

BIOLOGY OF THE STINGLESS BEES

Alvaro Wille

Museum of Entomology, University of Costa Rica, Costa Rica

The stingless bees belong to the Meliponinae, one of three subfamilies of the family Apidae (49). In general, stingless bees are easily distinguished from other bees by the following three characters: 1. Reduction and weakness of the wing venation. 2. Presence of the penicillum, a brush of long, stiff setae located anteriorly on the outer apical margin of the hind tibia. (This structure is unique to the Meliponinae; it is absent or much reduced and soft, however, in the subgenus *Hypotrigona* and the parasitic genera *Les-trimelitta* and *Cleptotrigona*.) 3. Reduction of the sting.

In recent years (46) the subfamily Meliponinae has been divided into the tribes Meliponini and Trigonini; this was due to the discovery of a series of apparently valid taxonomic characters (24), primarily relating to external morphology but reinforced by characters concerned with general biology, nest architecture, the dorsal vessel, the ventral nerve cord, and the alimentary canal. The differences between Trigonini and Meliponini are enumerated elsewhere (46); see also Table 1. The last three anatomical characters, which are striking and important differences between the tribes, are explained in the following paragraphs.

In the tribe Meliponini and one African species of Trigonini, *Meliponula bocandei* (42), the thoracic portion of the dorsal vessel forms an arch between the longitudinal muscles of the thorax. The entrance between the longitudinal muscles is close to the anterior ventral border of the second phragma, and the ascending portion of the vessel lies along its midline. There is a horizontal portion, which runs along and in the middle of the longitudinal dorsal muscles of the mesothorax. The descending portion

slopes gently and is not well differentiated from the horizontal one. In all the other genera and subgenera of Trigonini the thoracic portion of the dorsal vessel is straight, running along and dorsal to the gut, and never between the longitudinal thoracic muscles. This arrangement is referred to as Type 1, and the one that makes a small loop in the thorax as Type 2. A logical question is why *Meliponula*, which belongs to the Trigonini, differs from other members of its tribe in the position of the dorsal vessel. The answer is suggested by a comparative study of the dorsal vessel in other bees (39, 46), which shows that most bees with the Type 1 vessel are slender and weak fliers. On the other hand, bees with a dorsal vessel of Type 2 tend to be more robust and larger, at least relative to the members of the same family or tribe. Among the Trigonini, *Meliponula bocandei* is the only species similar to the Meliponini (by convergence) in being large and robust and in having relatively short wings and dense pubescence. This suggests a correlation between apparently more effective flight mechanisms (therefore stronger thoracic muscles) and dorsal vessels of Type 2. One possible basis for this correlation is that bees with stronger flight mechanisms may need a more effective blood irrigation or heat exchange mechanism in the thorax.

It is only in the tribe Meliponini that the abdominal ganglia have migrated two to four segments forward from their usual segmental positions (40). As a result, ganglion 3, which in primitive bees is located in the second abdominal segment (first metasomal segment), has moved well inside the thorax. Among other bees ganglion 3 has a thoracic position only in the subfamily Bombinae.

Finally, the digestive tract in the tribe Meliponini is relatively longer than that of Trigonini (4). In *Trigona* the shortening is due to the reduced length of the hind gut, whereas in *Lestrimelitta* the mid gut is also shortened.

For many years there have been major differences of opinion among taxonomists as to the number of genera and subgenera of stingless bees. Up to 1934 Cockerell (2) recognized 2 genera and 7 subgenera. In 1948 Schwarz (35) recognized 3 genera and 18 subgenera. Moure (24), in 1951, recognized 16 genera and 20 subgenera. The same author (25) in 1961 recognized 32 genera and 26 subgenera. In view of these discrepancies, I proposed a new classification for the subfamily Meliponinae, in which I recognized 8 genera and 15 subgenera (46).

