc. Aside from the outside covering of exposed nests, the construction consists principally of brood cells, which are mass provisioned. There are no storage pots or storage cells as in other apid subfamilies. Construction materials are resin *(Euglossa),* resin often mixed with bark fragments *(Eufriesea),* and mud or feces perhaps with resin *(Eulaema).*

Social behavior: Some species are solitary *(Euglossa, Eufriesea).* Some species of *Eufriesea* often produce aggregations of cells in protected places. Some species of *Euglossa* and perhaps all *Eulaema* regularly have several females per nest. The nature of the interactions among them are diverse and little known, but the colonies are seemingly not eusocial.

The genus *Aglae* is cleptoparasitic in the nests of *Eulaema; Exaerete* is cleptoparasitic in nests of *Eulaema* and *Eufriesea.*

These and other aspects of euglossine biology are summarized by Dressler (1982a).

Distribution: Except for *Aglae,* which is known from eastern Panamá to Bolivia, each genus ranges from Mexico to Argentina, mostly in the moist forests.

Relationships among Euglossine Genera

History: The genera of this subfamily, although rather diverse in appearance, are remarkably uniform in many features, and all the nonparasitic species were included in *Euglossa* early in this century by most authors. The opposite extreme was achieved by Moure (1944b) who placed the five genera here recognized in five monogeneric tribes and two subfamilies. Moure himself (1950b) retreated from this extreme, however, recognizing only two tribes, Exaeretini for the cleptoparasites, Euglossini for the others, replacing his two subfamilies of 1944. Since the two cleptoparasitic genera seem to be independently derived from nonparasitic ancestors, there is no justification for these tribes.

Females of the parasitic forms lack corbiculae and other pollen carrying and manipulating structures. The hind tibiae are therefore slender, not excessively broadened as in females of nest-making genera. Interestingly, males of the parasitic genera also have slender hind tibiae, not swollen like those of the non-parasites. Since the hind tibiae of males receive the aromatic compounds collected by males, and this function is probably related somehow to mating behavior, one wonders why males of parasitic genera would not have hind tibiae as enlarged as those of other genera. Perhaps the slender hind tibiae of males are plesiomorphic features preserved in parasitic forms, as occurs in various other groups of parasitic bees.

Analysis: Kimsey (1982, 1987) presented two different cladograms for the genera of Euglossinae. Unfortunately, in presenting the second one, she did not discuss the first cladogram or the reasons for changes. The difference between the two is that in 1982 she placed *Aglae* as the sister group to all other genera, while in 1987 she placed it as the sister to *Eulaema* only. The reason for this change is a change in polarization of a single character, the thickness of S8 in profile.

The following comments refer only to the 1987 cladogram. It is based on 25 characters, 16 of which consist of a character state of a single genus, contrasting with all the rest; these states are presumably autapomorphies. Character states of single genera of course could be plesiomorphic (the other genera being united by the alternative synapomorphies) but Kimsey's interpretations (that they are derived) seem reasonable in all cases. The remaining 9 characters involve synapomorphies and are therefore potentially useful in cladogram construction. These are her characters 1, 3, 4, 5, 9, 14, 16, 19, and 25. Kimsey correctly emphasizes that, because most euglossine characters have no homologues in other subfamilies or families of bees, polarization based on out-group comparisons is often impossible. For example, on the outer surface of the mid tibia of males there are velvety areas whose number, size, and shape provide generic character states (Kimsey's characters 6 and 7). And on the hind tibia of males there is a hairy slit (Kimsey's characters 13-15) into which the aromatic compounds collected by males are placed. No homologues of these structures are found in other bees. If polarization is to be done, it must be by methods other than out-group comparisons. Kimsey uses the notion that a widespread character state is plesiomorphic relative to a less widespread alternative, but as is well known, this is often unreliable. I can see no logical basis for concluding that two adjacent midtibial velvety areas, one large and one small, is ancestral to other arrangements, or that a large, long hind tibial slit is ancestral to a short one. On bases such as these, I consider that polarization of Kimsey's characters 3, 5, 9, and 14 is in doubt.

The single supposed synapomorphy uniting *Euglossa* and *Exaerete* in Kimsey's cladogram is 14, curvature of the hind tibial slit of the male. Since both its polarity and the homology of the rather different looking curvature is in doubt, the reasonable course is to consider that *Euglossa, Exaerete,* and the remaining genera are connected at a trifurcation rather than showing the weakly justified additional cladistic structure. Synapomorphies 19 and 25, as well as 16 with a reversion for *Aglae,* seem to unite the three remaining genera, but the four synapomorphies used by Kimsey to unite *Aglae* and *Eulaema* as the sister group to *Eufriesea* turn out to be dubious. Numbers 3, 5, and 9 are not reliably polarizable, and 1 is not a unique synapomorphy for it is a loss (of two palpal segments) that occurs also in some species of *Exaerete;* it could have arisen independently in *Aglae* and *Eulaema.* The conservative course, showing only what is not too speculative, is to unite *Aglae, Eufriesea,* and *Eulaema* at an unresolved trifurcation. Thus the best cladogram now possible can be summarized thus: *(Euglossa, Exaerete, (Eufriesea, Eulaema, Aglae)).* This is not as satisfying as a fully dichotomous cladogram but better demonstrates our current ignorance.

Taxonomic Account of Euglossinae

This subfamily contains five genera that are separable by the key given below. For the most part they are easily separable in general appearance also: *Exaerete* species are large, all green, not conspicuously hairy; *Aglae* is slender, blue; and *Euglossa* is small and usually brilliantly metallic (but there are a few dull colored species). *Eufriesea* and *Eulaema* are similar superficially, large and conspicuously hairy, except that some species of *Eufriesea* are less hairy and brilliantly metallic, resembling *Euglossa*. There are cases of probable Müllerian mimicry involving *Eufriesea* and *Eulaema* (Dressler, 1979) so that close examination may be needed to recognize the usually rarer *Eufriesea*.

Key to the Genera of Euglossinae
(modified from Kimsey, 1987)

1. Hind tibia three or more times as long as broad in both sexes; female hind tibia somewhat inflated, without corbicula; cleptoparasitic species 2

—Hind tibia twice as long as broad or less in both sexes; female hind tibia flat and shield-like with enormous corbicula (Fig. 188); nonparasitic species 3

2. Hind femur swollen and usually denticulate ventrally; hind tibia curved and expanded apically; scutellum dorsally convex, with sublateral tubercle or welt . . . . *Exaerete*

—Hind femur slender and unmodified; hind tibia straight and apically narrowed; scutellum flat. . . . . *Aglae*

3. Labrum whitish with two large, dark oval spots; male hind tibial slit short, not reaching apical margin of tibia, and basally curved; male midtibia with two, or less commonly 1 or 3, small felty patches in basal end of large patch; female with median, black scutellar tuft . . . . *Euglossa*

—Labrum dark in color; male hind tibial slit long, reaching apical margin, broad and not curved basally; male midtibia with one relatively large basal felty patch adjacent to large patch; female with *(Eulaema)* or without *(Eufriesea)* scutellar tuft. 4

4. Labial palpus 4-segmented; face metallic without white markings; clypeal ridging various, usually without single medial ridge. . . . . *Eufriesea*

—Labial palpus 2-segmented; face black or brown, often with white markings; clypeus with single strong medial ridge . . . . *Eulaema*

Genus *Eufriesea* Cockerell
(Figs. 174, 179, 192)

Plusia Hoffmannsegg 1817: 52 (not Hübner, 1806). Type species: *Plusia superba* Hoffmannsegg, 1817 (monobasic).

Eumorpha Friese 1899: 126 (not Hübner, 1807). Type species: *Euglossa pulchra* Smith, 1854, by designation of Cockerell, 1908: 41.

Eufriesea Cockerell 1908: 41 (new name for *Eumorpha* Friese, 1899). Type species: *Euglossa pulchra* Smith, 1854 (autobasic).

Euplusia Moure 1943: 189 (new name for *Plusia* Hoffmannsegg, 1817). Type species: *Plusia superba* Hoffmannsegg, 1817 (autobasic).

This genus, most species of which were placed in *Euplusia* from 1943 to about 1980, was revised by Kimsey (1982). She showed (1979b) that the broad, flat scutellum formerly thought to separate *Eufriesea* from *Euplusia* cuts across natural groups and is not a useful generic or subgeneric character state. There are about 52 species, many of them brilliantly metallic but others with colorful yellow and black hairs and superficially resembling *Eulaema* except for weak metallic reflections at least on the face.

Nests consist of linear or branched series of cylindrical cells of resin often mixed with bark fragments. They are located in protected crevices or cavities, under overhangs of rocky banks, under buildings, in pre-existing burrows in wood, in termite nests, etc. Although such nests are sometimes aggregated, there is no evidence of social organization. Kimsey (1982) summarizes what is known about the nests.

Genus *Aglae* Lepeletier and Serville

Aglae Lepeletier and Serville, 1825: 105. Type species: *Aglae caerulea* Lepeletier and Serville, 1825 (monobasic).

This is a monotypic genus of relatively slender, steel blue bees reported to be cleptoparasites of *Eulaema*. It is the most distinctive euglossine genus, as indicated by Kimsey (1982) who considered it the sister group of all the other genera, and Kimsey (1987) who documents its many autapomorphies. In the latter work she regards it as the sister group of *Eulaema*, but see my comments above on relationships among the genera.

Genus *Euglossa* Latreille

(Fig. 188)

Euglossa Latreille, 1802a: 436. Type species: *Apis cordata* Linnaeus, 1758, by designation of Blanchard, 1849: 219.
Cnemidium Perty 1833: 148, not Goldfuss, 1826. Type species: *Cnemidium viride* Perty, 1833 (monobasic).
Euglossa (Glossura) Cockerell 1917b: 144. Type species: *Euglossa piliventris* Guérin, 1845, by original designation.
Euglossa (Euglossella) Moure 1967: 401. Replacement for *Cnemidium* Perty, 1833. Type species: *Cnemidium viride* Perty, 1833 (autobasic).
Euglossa (Dasystilbe) Dressler, 1978: 193. Type species: *Euglossa villosa* Moure, 1968, by original designation.
Euglossa (Glossurella) Dressler, 1982b: 131. Type species: *Euglossa bursigera* Moure, 1970, by original designation.

This genus consists of moderate-sized (the smallest of Euglossinae) to rather large, usually brilliantly metallic species. With 103 species described, it is the largest genus of the subfamily. Dressler (1978) provided a classification of the species, placing them in 12 species groups organized into four subgenera (*Dasystilbe* Dressler, *Glossura* Cockerell, *Euglossa* Latreille, s. str., and *Euglossella* Moure). The subgenera are seemingly natural groups but there is some intergradation among them. Later Dressler (1982b) elevated another group to subgeneric status under the name *Glossurella*. As I have nothing to dd to Dressler's classification, further comment seems unnecessary.

Nests of some species are constructed of resin and located on stems or twigs in the open. The cells are packed into the interior of a more or less spherical resinous envelope. Other species construct cells, isolated or in small clumps, in small cavities in tree branches or trunks, earthen banks, or in buildings. Some nests are built and occupied by lone females while others contain several females seemingly living more or less cooperatively (Roberts and Dodson, 1967).

Genus *Exaerete* Hoffmannsegg

(Figs. 174, 178)

Exaerete Hoffmannsegg, 1817: 53. Type species: *Apis dentata* Linnaeus, 1758 (monobasic).
Chrysantheda Perty, 1833: 147. Type species: *Chrysantheda nitida* Perty, 1833 (=*Apis dentata* Linnaeus, 1758) (monobasic).
Caliendra Gistel 1848: viii. Type species: *Chrysantheda nitida* Perty, 1833 (=*Apis dentata* Linnaeus, 1758) (autobasic) (unnecessary replacement for *Chrysantheda* Perty).

This is a genus of large, brilliant green, cleptoparasites of *Eufriesea* and *Eulaema*. The six species were revised by Kimsey (1979a). Its closest relative remains undetermined, although Kimsey (1987) places it as a sister group of *Euglossa*.

Genus *Eulaema* Lepeletier

(Fig. 180)

Eulaema Lepeletier, 1841: 11. Type species: *Apis dimidiata* Fabricius, 1793 (=*Apis meriana* Olivier, 1789) by designation of Taschenberg, 1833: 85.
Eulaema (Apeulaema) Moure 1950b: 184. Type species: *Eulaema fasciata* Lepeletier, 1841 (=*Centris cingulata* Fabricius, 1804), by original designation.

This genus was at one time called by the name *Centris* Fabricius (1804) (Sandhouse, 1943; Michener, 1944) because of an early and usually ignored type designation for *Centris*. However, the usual meanings of the names *Centris* and *Eulaema* have been preserved, thanks to Opinion 567 of the International Commission on Zoological Nomenclature. Sandhouse (1943) lists two unjustified emendations of the name *Eulaema*.

This genus consists of about 13 species of large bees, all black or with conspicuous patterns of yellow or orange hair, sometimes with limited metallic tints, usually on the metasoma.

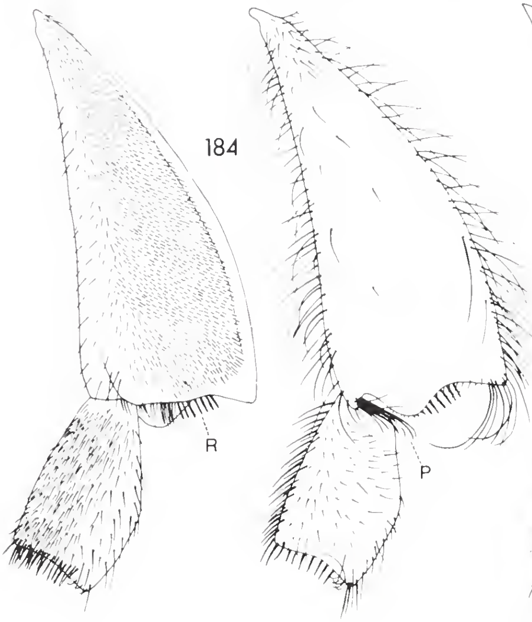
Nests consist of clusters of oval cells made of mud, feces, and probably resin, located in cavities in soil, banks, tree trunks, etc. Often more than one female works simultaneously in a single nest, but details of interactions among individuals remain little known (Michener, 1974).

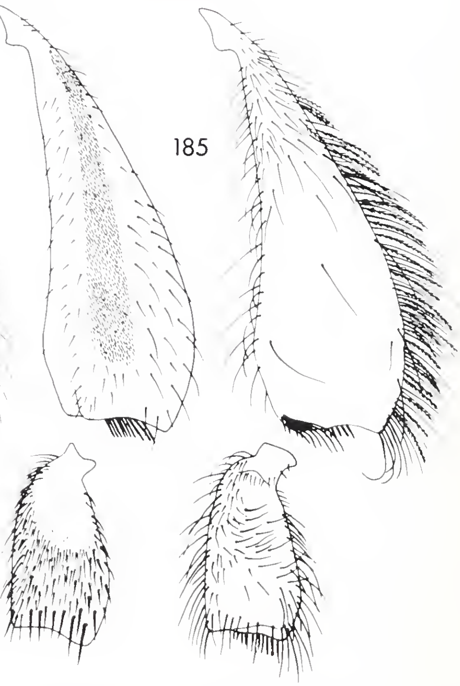
The genus was revised by Moure (1950b) and Dressler (1979). Moure (1950b) gives the distinctions in detail between the subgenera *Eulaema* s. str. and *Apeulaema*. R. L. Dressler (in litt.) indicates that there are four species groups; it is not clear whether any of them justify subgeneric status.

SUBFAMILY BOMBINAE

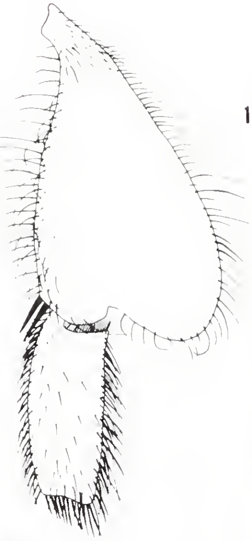
This subfamily consists of the bumble bees. Except for the parasitic species, all are primitively eusocial. The approximately 250 species are morphologically monotonous compared to the Euglossinae and especially to the Meliponinae. Nonetheless there is interesting diversity in a few structures—the male genitalia, stings, mandibles, etc. Most of the classification of the group is based on the male genitalia.

Description: Middle sized (9 mm long) to very large (22 mm long), robust, hairy bees. Claws of female cleft; arolia small but present; hind tibial spurs present. Strigilis with prong or strong elevation on inner margin. Hind tibia and basitarsus of female as in Apinae except in social parasites *(Psithyrus)*. Forewing with complete strong venation; marginal cell somewhat longer than distance from its apex to wing tip; stigma





Figures 184-185. Hind tibiae and basitarsi of meliponine workers, inner surface (without marginal hairs) at left. 184, *Plebeia (Plebeia) frontalis* (Friese). 185, *Trigona (Trigona) amalthea* (Olivier). R = rastellum, P = penicillum.



Figures 186-189. Hind tibiae and basitarsi of female Apidae (workers of social species), outer surfaces. 186, *Trigonisca longitarsis* (Ducke). 187, *Partamona* near *cupira* (Smith). 188, *Euglossa imperialis* Cockerell. 189, *Bombus pennsylvanicus* (Degeer).

Figures 190, 191. Dorsal views of scutellum of meliponine workers. 190, *Scaptotrigona mexicana* (Guérin). 191, *Partamona* near *cupira* (Smith).

small, little if any longer than prestigma, vein r arising near or beyond middle, margin within marginal cell straight or usually concave. *Hind wing without jugal lobe* (Fig. 181). Clypeus slightly convex, weakly to moderately protuberant. Maxillary palpus two segmented. Male S8 well developed, sclerotized, with median apical, truncate or emarginate, hairy process, body of sternum not thickened and excavated as in most Euglossinae, apodemes distinct, directed laterally or posterolaterally. S7 with disc rather broad, like preceding sterna but smaller, apical margin rounded or slightly bilobed (for this and associated structures, see series of illustrations by Ito, 1983, 1985). Male genitalia well sclerotized with distinct gonobase broadly interrupted midventrally; large gonocoxite; short and broad, often variously angulate, gonostylus (squama); and broad, hairy volsella attaining the apex of the gonostylus or exceeding it and also extending far toward the base of the gonocoxite on the lower surface.

The homologies and terminologies for the male genitalic parts have been confusing in Bombinae and are the subject of a separate section below.

Larva: With small pointed dorsolateral tubercles on thoracic segments. Mandible heavily sclerotized, apex bluntly rounded or minutely denticulate, acute in *Psithyrus,* with small preapical tooth on upper margin, with large apical concavity on inner surface.

Larvae have been described and illustrated in detail by Ritcher (1933), Cumber (1949), Michener (1953), Stephen and Koontz (1973), and others. There is significant variability among them that may clarify relationships among groups of *Bombus.*

Nest: A summary of nest architecture is given by Michener (1974). Nests are commonly in rodent nests, bird nests, cavities under bunch grass or other vegetation, etc. There may or may not be a thin wax (and pollen) covering over the nest. The cells are totally different from those of all other bees, for they are closed (sometimes incompletely) but grow with the growing larvae, commonly contain several eggs and later larvae, develop a separate bulge for each larva, and may even become divided into several cells as the larvae mature. Katayama (1989) has discussed such cells and their possible evolutionary origin in detail. Larvae are fed progressively, either by food introduced through the tops of the cells or by food pressed in through pockets at the bases of the cells and forming the cell floors. Both methods may occur in the same species, usually at different seasons. Both honey and pollen are stored in pots separate from brood cells; they are often made of old cocoons but may be wholly constructed by the bees. In *B. mendax* Gerstacker, unlike most species, the cocoons are wholly destroyed and honey storage is in a series of crowded (therefore sometimes hexagonal) pots separate from the pollen pots (Haas, 1976).

Social behavior: Except for the social parasites, the Bombinae are all eusocial. Their colonies are usually annual. Each is started by a single queen; in temperate and arctic climates this is in the spring. Her early progeny are all workers, usually much smaller than the queen but morphologically similar. Males and young queens are produced later; they mate, the colony fades away, and the young queens hibernate until the following spring. In the tropics this sort of cycle is sometimes modified, but it never attains the major features of highly social bees whose queens never live alone and are morphologically very different from workers. Other features of *Bombus* behavior are described by Michener (1974), Free and Butler (1959), Morse (1982) and others.

A few species of Bombinae are workerless social parasites in nests of species of *Bombus.* Most of the parasites are in the genus *Psithyrus;* females of this genus lack the pollen gathering and manipulating structures characteristic of *Bombus* and the apex of the metasoma is more pointed than in *Bombus* and curled downward, housing a powerful sting. The female social parasite dominates or kills the host queen and may become, in essence, the queen of a colony consisting of herself and workers of the host species. Fisher (1987) gives a recent study of one species with references to older works.

Distribution: Bumble bees are for the most part adapted to cool climates and thus are uncommon in places where Euglossinae are common. They are most abundant in the cool temperate parts of the holarctic region, with many more species and subgenera in Eurasia than in North America. Williams (1985) indicates that there are 199 species in Asia, 58 in Europe, 41 in North America, and 43 in Mexico, Central and South America. Northward, they range in small numbers as far as there is land. Southward they occur in North Africa but not in subsaharan Africa. There is one specimen of what appears to be a South American species reported from Cameroon (Tkalců, 1966); it was no doubt mislabeled or introduced. To the east they are numerous in the Himalayas but absent below 1000 m altitude in India (Williams, 1985); to the southeast a few species occur in the mountains of Southeast Asia, as far as Java and the Philippines, but they are absent from the lowlands. In the Western Hemisphere there is a rather small *Bombus* fauna all the way to Tierra del Fuego, mostly in montane areas or temperate latitudes, but unlike the situation in Africa and Asia, a few species occur in the lowland moist tropics.

It is curious that close to the center of diversity [and the area where the most plesiomorphic species occur, according to Williams (1985)], i.e., the Palearctic region, the lowland tropics seem to have been an absolute barrier to Bombinae. Moreover, in spite of widespread mesic Pleistocene conditions in what is now the Sahara, they did not reach the mountains and highlands of East Africa, as have other mesic northern groups like *Andrena*. On the other hand, in the Western Hemisphere, with poorer northern bombine diversity, they range almost as far south as there is land, and occur in the lowland tropics, e.g., the Amazon Valley.

Relationships among Bombine Genera and Subgenera

History: Traditionally two genera of Bombinae have been recognized, *Bombus* and *Psithyrus,* the latter consisting of social parasites of the former. Indeed, because of their divergent habits and the structures relating to pollen collecting, or lack of them in *Psithyrus,* some older authors (Ashmead, 1899; Friese, 1923) placed *Psithyrus* in a different subfamily or family from *Bombus.*

As to *Bombus,* although various subgeneric names had been proposed earlier (starting with Dalla Torre, 1880), and Robertson (1903) had proposed *Bombias* as a genus, it was Skorikov (1922) who divided *Bombus* into numerous genera. Most authors did not follow him, for the genera were hard to tell apart. Milliron (1961) divided *Bombus* into three genera and Tkalců (1972) recognized eight genera. These genera, likewise, are hard to distinguish, intergrade, and have little usefulness. The smaller supraspecific units, subgenera or species groups, however, based primarily on male genitalic character states, are more stable and for a *Bombus* specialist are useful. There are about 35 such units in the genus *Bombus,* all with subgeneric names. Some of them such as *Fervidobombus* are still quite diversified and may not represent unified recognizable groups. Ito (1983, 1985) gives a detailed and useful historical account, while a briefer one is provided by Richards (1968). Given the morphological homogeneity of *Bombus,* most authors have continued to use it in the traditional broad sense. Efforts to find a few recognizable units have failed because of intergradation and discordance in character state distributions, a problem that plagues even some of the finer divisions (subgenera or species groups). Moreover, the species of *Bombus* s.l., as noted above, are very much alike, not superficially separable into genera or subgenera, and have many distinctive behavioral attributes. Richards (1968) described the 35 subgenera that he recognized, gave keys, and thus for the first time provided a worldwide classification for subgenera of *Bombus.*

Many authors have speculated on the relation of *Psithyrus* to *Bombus.* Because of the superficial similarity of some Palearctic *Psithyrus* to their hosts, the suggestion that *Psithyrus* species arose polyphyletically from different groups of *Bombus* was made, for example by Richards (1927). The similarities of *Psithyrus* species would thus have to be a result of convergence. Recent studies by Ito (1983, 1985), Ito and Sakagami (1985), and Williams (1985) placing emphasis on male genitalia and hidden sterna, which are unlikely to evolve convergently, show decisively that *Psithyrus* is a monophyletic unit related to certain groups of *Bombus.* Electrophoretic studies of genetic relationships support the cohesiveness among *Psithyrus* species (Pamilo, Pekkarinen and Varvio, 1987; Obrecht and Scholl, 1981).