Taxonomists who specialize in any given group may tend to use many genera or subgenera. Other biologists, on the contrary, may tend to recognize few taxonomic groups for the sake of simplicity. In dealing with the stingless bees I have followed an intermediate course between the so-called splitters and lumpers. In my opinion, among the Meliponinae there are important advantages in retaining all members of the *Trigona* line in the

single genus *Trigona*, except for *Lestrimelitta* and the African groups, instead of breaking the subfamily into some 32 genera as has been done. All these bees have essentially similar biologies, and they are similar in appearance and basic morphology, in spite of the differences that exist—differences that can be employed as subgeneric or group characters. In the broad sense used here, *Trigona* has a meaning to entomologists and biologists that it would lose if it were dismembered. I know of no comparable advantages that would result from division of the genus.

I have omitted from this review consideration of papers on foraging and ecology; these are to be the subject of a review by others.

Area of Origin and Dispersion

Relevant evidence suggests that the Meliponinae had their center of origin and dispersion in Africa (46). Three major and significant factors indicate that Africa could be the center of origin of the stingless bees. 1. The wide acceptance of plate tectonics and continental drift. The stingless bees probably arose at about the Cretaceous-Tertiary boundary. 2. The recent discovery of European fossils from the early Tertiary (late Eocene), described by Kelner-Pillault (14), shows that Meliponinae were not restricted to America at that time. The finding of stingless bees in Europe in the late Eocene suggests that they originated in Africa, since South America was then completely isolated after separation from Africa, until the Pliocene-Pleistocene, when a connecting bridge between North and South America was established. 3. The primitiveness of several African Meliponinae [Africa is the only area where some of the stingless bees have a better developed sting than the majority of the group; for other primitive characters see (46).]

Since the stingless bees apparently originated in and dispersed from Africa, the presence of a stingless bee in Europe in the early Tertiary could indicate that the Meliponinae migrated first to the North, possibly during the Eocene, when tropical moist climates had wide development. Since Europe was presumably still in contact with North America, these bees probably soon migrated to that continent, as well as into Asia.

Although Africa has at present comparatively few species (about 35) of Meliponinae, it is possible that during the early Tertiary the number of species was higher. The number may have been greatly reduced by late Tertiary aridity. The Kalahari desert covered Angola and almost reached the Congo River, and the Sahara was also enlarged considerably. Obviously, the Meliponinae found environmental conditions to be more favorable in South and Central America than in Africa. Spreading over a whole continent with highly varied environments, the stingless bees speciated profusely. Different lines became adapted to diverse ecological roles. In short, they underwent, an adaptive radiation on a grand scale. This is supported by the

presence in the Neotropical region of a greater diversity of groups than in other areas, a far greater number of species (200–300), and the most highly specialized group, *Melipona*.

Phylogeny of the Stingless Bees

Some of the earliest Meliponinae were very likely minute *Plebeia*-like bees that were already undergoing reduction of the sting apparatus and the veins of the fore wing and that had the primitive characters listed elsewhere (46). Two groups can be regarded as the most primitive, *Axestotrigona* and *Meliplebeia*; three as primitive, *Hypotrigona*, *Plebeia*, and *Nogueirapis*, four as specialized, *Lestrimelitta*, *Trigona*, *Nannotrigona*, and *Dactylurina*; and one as very specialized, *Melipona*. The others can be considered intermediate. In order to evaluate the evolutionary levels of specialization among the different groups of Meliponinae, relative values of characters can be established. Diagram 1 is a phylogenetic tree indicating the levels of specialization among the different groups; numbers in parentheses indicate derived characters; the thickest lines of the tree refer to African origin.

It seems reasonable to separate a tribe Meliponini, containing only *Melipona*, from a paraphyletic tribe Trigonini. The major biological differences between these tribes, but not the morphological differences, are listed in Table 1.