Recent studies by Ito (1983, 1985) and Williams (1985) provide a wealth of information as well as interpretations. Ito gives excellent illustrations of male sterna and genitalia of nearly all groups. His analyses (based on genital character states of males) are phenetic; they show six groups of *Psithyrus* together but in the midst of *Bombus* groups, and closest to groups called *Mucidobombus, Eversmannibombus,* and *Orientalibombus.* A cladistic study of the problem by Ito and Sakagami (1985) indicates a relationship of *Psithyrus* to *Orientalibombus* and some species of *Fervidobombus,* especially *Bombus dahlbomii* Guérin.

Williams (1985) developed a cladogram for all groups of Bombinae, based on male genitalic character states. He utilized 14 characters, with 2 to 33 states per character. Polarities were judged by comparison with Euglossinae, although the characters with 24, 27, and 33 states were not ordered; they are branching characters.

Although a different method of coding, with more characters and fewer states per character, would seem desirable and would probably permit better polarization, Williams' study is interesting and valuable and his major phylogenetic conclusions are probably correct. *Mendacibombus* appears in his study as the sister group of all other Bombinae; *Psithyrus* is the next branch, the sister group of all but *Mendacibombus*. On this basis, following the practice of those who base classifications on cladograms only, Williams recognized three genera, *Mendacibombus, Psithyrus,* and *Bombus*. Ito (1983, 1985) also recognized *Mendacibombus* as a distinctive group, but in all but one of his phenograms it was closely associated with other groups of *Bombus*. Richards (1968) did not consider *Mendacibombus* unusual.

I regard Williams' cladogram as important but, as his title and introduction indicated, preliminary. His classificatory response seems to me premature. First, *Mendacibombus* is recognized on his cladogram by a single synapomorphy plus three plesiomorphies that distinguish it from the rest of the subfamily. Furthermore, about two thirds of all the other segments of the tree are also defined by single synapomorphies. Thus while the tree is in general convincing because some of the major groups of subgenera recognized by other authors tend to come out together, it is no doubt subject to change when other characters and taxa are added to the study. One objective of classification is stability; to base a classification on such fragile evidence is a mistake. Williams indicates (in litt., 1989), however, that the male genitalia of numerous species not available to him in 1985 have modified his cladogram in detail but the general form of the tree remains about the same.

Second, Williams (in litt.) reports that with other species now available, he finds *Mendacibombus* to represent more than one clade; it is therefore paraphyletic. If it were to be subdivided, one would have genera scarcely distinguishable from one another.

Third, Williams' cladogram is based exclusively on character states of male genitalia. A cladogram to be used as a basis for classification should be based on all available synapomorphies, or at least not on one single set of characters that in theory might exhibit convergences. Williams defends his limited character set on the basis that the genitalic character states selected are those likely to be more conservative than those involving other structures that do not fit the female securely to prevent interruption of copulation. In short, he argues that his characters are unlikely to exhibit convergence; he is probably right.

Fourth, lack of characters is illustrated by branches *(Mucidobombus, Rhodobombus)* that lack synapomorphies. From the viewpoint of Williams' cladogram, these groups should be regarded as paraphyletic. It should be noted, however, that Williams' cladogram was based on certain species, and that the traditional subgeneric names were then added; he is not responsible for these "subgenera."

Fifth, the genitalic characters themselves often involve minor changes whose polarity is subject to judgement. *Bombus (Mendacibombus) mendax* Gerstaecker not only looks like a *Bombus* but its genitalia are similar to those of other *Bombus*. Polarization of characters by outgroup comparison using Euglossinae is not only difficult, but may be deceptive since most similarities of Euglossinae and Bombinae are due to plesiomorphies, and the Euglossinae have many more autapomorphies (at the subfamily level) than do the Bombinae. Thus comparison of the states of a character is likely to be between a plesiomorphic state in Bombinae and a derived homologue in the Euglossinae.

Finally, I do not believe that the unified and homogeneous group *Bombus,* which has an enormous number of common character states and for which predictions concerning characteristics of little-studied species can be made, is any less useful because it can be shown to have given rise to another genus. In short, paraphyletic taxa are sometimes useful. One needs to know that they are paraphyletic, but the classification should often reflect other things than the cladistic pattern.

Given the problems described above, and noting that very intensive studies of Bombinae have been made and that additional useful characters are hard to find, I believe that those who rigidly wish classifications to be redundant, i.e., to duplicate information in cladograms, have no choice but to incorporate *Psithyrus* into *Bombus*. This would mean that many statements about *Bombus* must contain alternatives—either with a corbicula or without, with a rastellum or without, etc.

The alternative which I follow is to recognize a paraphyletic genus *Bombus*. I think this solution is correct not only currently, until a cladogram with more characters is devised, but also in the long term, because a classification that simply duplicates the cladistic pattern is redundant. The classification should be as useful as possible, and thus reflect information beyond that in the cladogram, in this case the phenetic distinctness of *Bombus* s.l. from *Psithyrus*.

Genitalia of the Bombinae

Partly because the Bombinae were among the first bees whose male genitalia were investigated, and partly because of problems in recognizing the homologies of certain parts, special terminologies often have been used in describing bombine genitalia. The greatest problems concern the identity of the volsella.

At one stage I believed that the structure called the volsella by Williams (1985) was in fact the lower branch or lamina of the gonostylus. In Bombinae it extends apicad and is hairy like a gonostylus, and its base is not very different from the base of the lower gonostylus of halictids like *Nomia melanderi* Cockerell. The presence of two gonostyli (really upper and lower and largely separate gonostylar structures) is widespread and presumably plesiomorphic in anthophorid bees, and seemed to explain the two apical processes from the bombine gonocoxite. Two gonostyli are well developed and distinct, for example, in *Tapinotaspis* (Exomalopsini), *Epicharis* (Centrini), *Diadasia* (Emphorini) in the Anthophorinae; in *Nomada* and other Nomadinae; and in *Manuelia postica* (Spinola) but not other *Manuelia*, in the Xylocopinae. As indicated by Sakagami and Michener (1987), *Manuelia* is close to the ancestor of the Apidae. It therefore would not be surprising to find the same structures in the apids that have most plesiomorphies, i.e., the Bombinae and Euglossinae.

Euglossinae (e.g., *Eufriesea pulchra* Smith, Fig. 192) clearly have the two gonostyli. In addition, however, they have a minutely hairy sclerite more basad along the lower inner margin of the gonocoxite; it appears to represent the volsella. In *Epicharis elegans* Smith (Anthophoridae) the two gonostyli are also clearly present, and in addition the volsella, as a separate small sclerite with a long, minutely hairy, apical process. The volsellae of *Eufriesea* and *Epicharis* cannot represent the lower gonostyli, which are easily recognizable; these volsellae are clearly homologous to the volsella of Bombinae (Fig. 193) as recognized by Williams. There are not two distinct gonostyli in Bombinae, but the gonostylus often appears bilobed, with a mesal and an apical projection, which may represent the two gonostyli of some other bees. The volsella was correctly identified by some earlier authors, e.g., Boulangé (1924, as voselle) and Smith (1970) who considers the structure in Bombinae to be the cuspis of the primitive chelate volsella.

I here accept the terminology of Williams (1985); its relation to certain other terminologies of bombine genitalia is indicated in Table 5.

TABLE 5. Terminology of bombine male genitalia.

Snodgrass (1941)	Michener (1944)	Richards (1968)	Ito (1985)	Williams (1985)
Basal ring	Gonobase	Cardo	Gonobase	Gonobase
Lamina parameralis	Gonocoxite	Stipes	Gonocoxite	Gonocoxite
Paramere	Gonostylus	Squama	Squama	Gonostylus
Paramere	Gonostylus	Lacinia	Gonostylus	Volsella
Dorsal plate of penis	Spatha	Spatha	Spatha	Spatha
Sagitta	Penis valve	Sagitta	Penis valve	Penis valve

Fossil Bombinae

None of the fossils that have been attributed to Bombinae can be reliably placed there except probably the Oligocene and Miocene species placed in *Bombus* (Zeuner and Manning, 1976).

Taxonomic Account of Bombinae

As indicated above, I recognize two bombine genera, with the clear understanding that one of them, *Bombus,* is paraphyletic.

Key to the Genera of Bombinae

1. Female hind tibia with corbicula and rastellum; hind basitarsus with strong auricle; apex of metasoma of female not curved downward, S6 without carinae; hind tibia of male often bare and shiny; gonostylus and volsella usually hardened, volsella often not greatly exceeding gonostylus, usually variously angulate . . . . *Bombus*

—Female hind tibia convex, hairy on outer surface, so that corbicula is absent; rastellum absent; hind basitarsus without auricle; apex of metasoma of female curved downward, S6 with lateral carina; hind tibia of male with abundant short dark hair; gonostylus and volsella more membranous, volsella extending well beyond gonostylus, simple, flat, without angles or teeth . . . . *Psithyrus*

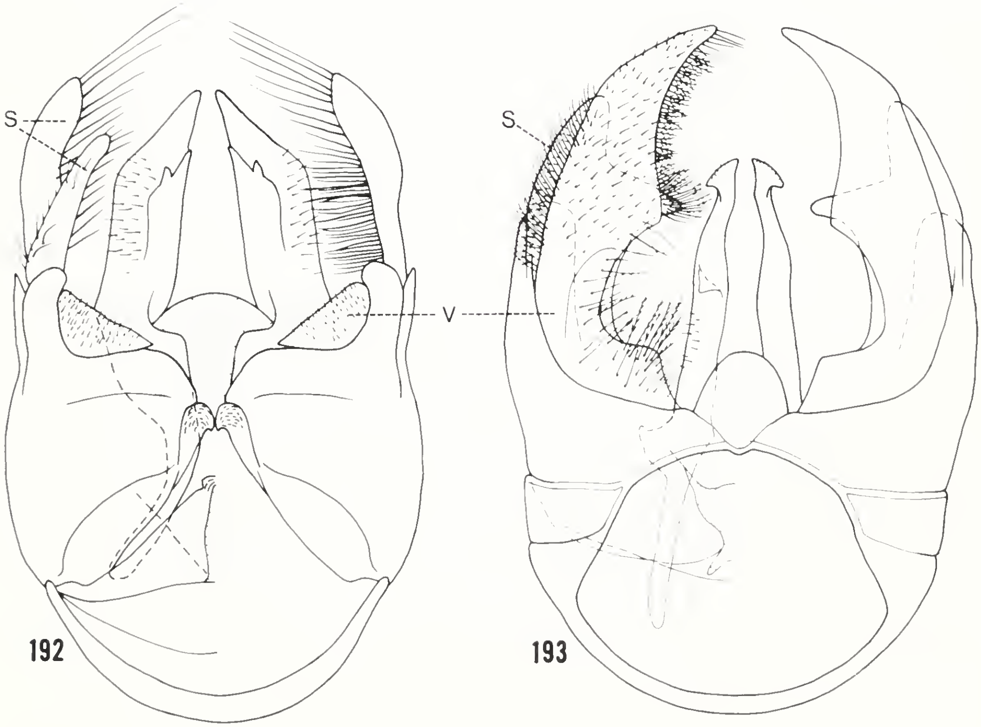
Genus *Bombus* Latreille

(Figs. 173, 177, 181, 189)

Bombus Latreille, 1902b: 385. Type species: *Apis terrestris* Linnaeus, 1758 (monobasic).

The enormous list of synonymous or subgeneric names has been given elsewhere (Richards, 1968; Ito, 1983, 1985; Williams, 1985). It seems unnecessary to repeat here these lists, type species, etc. The following are names proposed since Richards' paper:

Pyrobombus (Festivobombus) Tkalců, 1972: 27. Type species: *Bombus festivus* Smith, 1861, by original designation.



Figures 192, 193. Ventral views of male genitalia. 192, *Eufriesea pulchra* (Smith), lower gonostylus omitted on right side. 193, *Psithyrus variabilis* (Cresson). S = gonostylus, V = volsella.

Bombus (Digressobombus) Laverty, Plowright and Williams, 1984: 1051. Type species: *Megabombus digressus* Milliron, 1962, by original designation.

Bombus (Brachycephalibombus) Williams, 1985: 247. Type species: *Bombus brachycephalus* Handlirsch, 1888, by original designation.

Bombus (Dasybombus) Labougle and Ayala, 1985: 49. Type species: *Bombus macgregori* Labougle and Ayala, 1985, by original designation.

The scope of this genus is indicated above in the section on relationships among bombine genera and subgenera. Its distribution is that of the subfamily. It contains all the nonparasitic species of the subfamily, and in addition a very few parasitic species (Richards, 1973; Yarrow, 1970).

The named subgenera are less different from one another than are subgenera in most groups of bees. In fact, the homogeneity of the species in the genus is outstanding. These bees have been carefully studied to find group character states by diverse specialists (Richards, 1968; Sakagami and Ito, 1981; Ito, 1983, 1985; Williams, 1985). I do not consider recognition of the subgenera essential. The only key (except regional ones) is that of Richards (1968).