Parallel Evolution

The African genera and several groups of stingless bees from other continents appear to exhibit parallel evolution. For example, the resemblance between *Dactylurina* (African) and *Tetragona* (Neotropical and Oriental region) is the result of parallelism. There is also parallelism between the robber genera *Lestrimelitta* (Neotropical) and *Cleptotrigona* (African) and between *Melipona* (Neotropical) and *Meliponula* (African). To some extent there is also parallelism between *Partamona* (Neotropical) and *Axestotrigona* (African), and between *Plebeia* (Neotropical and Australian) and *Meliplebeia* (African). [*Plebeiella* and *Apotrigona* are included in *Meliplebeia*, Wille (46).] In each of these cases the members of the group acquired similar characteristics independently, although stemming from related ancestral stocks.

The Nest Architecture

The nest is mainly constructed with cerumen, which is a mixture of wax with resins and gums (usually called propolis) collected from plants and brought to the nest. Other materials used are mud, vertebrate feces, plant fibers, and chewed leaf material. There are three major types of nest architecture, with many variations among them. For a detailed description of the nest architecture see Wille & Michener (47).

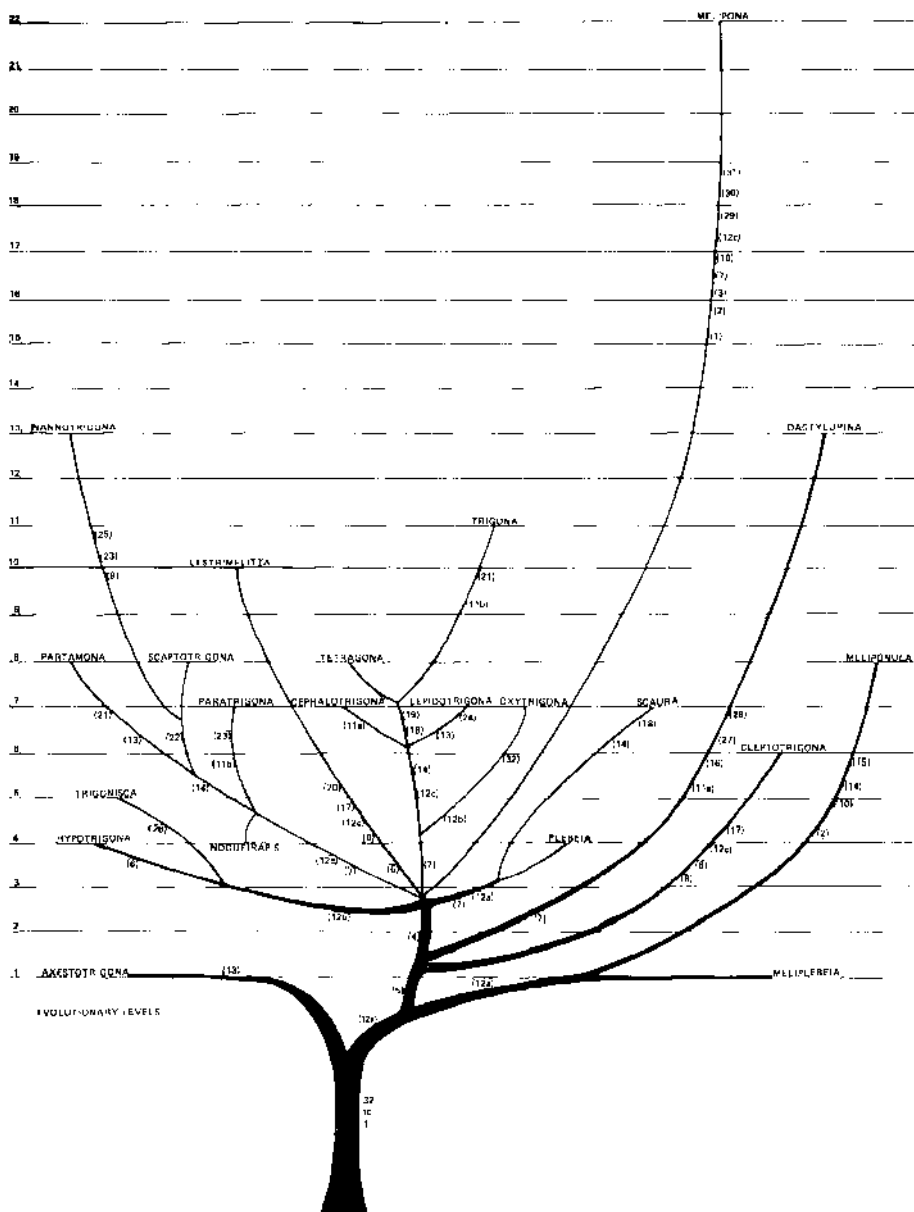


Table 1 Tribal differences in nest structure and reproductive biology

Characters	Trigonini	Meliponini
Nature of the nest entrance and batumen plates	Usually made of cerumen	Usually made of mud; nest entrance often with radial striations on outside surface
Royal cells	Nest with specialized queen cells, larger than those of workers and males	Nest without specialized queen cells
Location of queen cells	Usually found near periphery of combs or in the outer parts of cell clusters	Intermingled in the combs with cells of workers and males
Size of virgin queens	Larger than workers; thorax notably wider	Smaller than workers; thorax not notably wider
Ovaries of the newly emerged queens	Well developed	Underdeveloped
Rate of production of queen	Relatively rarely produced	Frequently produced
Determination of workers and queens	Presumably trophically determined	Supposedly trophically and genetically determined

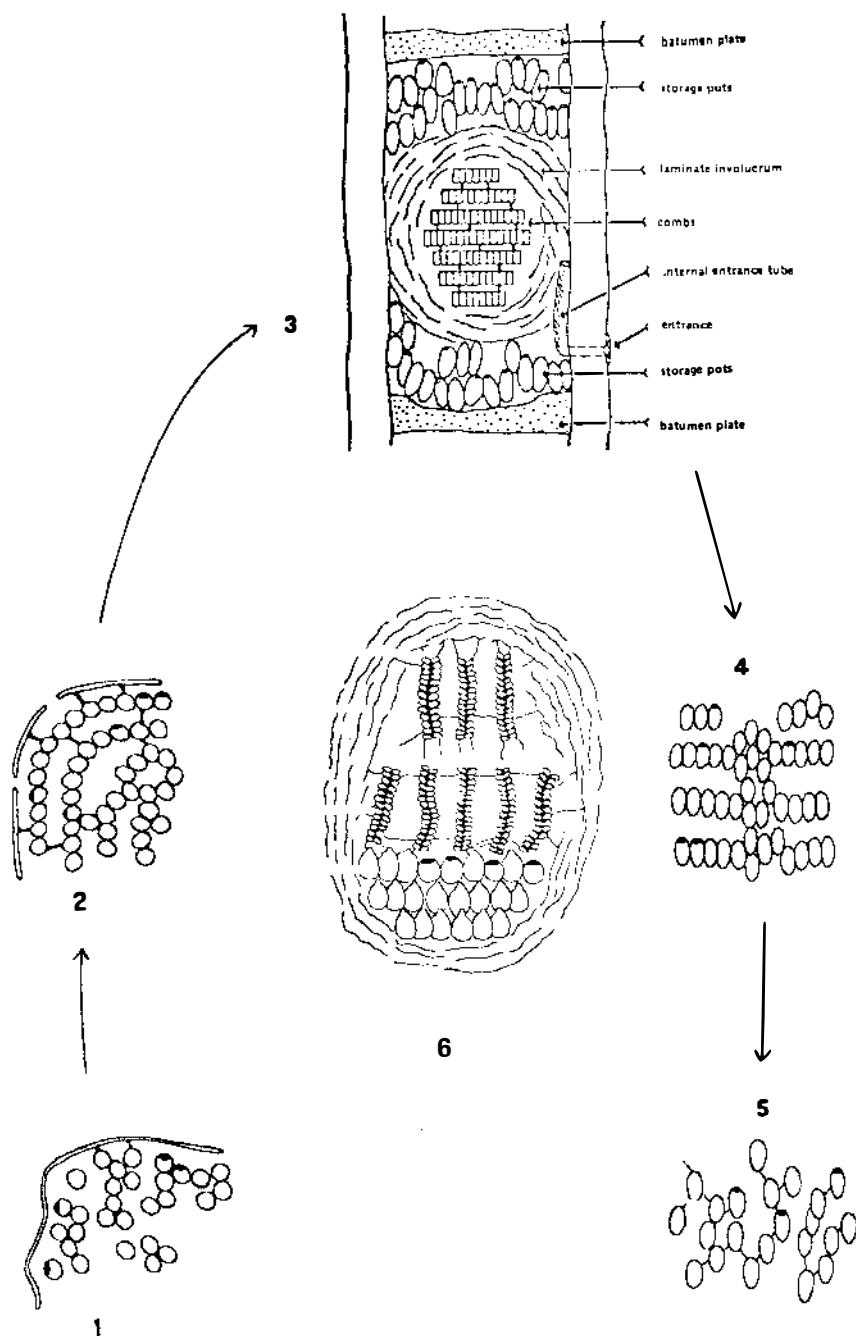
NESTS WITH HORIZONTAL COMBS The most common type of nest is that found in tree cavities, with several horizontal combs (cells or cocoons) in the center of the nest (Figure 3). The group of combs is the main feature of the brood chamber, which is commonly surrounded by a sheath of soft or rarely hard cerumen; this sheath is called the involucrum. Many nests have laminate involucri, consisting of several layers with spaces between them. The storage pots are containers of honey or pollen and are usually found above and below the involucrum. The hollow is often limited by special plates called batumen, usually made of hard cerumen, mud, or a mixture of these. The walls of the nest cavity are frequently lined with a thin layer of resin or cerumen (lining batumen). The entrance of the nest may be a simple hole. It is, however, often extended from the nest as an external entrance tube; its length varies from a few millimeters to a meter, the latter observed in one nest of *Trigona* (*Scaptotrigona*) *pectoralis*. Frequently this tube continues inside the nest cavity along the inner wall of the entrance cavity. Inside the nest there are pillars and connectives, which support all other structures within the batumen. Pillars are vertical and connectives are more or less horizontal. The cells of the combs are in contact with one another; sometimes, however, they are connected by small pillars or connectives of soft cerumen. Pillars connect the combs with one another and with surrounding structures. In a few species, like *Trigona*