Further studies of behavioral characters like those of Hobbs (1964), Sakagami (1976) and Katayama (1989) may help in the delineation of more useful units. Such studies are needed for many more groups. Katayama (1989) recorded in admirable detail the often subgenus-specific behaviors in cell construction and egg laying, but the sampling of species was necessarily limited. Particularly, more data are needed on the earliest stages of colony development, when some of the most important characters are manifest.

As biochemical methods of determining genetic relatedness have evolved, various authors have used such methods to indicate relationships among species of *Bombus*. Such studies usually reinforce the groups or subgenera based on morphological differences, showing that most of these groups are useful monophyletic or paraphyletic units (Pamilo, Pekkarinen and Varvio, 1987).

Important regional treatments of species are by Franklin (1912, 1913), Krueger (1917), Burks (1951), Moure and Sakagami (1962), Thorp, Horning and Dunning (1983), Labougle (1990) and many others.

Genus *Psithyrus* Lepeletier

(Figs. 173, 193)

Psithyrus Lepeletier, 1832: 373. Type species: *Apis rupestris* Fabricius, 1793, by designation of Curtis, 1833: pl. 468.

As for *Bombus,* the subgeneric (really synonymous) names seem not worth listing as they have been listed by Ito (1983, 1985) and Williams (1985). The following is a recent addition to the list:

Citrinopsithyrus Thorp, in Thorp, Horning and Dunning, 1983: 50. Type species: *Apathus citrinus* Smith, 1854, by original designation. (Replacement for *Laboriopsithyrus,* the type species of which turns out to be an anthophorid bee of the genus *Habropoda.*)

As shown by both Ito and Williams, the subgenera in *Psithyrus* are even more similar than those of *Bombus;* I consider them synonyms of *Psithyrus.* They were treated in detail by Popov (1931).

As indicated earlier, *Psithyrus* consists of social parasites in the nests of *Bombus,* and lacks a worker caste.

Psithyrus is a holarctic genus found in the areas where *Bombus* is most abundant, but not ranging into the high arctic or into the mountains of southeast Asia and nearby islands, and in the New World, probably not ranging south of Guatemala.

Regional treatments of *Psithyrus* species are usually included in the regional accounts of *Bombus* cited above; see also Popov (1931).

ACKNOWLEDGMENTS

For the loan of type material important for this study, I am indebted to Frank Koch, Museum für Naturkunde der Humboldt Universität, Berlin. David W. Roubik of the Smithsonian Tropical Research Institute sent preparations of meliponine mouthparts as well as males of various species not otherwise available to me.

Michael Prentice and Howell V. Daly of the University of California sent me copies of their as yet incomplete manuscript (and illustrations) on the relationships of the subfamilies of Apidae. This work was of great value in modifying my ideas on this subject.

S. F. Sakagami of the University of Hokkaido, J. M. F. Camargo of the Faculdade de Filosofia, Ciencias e Letras, Universidade de São Paulo, and Ricardo Ayala of the Estacion Chamela, Universidad Nacional Autonoma de México, reviewed the section on Meliponinae, made many useful suggestions, and called my attention to characters than I had not previously recognized.

Byron Alexander of the University of Kansas reviewed the section on Apinae and made useful suggestions.

Robert L. Dressler of the University of Florida provided helpful information for my treatment of Euglossinae; Paul Williams of the Natural History Museum London reviewed the section on Bombinae and has been most helpful in providing unpublished materials on this subfamily, in patiently correcting my misinterpretation of homologies of bombine male genitalia, and in explaining his classification of this group.

Analyses using Hennig 86 were by James Pakaluk; those using PAUP were in collaboration with Stephen Reyes and Arturo Roig-Alsina; the use of PAUP 3.0 was through J. S. Ashe.

Joetta Weaver and Virginia Ashlock have done excellent secretarial and editing work, which I much appreciate.

This study is a product of National Science Foundation Grant BSR 87-16817.

APPENDIX: *TRIGONA GENALIS* FRIESE, A HITHERTO UNPLACED NEW GUINEA SPECIES

by Charles C. Michener and Shôichi F. Sakagami

In his seminal work on the classification of Old World stingless bees (Meliponinae), Moure (1961) did not include certain species from New Guinea. Two of these (*T. genalis* Friese and *atricornis* Smith) are the principal subject of this Appendix. Although these two species are deceptively similar, the first is so unusual that each of us independently described it in manuscript as a new subgenus of *Trigona,* here named *Papuatrigona* Michener and Sakagami. *T. atricornis* also is unusual within its group. In the body of the text it is included by CDM in the subgenus *Heterotrigona,* but as indicated there, SFS places it as an unusual species of *Platytrigona.* It does not agree with Moure's characterization of *Platytrigona,* the definition of which must be broadened to include *T. atricornis.*

Most of the descriptive material on the subgenus *Papuatrigona* is the work of CDM; the discussion and comparative material is by both of us, and the specific descriptions and illustrations (Figs. 194 to 219) are by SFS. The subgenus is incorporated into the body of this work; the Appendix provides added details including descriptive material comparable to that of Moure (1961).

A third species, *T. keyensis* Friese, described from the Kepulavan Kai but also found in New Guinea, is a member of the group of *Platytrigona* defined by Moure (1961), i.e., a relative of *T. planifrons* Smith and *flaviventris* Friese with the basal area of the propodeum hairy throughout. It differs from the species known to Moure by certain characters listed in the body of the text, under *Heterotrigona.* Although *T. keyensis* also has the reddish yellow body coloration like *T. genalis* and *atricornis,* it is not discussed further here except to give the following New Guinea collection data: Northeast New Guinea: Wagu/Black River, Western Highlands, Oct. 3, 1972 (Hohmann).

Papuatrigona Michener and Sakagami, new subgenus

Type species: *Trigona genalis* Friese, 1908.

To facilitate comparison with other taxa, the lettering system of Moure (1961) is utilized.

a) Integument rather shiny but head and thorax minutely punctured throughout, punctures separated by about a puncture width in most areas, clypeus and lower paraocular area not more coarsely punctured than rest of face. Integument largely testaceous, yellow marks absent.

b) Head as broad as thorax. Interocular distance greater than eye length; inner orbits converging upward in upper thirds, gently converging downward in lower third so that upper and lower interorbital distances are about equal (Table 6). Upper alveolar tangent well below middle of face; interalveolar distance scarcely greater than half alveolorbital distance. Frontal line a fine groove; frons gently convex.

c) Clypeus gently convex, slightly more than twice as broad as long; lateral parts of epistomal suture incurved below.

d) Mandible with two small denticles in upper fourth of apical margin, the lower one smaller than upper and almost evanescent. Labrum simple. Malar area as long as about 1.5 flagellar diameters; clypeocular distance two flagellar diameters. Gena rounded, almost as wide as eye in side view. Labial palpus with about five large, sinuous setae on first segment, six on second; second segment more than half length of first, less than three times as long as wide, extending slightly beyond base of third segment; segments three plus four about as long as two. Galea with numerous straight or weakly hooked setae.

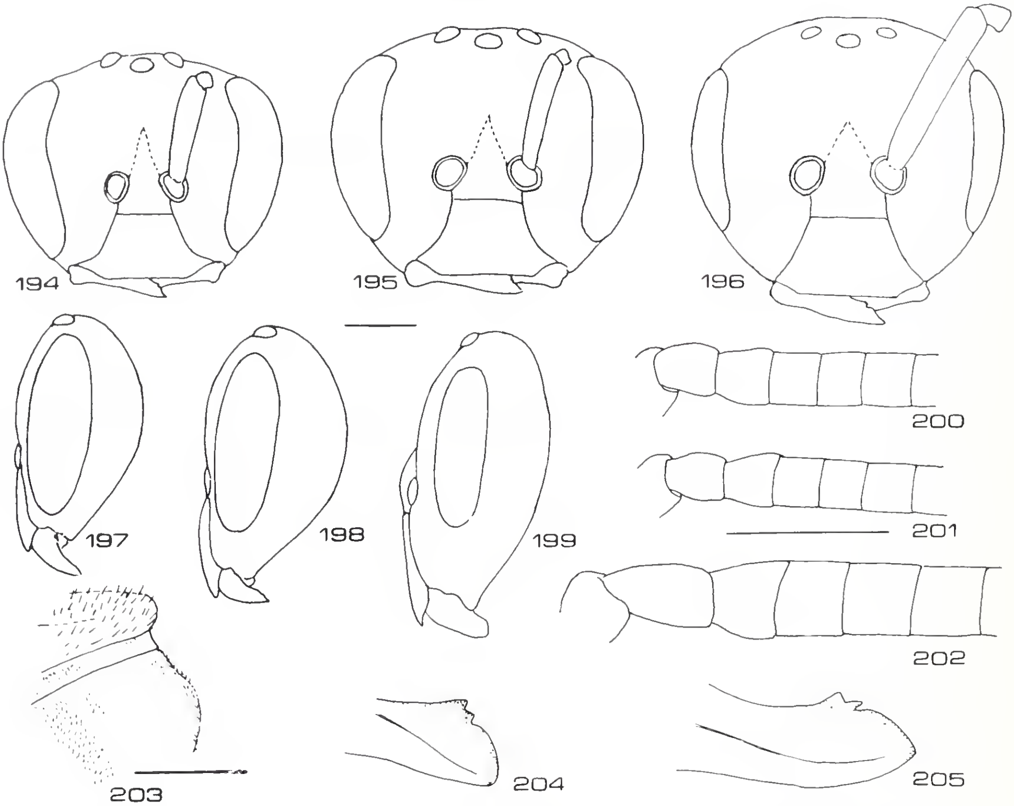
e) Vertex weakly procurved behind ocelli, not produced or ridged; ocelloccipital distance about equal to ocellar diameter and half of ocellocular distance, orbitoccipital distance and interocellar distance, which are about equal to one another.

f) Scape shorter than alveolocellar distance, not reaching median ocellus. Flagellar segments mostly slightly longer than broad, second slightly longer than first which is about as long as wide.

g) Notaulus and median line visible but not impressed; parapsidal line small. Scutellum short, rounded, slightly overhanging steeply sloping metanotum.

h) Forewing extending well beyond apex of metasoma; stigma moderate sized, prestigma shorter than width of stigma. Marginal cell over four times as long as broad, acute at base, only narrowly open at apex where Rs bends apicad almost parallel to wing margin. M-Cu bifurcation coincident with or rarely slightly basal or apical to m-cu; Cu strong; transverse cubitals almost unrecognizable so that submarginal cells are almost confluent; submarginal angle (between Rs and M at base of first submarginal cell) very slightly obtuse; M bent at first recurrent vein and continuing almost to wing margin. Hamuli seven per wing; jugal lobe one-third as long as vannal lobe, half as long as cubital cell.

i) Hind tibia more than 2.5 times as long as wide, posterior margin convex (almost straight in basal half), posterior distal angle obtuse and somewhat rounded; hair on posterior margin mostly simple and of moderate length but plumose hairs intermixed in distal fifth or sixth of margin; corbicula occupying distal half. Inner surface with keirotrichiate zone at widest point



Figures 194-205. *Trigona atricornis* Smith and *T. genalis* Friese. 194, Face of worker, *T. atricornis.* 195, 196, Faces of worker and queen, *T. genalis.* 197-199, Lateral views of heads of *T. atricornis* and *genalis,* workers, and *T. genalis,* queen. 200-202, Apex of scape, pedicel, and base of flagellum, *T. atricornis* worker and *T. genalis* worker and queen. 203, Posterolateral view of propodeum of worker of *T. genalis.* 204, 205, Mandibles of worker and queen, *T. genalis.* (Drawings by S. F. Sakagami.) Scale line = 0.5 mm; one applies to all heads, another to antennae and mandibles, and the third to the propodeum.

(about two-thirds of length of tibia from base) nearly twice as wide as shiny posterior marginal zone, not reaching apex of tibia, on distal part of tibia sloping gradually to marginal zone, the latter more depressed in middle of tibia so that there is slope at edge of keirotrichiate zone, this slope extending onto basal fourth of tibia. Penicillum and rastellum strong; bristles of rastellum robust, mostly blunt tipped.

j) Hind basitarsus about two times as long as wide, about two thirds as wide as tibia, inner surface uniformly setose.

k) Propodeum rather short, basal area steeply inclined, medially smooth, shiny, and glabrous but with small, isolated patch of hairs sublaterally, above. Metasoma narrower than thorax, not particularly elongate, first four terga smooth, shiny.