(*Oxytrigona*) *tataira*, the combs form a spiral (Figure 7). The spiral pattern is not necessarily a specific character; it may be present in some nests of a species but not in others. In some species, like *Trigona* (*Trigona*) *fulviventris*, the combs are rather irregular. Major nest variations of the type with horizontal combs are the exposed or aerial nests and the subterranean nests.

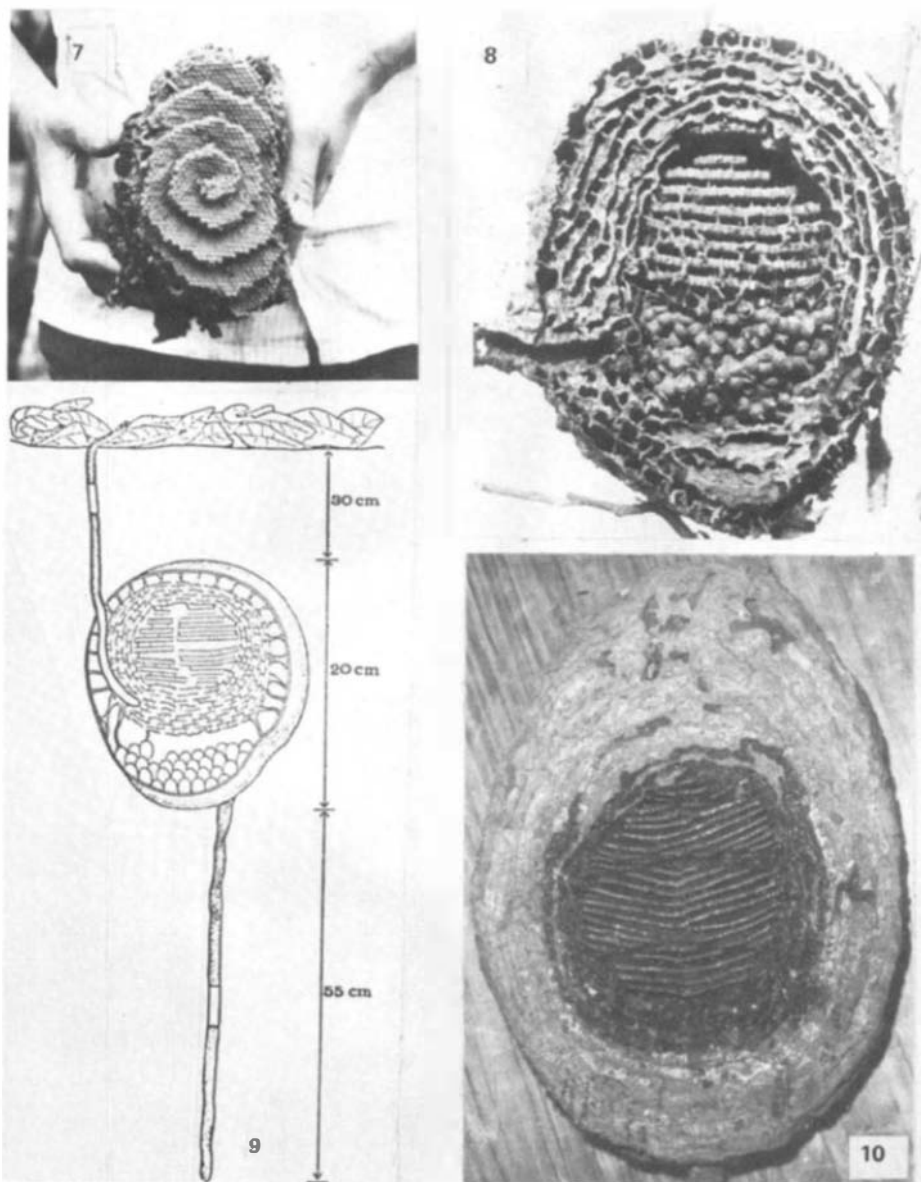
EXPOSED NESTS Exposed or partially exposed nests are entirely or partially surrounded by bare batumen (Figures 8 and 10). In the fully exposed nests the layers of batumen are numerous and mostly strong and are firm and sometimes brittle. The most typical ones are those of certain species of the subgenus *Trigona*. In these nests deposits of bees' feces or earth and vegetable fibers are found between the batumen layers; in some species the spaces between batumen layers are largely filled in some parts of the nest. When the deposition appears to start on one side of the nest it is called a scutellum (*Trigona spinipes*). In other cases (Figure 10) all the spaces between layers are completely filled in old nests, while young nests lack such material. In one nest of *Trigona corvina* found in Costa Rica, spaces between batumen layers were completely filled; according to the local people it had been in place for more than ten years. This nest measured 85 cm long by 55 cm wide and weighed 162 pounds (Figure 10). It had to be opened with a hatchet and is so unusual that it is on exhibit in the Entomological Museum of the University of Costa Rica. However, the outer layer of all these nests is commonly thin and delicate or brittle. The outer layer of nests of *Trigona nigerrima* is made of vertebrate feces; this is one of the few species with exposed nests and also with a well-formed entrance tube (Figure 8). Some forms with small exposed nests do not have laminate batumen, like *Trigona* (*Paratrigona*) *peltata peltata* and *Trigona* (*Paratrigona*) *guatemalensis*. The batumen of these nests is of only one layer.

Partially exposed nests, like those of most species of the subgenus *Partamona*, have laminated batumen. Sometimes, parts of nests of *Partamona* have only a single batumen layer, but at least where the nest is exposed the batumen is laminate.