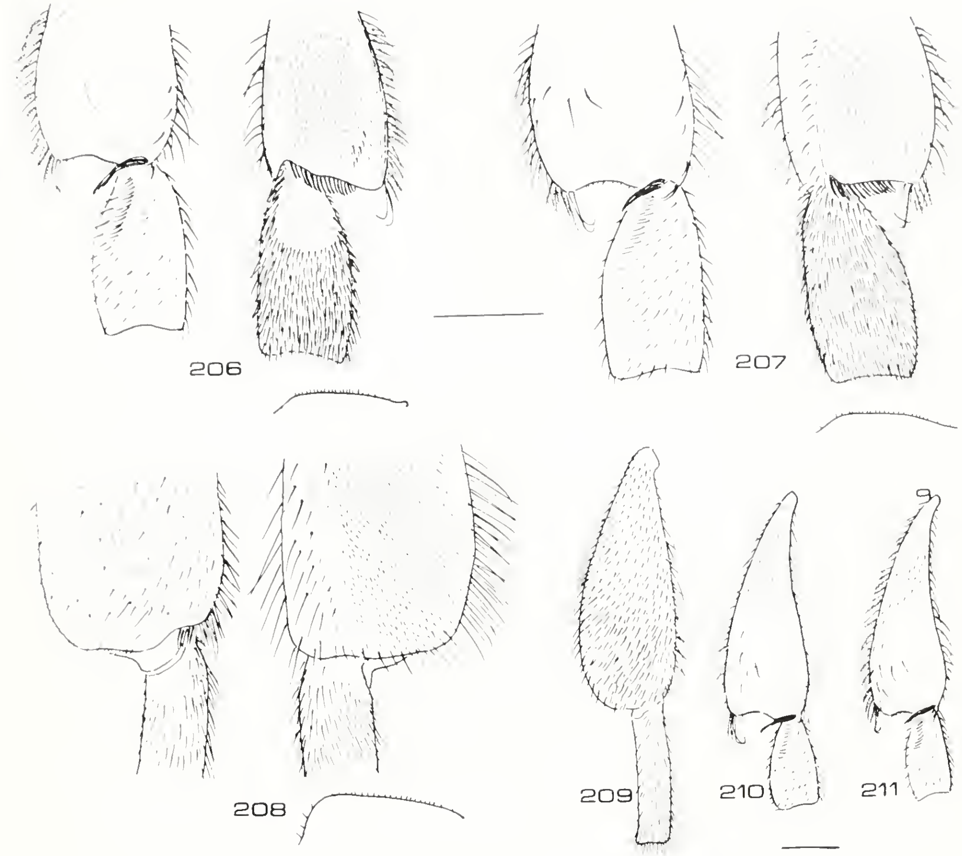
The name of this subgenus is based on Papua, a part of New Guinea, plus *Trigona.*

Trigona (Papuatrigona) genalis Friese

Because neither *T. genalis* nor *T. atricornis* has been fully described, we present a description, including metric information for both species (Table 6). The description is for *T. genalis,* with comparative information for *T. atricornis* added in parentheses; subgeneric characters listed above are mostly not repeated.

WORKER: *Color.* Pale honey brown, apical terga and apex of mandible darker. Pedicel except base, first flagellomere (often except apex), and rest of flagellum dusky, paler beneath. Middle and hind basitarsi and posterior margin of hind tibia often dusky or blackish (*T. atricornis* pale form nearly identical, dark form chestnut brown, mesoscutum dark brown, epistomal suture black; malar space, hind tibia and basitarsus, and apical terga sometimes blackish).

Pilosity. Occiput and vertex with moderately



Figures 206-211. *Trigona atricornis* Smith and *T. genalis* Friese. 206, 207, Outer views and inner views of basitarsus and apex of tibia and cross-section of inner tibial surface of workers of *T. atricornis* and *genalis*. 208, Same, queen of *T. genalis*. 209-211, Outer views of tibia and basitarsus, *T. genalis* queen and worker, *T. atricornis* worker. (Drawings by S. F. Sakagami.)

dense, pale brown bristles, up to about 200 μ long. (In. *T. atricornis* brown, up to about 150 μ long.) Ocellocular area with similar but shorter and sparser hairs. Short appressed pale brown hairs on upper face; more conspicuous on lower face, some plumose, silvery in some positions; on apex of clypeus some erect hairs. Mesoscutum with sparse, erect hairs, 50-75 μ long (in *atricornis* denser and 125-150 μ) and denser fine semiappressed hairs ± 25 μ long (in *atricornis* ± 50 μ). Scutellar bristles up to 175 μ long (in *atricornis* to 250 μ), rather sparse. Pleura with fine, dense hairs 25-30 μ and sparser, semierect, plumose white hairs over 50 μ long above to 300 μ below. Propodeum above broadly glabrous medially, laterally with small patch of sparse hairs (Fig. 203) (this patch also present in *T. atricornis* as well as in *T. moorei* Schwarz). T1 and T2 discs virtually glabrous with few fine pale brown hairs up to 20 μ long; T3 similar but apical fimbria more distinct and laterally with sparse pale brown bristles to 50 μ; T4 and 5 similar but hairs on discs slightly denser. T6 with pale brown bristles to 150 μ. Sterna with simple hairs, some slightly curved apically, to 175 μ.

Structure. See measurements, Table 6, and subgeneric description. Lateral ocellus less protuberant than in *T. atricornis* (Figs. 194, 195). Sculpture coarser and less shining than in *atricornis* (see subgeneric description). Basal vein usually meeting cu-v of forewing, rarely basal or distal to cu-v (in *atricornis*, usually basal). Hind tibial and basitarsal character states illustrated for *genalis* and *atricornis*.

QUEEN: Entirely honey brown, with caste differences from worker common to many if not all known stingless bees: longer head, smaller ocelli, longer malar space, smaller eye, longer supraorbital part of head, longer scape, wider mesosoma, larger metasoma (cf. Figs. 195, 196), less reduced sting (Figs. 218, 219), more reduced mouthparts (Figs. 214-217), and hind tibia and basitarsus (Figs. 207-210).

SPECIMENS EXAMINED: CDM examined three specimens kindly lent by Dr. F. Koch of the Museum für Naturkunde, Berlin. Two bear Friese's orange "Typus" labels. The other has the red label, "Type," and we designate it as the lectotype. It (as well as the other two specimens) is labeled "Manikion 16.28.II.03" [Feb. 16-28, 1903] "*Trigona genalis* 1904 Friese det. m" [mihi]. Manikion was evidently on the north coast of Indonesian New Guinea; one of the specimens, in addition to the labels listed above, is labeled "N. Guinea, Holland. 03", presumably with reference to Hollandia (= Kotabaru = Sukarnapura = Djajapura).

Other specimens are as follows (all workers except one queen from Marua River): *Papua New Guinea:* 50 from nest 9, Marua River near Kerema, 6 May 1959 (C.D. Michener). *Northeast New Guinea:* One, Dreikikir, Sepik District, 350 m altitude, June, 1969 (J.L. and M. Gressitt). *Indonesian New Guinea:* 22, Bodem, 10-17 July 1959 (T.C. Maa); 22, Bodem, 11 km SE of Oefberfaren, 100 m altitude, 7-17 July 1959 (T.C. Maa); one, Bodem, Sarmi area, 10 July 1959 (T.C. Maa); two, Waris, south of Hollandia, 450-500 m altitude, 1-2 August 1959 (T.C. Maa); Klamono Oil Fields, 14-18 August 1948 (M.A. Lieftinck). The last specimens are in the Leiden Museum. All others are in the Bishop Museum, Honolulu; duplicates are in the Snow Entomological Museum, Lawrence, Kansas; the Universidade Federal do Paraná, Curitiba; and the S. F. Sakagami Collection, Hokkaido University, Sapporo.

Fragmentary information on the nest on the Marua River is given by Michener (1961).

TABLE 6. Measurements of *Trigona genalis* (G) and *T. atricornis* (A) workers (n = 10 for each species).

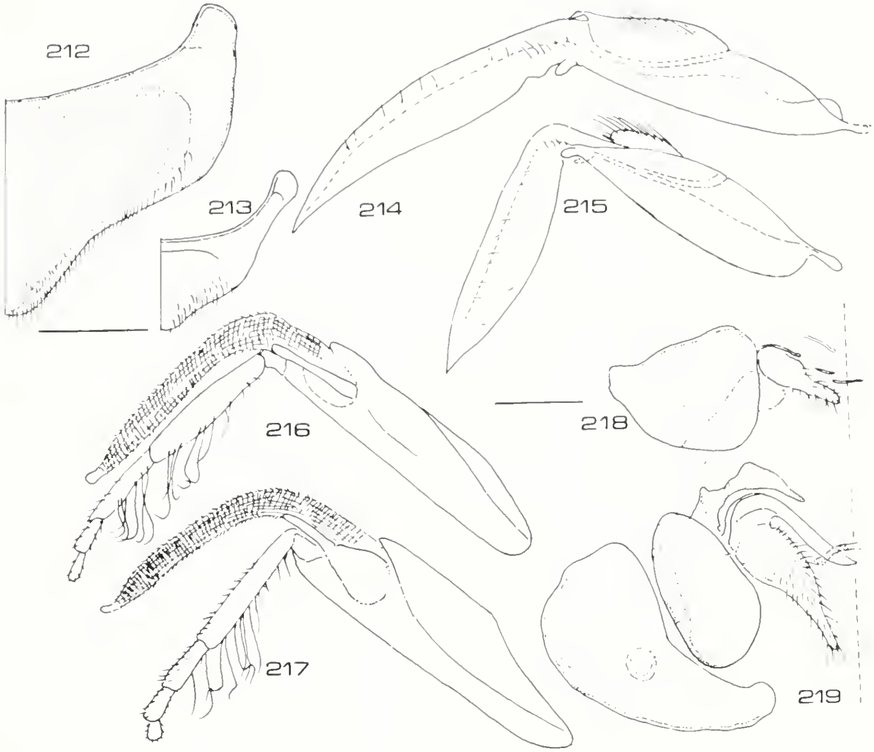
Feature	$\bar{X}$		SD		Range		Scale
	G	A	G	A	G	A	
Body length	51.50	46.70	3.01	3.74	45–56	40–55	10 = 1mm
Wing length with tegula	54.62	52.55	2.02	2.41	52–57	50–56	10 = 1mm
Mesoscutal width[a]	44.40	37.10	3.04	1.22	36–43	35–39	25 = 1mm
Mesoscutal length	31.21	29.45	0.83	1.31	29–32	27–31	25 = 1mm
Scutellar length	10.24	10.05	0.90	0.65	9–12	9–11	25 = 1mm
Metasomal width	44.40	41.36	3.04	2.10	37–48	38–45	25 = 1mm
Head width	54.27	50.18	1.69	1.64	53–56	47–52	25 = 1mm
Head length	43.60	41.05	1.20	1.01	41–45	40–43	25 = 1mm
Upper interorbital dist.	33.25	29.35	0.93	0.89	31–35	28–31	25 = 1mm
Max. interorbital dist.	37.65	34.60	1.23	1.18	35–39	32–36	25 = 1mm
Lower interorbital dist.	35.06	28.55	1.30	0.91	32–36	27–30	25 = 1mm
Eye length	31.65	32.25	0.87	1.01	30–33	31–34	25 = 1mm
Scape length	20.75	19.40	0.64	0.49	20–22	19–20	25 = 1mm
Interalveolar dist.[b]	7.70	7.25	0.46	0.40	7–8	7–8	40 = 1mm
Alveolorbital dist.	15.71	12.94	0.93	0.33	14–17	12–14	40 = 1mm
Interocellar dist.[c]	15.05	13.05	0.35	0.47	14–16	12–14	40 = 1mm
Ocellocular dist.[d]	12.60	10.77	0.66	0.58	11–13	10–12	40 = 1mm
Genal width	18.40	14.60	0.66	0.49	17–19	14–15	40 = 1mm
Malar length	9.10	4.45	0.66	0.52	8–10	3.5–5.0	40 = 1mm
Flagellomere 1 length	4.85	4.40	0.32	0.30	4.5–5.5	4–5	40 = 1mm
Flagellomere 2 length	5.25	4.80	0.28	0.24	5–6	4.5–5.0	40 = 1mm
Flagellomere 3 length	5.45	5.15	0.22	0.23	5.0–5.5	5.0–5.5	40 = 1mm
Flagellomere 2 width	6.05	5.43	0.35	0.11	5.5–7.0	5.0–5.5	40 = 1mm

[a] Greatest width in front of tegulae.

[b] Distance between antennal alveoli.

[c] Distance between posterior ocelli.

[d] Margin of lateral ocellus to nearest eye margin.



Figures 212-219. *Trigona genalis* Friese. 212, 213, S6 of queen and worker. 214, 215, Maxilla, worker and queen. 216, 217, Labium, worker and queen. 218, 219, Sting and associated structures, worker and queen. (Drawings by S. F. Sakagami.) Scale line for S6, 0.5 mm; for other structures, 0.25 mm.

LITERATURE CITED

Alexander, B. In press. A phylogenetic analysis of the genus *Apis*. Ann. Entomol. Soc. Amer.

Armbruster, L. 1938. Versteinerte Honigbienen aus dem obermiocänen Randecker Maar. Arch. Bienenkunde, 19: 1-48, 97-133.

Ashmead, W. H. 1899. Classification of the bees or the superfamily Apoidea. Trans. Amer. Entomol. Soc., 26: 49-100.

Ashmead, W. H. 1904. Remarks on honey bees. Proc. Entomol. Soc. Washington, 6: 120-122.

Baumgartner, D. L. and D. W. Roubik. 1989. Ecology of necrophilous and filth-gathering stingless bees (Apidae: Meliponinae) of Peru. Jour. Kansas Entomol. Soc., 62: 11-22.

Blanchard, E. 1849. Les Insectes, *in* G. Cuvier, Règne Animal, ed. 3, Paris, vol. 2.

Boulangé, H. 1924. Recherches sur l'Appareil Copulateur des Hyménoptères et Spécialement des Chalastogastres. Thèses Fac. Sci. Nancy, 1-444.

Brooks, R. W. and C. D. Michener. 1988. The Apidae of Madagascar and nests of *Liotrigona*. Sociobiology, 14: 299-323.

Brothers, D. J. 1976. Modifications of the metapostnotum and origin of the 'propodeal triangle' in Hymenoptera Aculeata. Syst. Entomol., 1: 177-182.

Burks, B. D. 1951. Tribe Bombini, pp. 1247-1255, *in* Muesebeck et al., Hymenoptera of America north of Mexico. Synoptic catalog. Agriculture Monogr., Washington, D. C.

Camargo, J. M. F. 1974. Notas sobre a morfologia e biologia de *Plebeia (Schwarziana) quadripunctata quadripunctata*. Studia Entomol. 17: 433-470.

Camargo, J. M. F. 1980. O grupo *Partamona (Partamona) testacea* (Klug): suas espécies, distribuição e diferenciação geográfica. Acta Amazonica (Suplemento), 10(4): 1-175.

Camargo, J. M. F. 1984. Notas sobre o gênero *Oxytrigona*. Bol. Mus. Paraense Emilio Goeldi, Zoologia 1: 115-124.

Camargo, J. M. F., W. E. Kerr, and C. R. Lopes. 1967. Morfologia externa de *Melipona (Melipona) marginata* Lepeletier. Papéis Avulsos, Zool., S. Paulo, 20: 229-258, pls. A-P plus one unlettered.

Camargo, J. M. F. and J. S. Moure. 1983.

Trichotrigona, um novo gênero de Meliponinae (Hymenoptera, Apidae), do Rio Negro, Amazonas, Brasil. Acta Amazonica, 13: 421-429.

Camargo, J. M. F. and J. S. Moure. 1988. Notas sobre os Meliponinae (Hymenoptera, Apidae) colecionados por Filippo Silvestri na bacia do Rio da Prata. Rev. Bras. Entomol., 32: 293-314.

Camargo, J. M. F., J. S. Moure, and D. W. Roubik. 1988. *Melipona yucatanica* new species (Hymenoptera: Apidae: Meliponinae); stingless bee dispersal across the Caribbean arc and post-Eocene vicariance. Pan-Pac. Entomol., 64: 147-157.

Cockerell, T. D. A. 1907. A fossil honey-bee. Entomologist, 40: 227-229.

Cockerell, T. D. A. 1908. Notes on the bee-genus *Exaerete*. Psyche, 15: 41-42.

Cockerell, T. D. A. 1917a. New social bees. Psyche, 24: 119-128.

Cockerell, T. D. A. 1917b. Some euglossine bees. Canadian Entomol., 49: 144-146.

Cockerell, T. D. A. 1922. Bees in the collection of the United States National Museum.—4. Proc. U.S. Natl. Mus., 60: 1-20.

Cockerell, T. D. A. 1934. Some African meliponine bees. Rev. Zool. Bot. Afr., 26: 46-62.

Cruz-Landim, C. da. 1967. Estudo comparativo de algumas glândulas das abelhas (Hymenoptera, Apoidea) e respectivas implicações evolutivas. Arq. Zool. S. Paulo, 15: 177-290.

Cruz-Landim, C. da. 1973. Tipos de glândulas salivares do tórax presentes em abelhas. Studia Entomologica, 16: 209-213.

Cruz-Landim, C. da, J. F. Höfling, and M. C. Zaniboni. 1972. Estudo comparativo do cordão nervoso ventral em abelhas, pp. 113-134, *in* Homenagem à Warwick E. Kerr. Rio Claro, Brazil.

Cruz-Landim, C. da and L. Rodrigues. 1967. Comparative anatomy and histology of the alimentary canal of adult Apinae. Jour. Apic. Res., 6: 17-28.

Cumber, R. A. 1949. Larval specific characters and instars of English Bombidae. Proc. Royal Entomol. Soc. London, (A)24: 14 19.

Curtis, J. 1833. British Entomology. Vol. 10, pls. 434-481.

Dalla Torre, K. W. (C. G.) v. 1880. Unsere Hummel- *(Bombus)* Arten. Die Naturhistoriker, 2, 30 and 40-41.

Danforth, B. N. 1989. The evolution of hymenopteran wings: the importance of size. Jour. Zool. London, 218: 247-276.

Dodson, C. H., R. L. Dressler, H. C. Hills, R. M. Adams, and N. H. Williams. 1969. Biologically active compounds in orchid fragrances. Science, 164: 1243-1249.

Dressler, R. L. 1978. An infrageneric classification of *Euglossa*, with notes on some features of special taxonomic importance. Rev. Biol. Trop., 26: 187-198.

Dressler, R. L. 1979. *Eulaema bombiformis*, *E. meriana*, and Mullerian mimicry in related species. Biotropica, 22: 144-151.

Dressler, R. L. 1982a. Biology of the orchid bees (Euglossini). Annu. Rev. Ecol. Syst., 13: 373-394.

Dressler, R. L. 1982b. New species of *Euglossa*. III. The *bursigera* species group. Rev. Biol. Trop., 30: 131-140.

Fisher, R. M. 1987. Queen-worker conflict and social parasitism in bumble bees. Anim. Behaviour, 35: 1026-1036.

Fletcher, D. J. C. and R. M. Crewe. 1981. Nest structure and thermoregulation in the stingless bee *Trigona (Plebeina) denoiti* Vachal. Jour. Entomol. Soc. South. Africa, 44: 183-196.

Franklin, H. J. 1912, 1913. The Bombinae of the New World. Trans. Amer. Entomol. Soc., 38: 177-486; 39: 73-200, pls. 1-22.

Free, J. B. and C. G. Butler. 1959. Bumblebees. Collins, London, xiv + 208 pp.

Friese, H. 1899. Monographie des Bienengattung *Euglossa*. Termész. Fuzetek, 22: 124-157.

Friese, H. 1903. Neue Meliponiden II. Zeitschr. Syst. Hymen. Dipt., 3: 359-361.

Friese, H. 1923. Die europäischen Bienen. Gruyter, Berlin and Leipzig, xvii + 456 pp., 33 pls.

Gistel, J. N. F. X. 1848. Naturgeschichte des Tierreichs für höhere Schulen, Stuttgart.

Haas, A. 1976. Paarungsverhalten und Nestbau der alpinen Hummelart *Bombus mendax*. Entomol. Germ., 3: 248-259.

Hobbs, G. A. 1964. Phylogeny of bumblebees based on brood-rearing behavior. Canad. Entomol., 96: 115-116.

Hoffmannsegg, G. J. C. von. 1817. Entomologische Bemerkungen bei Gelegenheit der Abhandlungen über amereikanische Insekten . . . . Widem Mag., 1: 8-56.

Horn, E. 1975. Mechanisms of gravity processing by leg and abdominal gravity receptors in bees. Jour. Insect Physiol., 21: 273-279.

Ihering, H. von. 1912. Zur Biologie der brasilianischen Meliponiden. Zeitsch. Wissenschaftliche Insektenbiol., 8(1): 1-5, (2): 43-46.

Illiger, J. C. W. 1806. William Kirby's Familien der Bienenartigen Insekten mit Zusätzen, Nachweisungen und Bemerkungen. Magazin für Insectenkunde, 5: 28-175.

Ito, M. 1983, 1985. Supraspecific classification of bumblebees based on the characters of the male genitalia. (1983), Zool. Sect., Inst. Low Temp. Sci., Hokkaido Univ., Sapporo, 247 pp. and (1985), Contrib. Inst. Low Temp. Sci., Hokkaido Univ., (B)20: 1-143.

Ito, M. and S. F. Sakagami. 1985. Possible synapomorphies of the parasitic bumblebees *(Psithyrus)* with some nonparasitic bumblebees *(Bombus)*. Sociobiology, 10: 105-119.

Jander, R. and U. Jander. 1970. Über die Phylogenie der Geotaxis innerhalb der Bienen. Zeitschr. vergl. Physiol., 66: 355-368.

Jurine, L. 1807. Nouvelle méthode de classer les Hyménoptères et les Diptères. Geneva, 320 + 4 pp., 14 pls.

Katayama, E. 1989. Comparative studies on the egg-laying habits of some Japanese species of bumblebees. Entomol. Soc. Japan Occasional Publ., No. 2: 1-161.

Kelner-Pillault, S. 1970. Une mélipone (s. l.) de l'ambre Balte. Ann. Soc. Ent. France (N. S.), 6: 437-441.

Kerr, W. E. 1969. Some aspects of the evolution of social bees. Evol. Biol., 3: 119-175.

Kerr, W. E. 1972. Numbers of chromosomes in some species of bees. Jour. Kansas Entomol. Soc., 45: 111-122.

Kerr, W. E. 1987. Sex determination in bees. XVII. Systems of caste determination in the Apinae, Meliponinae and Bombinae and their phylogenetical implications. Rev. Brasil. Genetica, 10: 685-694.

Kerr, W. E. and H. Esch. 1965. Comunicação entre as abelhas sociais brasileiras e sua contribuição para o entendimento da sua evolução. Ciencias e Cultura, 17: 529-538.

Kerr, W. E. and E. de Lello. 1962. Sting glands in stingless bees—a vestigial character. Jour. N.Y. Entomol. Soc., 70: 190-214.

Kerr, W. E. and V. Maule. 1964. Geographic distribution of stingless bees and its implications. Jour. N.Y. Entomol. Soc., 72: 2-17.

Kerr, W. E., J. F. Pisani, and D. Aily. 1967. Aplicação de princípios modernos à sistemática do gênero *Melipona* Illiger, com a divisão em dois subgêneros. Papéis Avulsos, Zool., S. Paulo, 20: 135-145.

Kimsey, L. S. 1979a. An illustrated key to the genus *Exaerete* with descriptions of male genitalia and biology. Jour. Kansas Entomol. Soc., 52: 735-746.

Kimsey, L. S. 1979b. Synonymy of the genus *Euplusia* Moure under *Eufriesea* Cockerell. Pan-Pac. Entomol., 55: 126.

Kimsey, L. S. 1982. Systematics of bees of the genus *Eufriesea*. Univ. Calif. Publ. Entomol., 95: i-ix + 1-125.

Kimsey, L. S. 1984. A re-evaluation of the phylogenetic relationships in the Apidae. Syst. Entomol., 9: 435-441.

Kimsey, L. S. 1987. Generic relationships within the Euglossini. Syst. Entomol., 12: 63-72.

Kimsey, L. S. and R. L. Dressler. 1986. Synonymic species list of Euglossini. Pan-Pac. Entomol., 62: 229-236.

Krueger, E. 1917. Zur Systematik der Mitteleuropaischen Hummeln. Entomol. Mitt., 6: 55-66.

Krueger, E. 1920. Beitrage zur Systematik und Morphologie der Mittel-europaischen Hummeln. Zool. Jb., Abt. Syst., 42: 289-464, tab. 3-7, 8 figs.

Labougle, J. M. 1990. *Bombus* of México and Central America (Hymenoptera, Apidae). Univ. Kansas Sci. Bull., 54: 35-73.

Labougle, J. M. and R. Ayala. 1985. A new subgenus and species of *Bombus* (Hymenoptera: Apidae) from Guerrero, Mexico. Folia Entomol. Mexicana, no. 66: 47-55.

Latreille, P. A. 1802a. Histoire Naturelle des Fourmis. Paris, pp. 1-445, pls. I-XII.

Latreille, P. A. 1802b. Histoire Naturelle Générale et Particulière des Crustacés et des Insectes. Paris, vol. 3, 467 pp.