SUBTERRANEAN NESTS Species that build their nests in underground cavities are relatively few among the stingless bees (Figure 9). It is significant that the greatest number known to be subterranean belong to the most primitive groups, e.g. four species of the genus *Meliplebeia*, two of *Plebeia*, and one of *Nogueirapis*. The specialized ground-nesting species include two forms of *Melipona*, one species of the subgenus *Trigona*, three species of *Tetragona*, two species of *Paratrigona*, and one species of *Cephalotrigona*. *Melipona schenki picandensis* and *Trigona* (*Trigona*) *fulviventris* nest preferentially among the roots at bases of trees. *Trigona* (*Tetragona*) *mombuca*



Figures 1-6 (1) Diagram of a primitive cluster type of nest, as in *Trigona (Plebeia) australis*; (2) Intermediate cluster type, as in *Trigona (Plebeia) cincta*; (3) Diagram of a meliponine nest with the structures labelled; (4) Irregular horizontal comb-type, as in *Trigona (Plebeia) schrottkyi*; (5) Specialized cluster-type, as in *Trigona (Plebeia) tica*; (6) Diagram of the nest of the African *Dactylurina staudingeri* showing vertical combs.



Figures 7-10 (7) Spiral combs of *Trigona (Oxytrigona) tataira*; (8) The nest of *Trigona (Trigona) nigerrima*, opened; the thin, brittle outer batumen layer is gone; (9) Diagram of a nest of *Trigona (Nogueirapis) mirandula* showing drainage duct; (10) Opened nest of *Trigona (Trigona) corvina* showing spaces between batumen layers completely filled. This large nest weighed 162 pounds.

and *Trigona* (*Paratrigona*) *lineata nuda* apparently take advantage of nests of *Atta*, and because of this their nests are generally more than one meter deep and frequently in hard soil. On the other hand, *Trigona* (*Paratrigona*) *subnuda* (= *petropolis*) makes its nest in soft soil and usually at less than one meter in depth.

Although species that build nests underground are relatively few, it is even less common to find these bees nesting in the soil of the tropical rain forest. This habitat is characterized by a prevailing high humidity and lack of light penetration to the lower strata of the forest, with the ground covered by a thick layer of organic debris. To date, the only bees known to me to nest in these conditions are *Trigona* (*Nogueirapis*) *mirandula* and *Trigona* (*Tetragona*) *buchwaldi* (43). Nests in the soil often have drainage ducts (Figure 9) or openings at the bottom of the nest. Such tubes are believed to drain away excess water. Drainage tubes of this type are known in *Meliplebeia tanganyikae medionigra*, *Meliplebeia lendliana*, *Meliplebeia denoiti*, *Trigona* (*Partamona*) *testacea testacea*, and *Trigona* (*Nogueirapis*) *mirandula* (not in all nests). In the case of *Meliplebeia tanganyikae medionigra*, such a burrow was 95 cm deep. In *Meliplebeia beccarii* a similar tube extends down from a sharp bend in the entrance burrow rather than from the nest itself. *Trigona mirandula* may have up to three short tubes instead of a single, long one. In *Trigona buchwaldi* several small holes at the bottom of the nest seem to take the place of the drainage tubes of the species listed above (43).

CLUSTER-TYPE NESTS This type of nest contains, instead of combs, a cluster or group of brood cells or cocoons irregularly arranged. It is found in three species of the subgenus *Plebeia*, in most of the subgenus *Hypotrigona*, in all the species of the subgenus *Trigonisca*, in *Trigona* (*Scaura*) *timida*, *Trigona* (*Partamona*) *testacea helleri*, *Cleptotrigona cubiceps*, and in twelve of the species of the subgenus *Tetragona*. Several variations exist, such as the following: primitive cluster-type (Figure 1) as in *Trigona* (*Plebeia*) *australis*, intermediate cluster-type (Figure 2) as in *Trigona* (*Plebeia*) *cincta*, irregular horizontal comb-type (Figure 4) as in *Trigona* (*Plebeia*) *schrottkyi*, and specialized cluster-type (Figure 5) as in *Trigona* (*Plebeia*) *tica* (44). Unlike nests with combs, cluster-type nests can take advantage of small and irregular spaces (22a, 30). *T. fuscobalteata*, for example, regularly spreads its cluster-type brood out in thin spaces between boards in wood buildings.