Latreille, P. A. 1810. Considérations Générales sur l'Ordre Naturel des Animaux Composant les Classes des Crustacés, des Arachnides et des Insectes . . . . Paris, 467 pp.

Laverty, T. M., R. C. Plowright, and P. H. Williams. 1984. *Digressobombus,* a new subgenus with description of the male of *Bombus digressus* (Milliron). Canadian Entomol., 116: 1051-1056.

Lepeletier, A. L. M. 1832. Observations sur l'ouvrage intitulé: Bombi Scandinaviae monographice tractato, et., a Gustav Dahlbom. Ann. Soc. Entomol. France, 1: 366-382.

Lepeletier, A. L. M. 1841. Histoire Naturelle des Insectes. Hyménoptères. Paris, vol. 2: 1-680.

Lepeletier, A. L. M. and A. Serville. 1825, *in* M. Diderot et al., Encyclopédie Méthodique, Histoire Naturelle, Insectes, Paris, vol. 10.

Linnaeus, C. 1758. Systema Naturae, ed. 10, 824 pp., Stockholm.

Maa, T. 1953. An inquiry into the systematics of the tribus Apidini or honeybees. Treubia, 21: 525-640.

Maddison, W. and D. Maddison. 1987. MacClade version 2.1. An Interactive, Graphic Program for Analyzing Phylogenies and Studying Character Evolution. Mus. Comp. Zool., Cambridge, Mass., 55 pp.

McEvoy, M. V. and B. A. Underwood. 1988. The drone and species status of the Himalayan honey bee, *Apis laboriosa*. Jour. Kansas Entomol. Soc., 61: 246-249.

Mello, M. L. S. and W. E. Kerr. 1984. Histochemistry of salivary gland and Malpighian tubule secretions contributing to the cocoon in *Plebeia droryana* and *Scaptotrigona postica*. Zool. Anz., 213: 177-189.

Michener, C. D. 1944. Comparative external morphology, phylogeny, and a classification of the bees. Bull. Amer. Mus. Nat. Hist., 82: 151-326.

Michener, C. D. 1953. Comparative morphological and systematic studies of bee larvae with a key to the families of hymenopterous larvae. Univ. Kansas Sci. Bull., 35: 987-1102.

Michener, C. D. 1961. Observations on the nests and behavior of *Trigona* in Australia and New Guinea. Amer. Mus. Novitates, no. 2026: 1-46.

Michener, C. D. 1965. A classification of the bees of the Australian and South Pacific regions. Bull. Amer. Mus. Nat. Hist., 130: 1 362, pl. 1-15.

Michener, C. D. 1974. The Social Behavior of the Bees. Harvard Univ. Press, Cambridge, Mass., xii + 404 pp.

Michener, C. D. 1981. Classification of the bee family Melittidae with a review of species of Meganomiinae. Contr. Amer. Entomol. Inst., 18: iii + 1-135.

Michener, C. D. 1982. A new interpretation of fossil social bees from the Dominican Republic. Sociobiology, 7: 37-45.

Michener, C. D. 1985. A comparative study of the mentum and lorum of bees. Jour. Kansas Entomol. Soc., 57: 705-714.

Michener, C. D. 1990. Phylogeny and biogeography of the Meliponinae. Proc. 11th Internat. Congr. Internat. Union Stud. Soc. Ins., Bangalore. In press.

Michener, C. D. and A. Fraser. 1978. A comparative anatomical study of mandibular structure in bees. Univ. Kansas Sci. Bull., 51: 463-482.

Michener, C. D. and D. A. Grimaldi. 1988a. A *Trigona* from Late Cretaceous amber of New Jersey. Amer. Mus. Novitates, no. 2917: 1-10.

Michener, C. D. and D. A. Grimaldi. 1988b. The oldest fossil bee: apoid history, evolutionary stasis, and antiquity of social behavior. Proc. Natl. Acad. Sci. USA, 85: 6424-6426.

Michener, C. D. and D. W. Roubik. In press. Observations on the labium of meliponine bees, *in* S. Yamane and T. Inoue, eds., Evolution of Insect Society—Festschrift of Professor S. F. Sakagami. Sisakusha, Tokyo.

Michener, C. D., M. L. Winston, and R. Jander. 1978. Pollen manipulation and related activities and structures in bees of the family Apidae. Univ. Kansas Sci. Bull., 51: 575-601.

Milliron, H. E. 1961. Revised classification of the bumblebees—a synopsis. Jour. Kansas Entomol. Soc., 34: 49-61.

Morse, D. H. 1982. Behavior and ecology of bumblebees, pp. 245-322, *in* H. R. Hermann, ed., Social Insects, vol. III. Academic Press, New York.

Moure, J. S. 1942. Abelhas de Salobra. Papéis Avulsos, Zool., S. Paulo, 2(21): 291-321.

Moure, J. S. 1943. Abelhas de Batatais. Arq. Mus. Paranaense, 3: 145-203, pl. XI.

Moure, J. S. 1944a. Abejas del Perú. Bol. Mus. Hist. Nat. "Javier Prado," 8(28-29): 67-75.

Moure, J. S. 1944b. Apoidea da coleção do Conde Amadeu A. Barbiellini. Rev. Entomol. [Rio], 15: 1-18.

Moure, J. S. 1946a. Contribuição para o conhecimento dos Meliponinae. Rev. de Entomol. [Rio], 17: 437-443.

Moure, J. S. 1946b. Melíponas do Brasil. Chacaras e Quintais, 74: 609-612.

Moure, J. S. 1950a. Contribuição para o conhecimento das espécies Brasileiras de *Hypotrigona* Cockerell. Dusenia, 1: 241-260.

Moure, J. S. 1950b. Contribuição para o conhecimento do gênero *Eulaema* Lepeletier. Dusenia, 1: 181-200.

Moure, J. S. 1951. Notas sôbre Meliponinae. Dusenia, 2: 25-70.

Moure, J. S. 1953. *Nogueirapis,* no grupo de Trigonini da região neotropical. Ciencia e Cultura, 5: 247-249.

Moure, J. S. 1960. Notes on the types of the Neotropical bees described by Fabricius. Studia Entomol., 3: 97-160.

Moure, J. S. 1961. A preliminary supra-specific classification of the Old World meliponine bees. Studia Entomol., 4: 181-242.

Moure, J. S. 1963a. Sôbre a identidade dos Meliponinos descritos por Spinola em 1853. Anais Acad. Bras. Cienc., 35: 257-269.

Moure, J. S. 1963b. Uma nova espécie de "*Trigona (Frieseomelitta)*" do norte do Distrito Tupi. Rev. Brasil. Biol., 23: 39-43.

Moure, J. S. 1967. A check-list of the known euglossine bees, *in* Atlas do Simpósio sôbre a Biota Amazônica, 5(Zool.): 395-415.

Moure, J. S. 1971. Descrição de uma nova espécie de *Tetragona* do Brasil Central. Bol. Univ. Fed. Paraná, Zool., 4: 47-50.

Moure, J. S. 1975. Notas sobre as espécies de *Melipona* descritas por Lepeletier em 1836. Rev. Brasil. Biol., 35: 615-623.

Moure, J. S. and J. M. F. Camargo. 1978. A fossil stingless bee from Copal. Jour. Kansas Entomol. Soc., 51: 560-566.

Moure, J. S. and J. M. F. Camargo. 1982. *Partamona (Nogueirapis) minor,* nova espécie de Meliponinae (Hymenoptera: Apidae) do Amazonas e notas sobre *Plebeia variicolor* (Ducke). Bol. Mus. Paraense Emilio Goeldi, n. ser.: Zool., No. 120: 1-10.

Moure, J. S., J. M. F. Camargo, and M. V. B. Garcia. 1988. Uma nova espécie de *Leurotrigona.* Bol. Mus. Paraense Emilio Goeldi (Zool.), 4: 145-154.

Moure, J. S. and W. E. Kerr. 1950. Sugestões para a modificação da sistemática do gênero *Melipona.* Dusenia, 1: 105-129, pls. II-III.

Moure, J. S. and S. F. Sakagami. 1962. As mamangabas sociais do Brasil (*Bombus* Latr.). Studia Entomol., 5: 65-194.

Obrecht, E. and A. Scholl. 1981. Enzymelektrophoretische Untersuchungen zur Analyse der Verwandtschaftsgrade zwischen Hummel- und Schmarotzerhummelarten. Apidologie, 12: 257-268.

Oliveira, B. L. 1965. Observações em larvas e pupas de *Plebeia (Plebeia) droryana* (Friese, 1900). Papéis Avulsos, Zool., S. Paulo, 18: 29-38.

Pamilo, P., A. Pekkarinen, and S.-L. Varvio. 1987. Clustering of bumblebee subgenera based on interspecific genetic relationships. Ann. Zool. Fennici, 24: 19-27.

Perty, J. A. M. 1833. Dilectus Animalium Articulatorium . . . Brasiliam, fasc. 3, pp. 125-224, pls. 25-40, München.

Plant, J. D. and H. F. Paulus. 1987. Comparative morphology of the postmentum of bees (Hymenoptera: Apoidea) with special remarks on the evolution of the lorum. Z. Zool. Syst. Evolut.-forsch., 25: 81-103.

Popov, V. B. 1931. Zur Kenntnis der paläarktischen Schmarotzerhummeln (*Psithyrus* Lep.). Eos, 7: 131-209.

Rafinesque, C. S. 1814. Principes Fondamentaux de Somiologie . . . , Palermo, 52 pp.

Rafinesque, C. S. 1815. Analyse de la Nature ou Tableau de l'Univers et des Corps Organisés. Palermo, 224 pp.

Richards, K. W. 1973. Biology of *Bombus polaris*

Curtis and *B. hyperboreus* Schonherr at Lake Hazen, Northwest Territories. Quaestiones Entomol., 9: 115-157.

Richards, O. W. 1927. The specific characters of the British bumblebees. Trans. Roy. Entomol. Soc. London, 75: 233-268.

Richards, O. W. 1968. The subgeneric division of the genus *Bombus* Latreille. Bull. British Mus. Nat. Hist. (Ent.), 22: 211-276.

Ritcher, P. O. 1933. The external morphology of larval Bremidae and key to certain species. Ann. Entomol. Soc. Amer., 26: 53-63.

Roberts, R. B. and C. H. Dodson. 1967. Nesting biology of two communal bees, *Euglossa imperialis* and *Euglossa ignita* including description of larvae. Ann. Entomol. Soc. Amer., 60: 1007-1014.

Robertson, C. 1903. Synopsis of Megachilidae and Bombinae. Trans. Amer. Entomol. Soc., 29: 163-178.

Roubik, D. W. 1979. Nest and colony characteristics of stingless bees from French Guiana. Jour. Kansas Entomol. Soc., 52: 443-470.

Roubik, D. W. 1980. New species of *Trigona* and cleptobiotic *Lestrimelitta* from French Guiana. Rev. Biol. Trop., 28: 263-269.

Roubik, D. W. 1982. Obligate necrophagy in a social bee. Science, 217: 1059-1060.

Roubik, D. W. 1983. Nest and colony characteristics of stingless bees from Panama. Jour. Kansas Entomol. Soc., 56: 327-355.

Roubik, D. W. 1989. Ecology and Natural History of Tropical Bees, x + 514 pp. Cambridge Univ. Press, Cambridge, U.K.

Roubik, D. W., S. F. Sakagami, and I. Kudo. 1985. A note on distribution and nesting of the Himalayan honey bee *Apis laboriosa* Smith. Jour. Kansas Entomol. Soc., 58: 746-749.

Roubik, D. W., B. H. Smith, and R. G. Carlson. 1987. Formic acid in caustic cephalic secretions of stingless bee, *Oxytrigona*. Jour. Chem. Ecol., 13: 1079-1086.

Ruttner, F. 1987. Biogeography and Taxonomy of Honeybees. xii + 284 pp., Springer, Berlin.

Sakagami, S. F. 1963. On the male of *Trigona (Tetragona) fimbriata* Smith. Jour. N.Y. Entomol. Soc., 71: 39-44.

Sakagami, S. F. 1966. Comparative ethology of Apidae. Japanese Soc. Syst. Zool., circular 35: 1-6 (in Japanese).

Sakagami, S. F. 1971. Ethosoziologischer Vergleich zwischen Honigbienen und stachellosen Bienen. Zeitschr. Tierpsychol., 28: 337-350.

Sakagami, S. F. 1975. Stingless bees (excl. *Tetragonula*) from the continental southeast Asia in the collection of the Bernice P. Bishop Museum, Honolulu. Jour. Fac. Sci. Hokkaido Univ., ser. VI, Zool., 20: 49-76.

Sakagami, S. F. 1976. Specific differences in the bionomic characters of bumblebees. A comparative review. Jour. Fac. Sci. Hokkaido Univ., Ser. VI, Zool., 20: 390-447.

Sakagami, S. F. 1978. *Tetragonula* stingless bees of the continental Asia and Sri Lanka. Jour. Fac. Sci. Hokkaido Univ., ser. VI, Zool., 21: 165-247.

Sakagami, S. F. 1982. Stingless bees, pp. 361-423, *in* H. R. Hermann, ed., Social Insects, vol. III. Academic Press, New York.

Sakagami, S. F. and T. Inoue. 1985. Taxonomic notes on three bicolorous *Tetragonula* stingless bees in Southeast Asia. Kontyu, 53: 174-189.

Sakagami, S. F. and T. Inoue. 1987. Stingless bees of the genus *Trigona* (subgenus *Trigonella*) with notes on the reduction of the spatha in male genitalia of the subgenus *Tetragonula*. Kontyu, 55: 610-627.

Sakagami, S. F. and T. Inoue. 1989. Stingless bees of the genus *Trigona* (subgen. *Geniotrigona*) (Hymenoptera, Apidae), with description of *T. (G.) incisa* sp. nov. from Sulawesi. Japanese Jour. Entomol., 57: 605-620.

Sakagami, S. F., T. Inoue, and S. Salmah. 1985. Key to the stingless bee species found or expected from Sumatra, pp. 37-43, *in* Ohgushi, R.-i., ed., Evolutionary Ecology of Insects in Humid Tropics, especially in Central Sumatra. Sumatra Nature Study (Entomology), Kanazawa Univ., Japan.

Sakagami, S. F., T. Inoue, S. Yamane, and S. Salmah. 1983. Nesting habits of Sumatran stingless bees, pp. 38-45, *in* Ohgushi, R.-i., ed., Ecological Study on Social Insects in Central Sumatra with Special Reference to Wasps and Bees. Sumatra Nature Study (Entomology), Kanazawa Univ., Japan.

Sakagami, S. F. and M. Ito. 1981. Specific and subgeneric variations in tibial corbiculation of male bumblebees (Hymenoptera: Apidae), an apparently functionless character. Entomol. Scand. Suppl., 15: 365-376.

Sakagami, S. F. and S. G. Khoo. 1987. Taxonomic status of the Malesian stingless bee *Trigona reepeni*, with discovery of *Trigona pagdeni* from northern Malaya. Kontyu, 55: 207-214.

Sakagami, S. F., T. Matsumura, and K. Ito. 1980. *Apis laboriosa* in Himalaya. The little known worlds largest honeybee. Insecta Matsumurana (NS), 19: 47-77.

Sakagami, S. F. and C. D. Michener. 1987. Tribes of Xylocopinae and origin of the Apidae. Ann. Entomol. Soc. Amer., 80: 439-450.

Sakagami, S. F., and S. Yamane. 1987. Oviposition behavior and related notes of the Taiwanese stingless bee *Trigona (Lepidotrigona) ventralis hoozana*. Jour. Ethol., 5: 17-27.

Sakagami, S. F., S. Yamane, and G. G. Hambali. 1983. Nests of some Southeast Asian stingless bees. Bull. Fac. Educ., Ibaraki Univ. (Nat. Sci.), no. 32: 1-21.

Sakagami, S. F., S. Yamane, and T. Inoue. 1983. Intranidal behaviors of *Trigona (Tetragonula) laeviceps* and *T. (Trigonella) moorei*, pp. 46-51, *in* Ohgushi, R.-i., ed., Ecological Study on Social Insects in Central Sumatra with Special Reference to Wasps and Bees. Sumatra Nature Study (Entomology), Kanazawa Univ., Japan.

Sandhouse, G. A. 1943. The type species of the genera and subgenera of bees. Proc. U.S. Nat. Mus., 92: 519-619.

Schönitzer, K. 1986. Comparative morphology of the antenna cleaner in bees. Z. Zool. Syst. Evolut.-forsch., 24: 35-51.

Schwarz, H. F. 1932. The genus *Melipona*. The type genus of the Meliponidae or stingless bees. Bull. Amer. Mus. Nat. Hist., 63: 231-460, pls. I-X.

Schwarz, H. F. 1934. The social bees (Meliponidae) of Barro Colorado Island, Canal Zone. Amer. Mus. Novitates, no. 731: 1-23.

Schwarz, H. F. 1937. Results of the Oxford University Sarawak (Borneo) expedition: Bornean stingless bees of the genus *Trigona*. Bull. Amer. Mus. Nat. Hist., 73: 281-328, pls. II-VII.

Schwarz, H. F. 1938. The stingless bees (Meliponidae) of British Guiana and some related forms. Bull. Amer. Mus. Nat. Hist., 74: 437-508, pls. LII-LXII.

Schwarz, H. F. 1939a. The Indo-Malayan species of *Trigona*. Bull. Amer. Mus. Nat. Hist., 76: 83-141.

Schwarz, H. F. 1939b. A substitute name for *Patera* Schwarz. Entomol. News, 50: 23.

Schwarz, H. F. 1940. Additional species and records of stingless bees (Meliponidae) from British Guiana based on specimens collected by the Terry-Holden Expedition. Amer. Mus. Novitates, no. 1078: 1-12.

Schwarz, H. F. 1948. Stingless bees (Meliponidae) of the Western Hemisphere. Bull. Amer. Mus. Nat. Hist., 90: i-xviii + 1-546.

Schwarz, H. F. 1949. The stingless bees (Meliponidae) of Mexico. Anales Inst. Biol. Mexico, 20: 357-370.

Skorikov, A. S. 1922. Les bourdons de la faune palé-arctique, Partie I. Biologie générale. Bull. Sta. Rég. Prot. Plantes, Petrograd, 4: 1-160, 11 figs., 17 maps (in Russian).

Smith, E. L. 1970. Evolutionary morphology of the external insect genitalia. 2. Hymenoptera, Ann. Entomol. Soc. Amer. 63: 1-27.

Snodgrass, R. E. 1941. The male genitalia of Hymenoptera. Smithsonian Misc. Coll., 99(14): 1-86, pls. 1-33.

Stephen, W. P. and T. Koontz. 1973. The larvae of the Bombini. I and II. Melanderia, 13: 1-12, 13-29.

Swofford, D. L. 1985. PAUP, phylogenetic analysis using parsimony, version 2.4, computer program. Illinois Natural History Survey, Champaign, Illinois.

Taschenberg, E. 1883. Die Gattungen der Bienen (Anthophila). Berliner Entomol. Zeitschr., 27: 37-100.

Thorp, R. W., D. S. Horning, Jr., and L. L. Dunning. 1983. Bumble bees and cuckoo bumble bees of California. Bull. Calif. Insect Survey, 23: i-viii + 1-79.

Tingek, S., M. Mardan, T. E. Rinderer, N. Koeniger, and G. Koeniger. 1988. Rediscovery of *Apis vechti* (Maa, 1953): the Saban honey bee. Apidologie, 19: 97-102.

Tkalců, B. 1966. *Megabombus (Fervidobombus) abditus* sp. n. aus äquatorial-Afrika. Casopis Moravského v Brne, 51: 271-274.

Tkalců, B. 1972. Arguments contre l'interprétation traditionelle de la phylogénie des abeilles, premiere partie. Bull. Soc. Entomol. Mulhouse, 1972 (Avr.-mai-juin): 17-28.

Torchio, P. F. and D. M. Torchio. 1975. Larvae of the Apidae (Hymenoptera, Apoidea). Part I. Apini, *Apis*. Research Rept. 20, Agric. Expt. Sta., Utah State Univ., pp. 1-36.

Tosi, A. 1896. Di nuovo genere di Apiaria fossile nell'ambra di Sicilia *(Meliponorytes succini,—M. sicula)*. Rev. Ital. Paleont., 2: 352-356.

Wille, A. 1956. Comparative studies of the thoracic musculature of bees. Univ. Kansas Sci. Bull., 38: 439-499.

Wille, A. 1958. A comparative study of the dorsal vessels of bees. Ann. Entomol. Soc. Amer., 51: 538-546.

Wille, A. 1959a. Comparative morphology and classification of the stingless bees. Ph.D. Thesis, Univ. of Kansas, Lawrence, 217 pp.

Wille, A. 1959b. A new fossil stingless bee (Meliponini) from the amber of Chiapas, Mexico. Jour. Paleontol., 33: 849-852, pl. 119.

Wille, A. 1960. A new species of stingless bee (Meliponini) from Bolivia. Rev. Biol. Trop., 8: 219-223.

Wille, A. 1961. Evolutionary trends in the ventral nerve cord of the stingless bees. Rev. Biol. Trop., 9: 117-129.

Wille, A. 1962. A new species of stingless bee (Meliponini) from Costa Rica. Rev. Biol. Trop., 10: 177-181.

Wille, A. 1963. Phylogenetic significance of an unusual African stingless bee, *Meliponula bocandei* (Spinola). Rev. Biol. Trop., 11: 25-45.

Wille, A. 1964. Notes on a primitive stingless bee *Trigona (Nogueirapis) mirandula*. Rev. Biol. Trop., 12: 117-151.

Wille, A. 1971. Notes on the morphology of the musculature of the salivary syringe and neck region of bees. Rev. Biol. Trop., 18: 33-51.

Wille, A. 1977. A general review of the fossil stingless bees. Rev. Biol. Trop., 25: 43-46.

Wille, A. 1979a. A comparative study of the pollen press and nearby structures in the bees of the family Apidae. Rev. Biol. Trop., 27: 217-221.

Wille, A. 1979b. Phylogeny and relationships among the genera and subgenera of the stingless bees (Meliponinae) of the world. Rev. Biol. Trop., 27: 241-277.

Wille, A. 1983. Biology of the stingless bees. Annu. Rev. Entomol., 28: 41-64.

Wille, A. and L. Chandler. 1964. A new stingless bee from the Tertiary amber of the Dominican Republic. Rev. Biol. Trop., 12: 187-195.

Wille, A. and C. D. Michener. 1973. The nest architecture of stingless bees with special reference to those of Costa Rica. Rev. Biol. Trop., 21(supl. 1): 1-278.

Williams, P. H. 1985. A preliminary cladistic investigation of relationships among the bumble bees. Syst. Entomol., 10: 239-255.

Winston, M. L. 1979. The proboscis of the long-tongued bees: a comparative study. Univ. Kansas Sci. Bull., 51: 631-667.

Winston, M. L. 1987. The biology of the honeybee. Harvard Univ. Press, Cambridge, Mass., x + 281 pp.

Winston, M. L. and C. D. Michener. 1977. Dual origin of highly social behavior among bees. Proc. Natl. Acad. Sci. USA, 74: 1135-1137.

Wu, Y.-r. and B. Kuang. 1986. A study of the genus *Micrapis*. Zool. Research, 7: 99-102 (in Chinese).

Wu, Y.-r. and B. Kuang. 1987. Two species of small honeybee—a study of the genus *Micrapis*. Bee World, 68: 153-155.

Yarrow, I. H. H. 1970. Is *Bombus inexpectatus* (Tkalců) a workerless obligate parasite? Ins. Soc., 17: 95-112.

Zeuner, F. E. and F. J. Manning. 1976. A monograph on fossil bees. Bull. British Mus. Nat. Hist. (Geol.), 27: 149-268, 4 pl.

ANNOUNCEMENT

The *University of Kansas Science Bulletin* (continuation of the *Kansas University Quarterly*) is an outlet for scholarly scientific investigations carried out at the University of Kansas or by University faculty and students. Since its inception, volumes of the *Bulletin* have been variously issued as single bound volumes, as two or three multi-paper parts or as series of individual papers. Issuance is at irregular intervals, with each volume prior to volume 50 approximately 1000 pages in length. Effective with volume 50, page size has been enlarged, reducing the length of each volume to about 750 pages.

The supply of all volumes of the *Kansas University Quarterly* is now exhausted. However, most volumes of the *University of Kansas Science Bulletin* are still available and are offered, in exchange for similar publications, to learned societies, colleges and universities and other institutions, or may be purchased at $30.00 per volume. Where some of these volumes were issued in parts, individual parts are priced at the rate of 3 cents per page. Current policy, initiated with volume 46, is to issue individual papers as published. Such separata may be purchased individually at the rate of 4.5 cents per page, with a minimum charge of $1.50 per separate. Subscriptions for forthcoming volumes may be entered at the rate of $30.00 per volume. All communications regarding exchanges, sales and subscriptions should be addressed to the Exchange Librarian, University of Kansas Libraries, Lawrence, Kansas 66045.

Reprints of individual papers for personal use by investigators are available for most recent and many older issues of the *Bulletin*. Such requests should be directed to the author.

The International Standard Serial Number of this publication is US ISSN 0022-8850.