NEST WITH VERTICAL COMBS Only the African species *Dactylurina staudingeri* has vertical, double combs, each consisting of two layers of horizontal cells opening in opposite directions, as in *Apis* (Figure 6).

TEMPERATURE HOMEOSTASIS The locations of nests in thick tree trunks or in the ground, and the multiple layers of batumen and involucre especially in exposed nests, suggest protection of the brood chamber from temperature fluctuations, and retention of heat produced by metabolism of the brood. Data summarized by Michener (23) support this view, and especially temperature homeostasis in *Trigona spinipes*. For certain other species there is no evidence of temperature homeostasis (D. W. Roubik, personal communication). If this is the general situation it may be a factor that limits stingless bees to tropical and subtropical areas. However, the nest architecture and the prevalence of fanning and buzzing, and of resultant air currents through nests (27), suggest behavior for which temperature control is the most reasonable explanation.

Mixed Colonies

Mixed colonies have been made artificially by several persons, as summarized by Michener (23). Roubik (31a) observed a naturally mixed colony of *Melipona fuliginosa* (= *nigra* = *flavipennis*) and *Melipona fasciata* in a tree trunk. From the general nest architecture, and especially the distinctive nest entrance, it was obvious that the nest was built by *M. fuliginosa*; *M. fasciata* had added storage pots and brood cells. No batumen plate was present at the top of the nest; an incomplete and thin batumen layer of resin mixed with mud was at the bottom of the nest and was not perforated; these are typical features of *M. fuliginosa* nests, whereas *M. fasciata* makes thick, perforated batumen plates (47). The three combs of *M. fasciata* were located beneath the colony food store and a space of 20 cm separated them from the two small brood combs of *M. fuliginosa*. The most interesting fact was that there were 300–400 workers of *M. fasciata*, but only 20 of *M. fuliginosa*. Besides one gravid queen of *M. fuliginosa*, there were four virgin queens of *M. fasciata*.

Associations of Stingless Bees With Termites and Ants

Associations of stingless bees with termites and ants are well known; for some species they are occasional events; for others, regular or invariable relationships. Several bees regularly use abandoned *Atta* nests, but this is merely a response to available cavities in the soil. Some bees get into cavities made by birds in aerial termite nests as in the case of *Meliplebeia nebulata komiensis* (6) in Africa and *Trigona* (*Trigona*) *fuscipennis* (47) in the Neotropics. In the latter species the termites are generally entirely gone. The former and a related species (*Meliplebeia denoiti*) also enter subterranean termite nests, or at least make subterranean nests associated with termites (37). Other species of *Trigona* make nests inside intact nests of termites and ants. A good example is *Trigona* (*Scaura*) *latitarsis*, which

regularly uses aerial *Nasutitermes* nests, and *Trigona* (*Paratrigona*) *peltata peltata*, which often uses aerial *Camponotus* ant nests. Such bees must make their own cavity in the material of the termite or ant nest. Wille & Michener (47) reported tube entrances of *Trigona latitarsis* built on the outside of *Nasutitermes* nests and assumed that from such entrance tubes the bees can extend their occupation into the termite nest and can wall off an area in the interior for their own use.

Foundation of New Colonies and Mating

The founding of new colonies is quite different from that of the honey bee, as suggested by Spinola (38) in 1840 and actually observed by Nogueira-Neto (28) from 1947 to 1951, and later by Kerr (15), Kerr et al (20), and Juliani (13). All these authors demonstrated that new colonies are formed in a progressive way. The necessary material, either for construction or for food, is transported from the mother nest; a young queen then flies to the new site from the mother nest [see Michener (23)]. The connection between the mother and daughter nests can last for weeks and even months.

Wille & Orozco (48) made a detailed study on the founding of a new colony of *Trigona* (*Partamona*) *cupira* in Costa Rica. On April 3, 1972, a group of bees was observed for the first time exploring and examining an abandoned nest of *Nasutitermes*, which formerly lodged a nest of *Trigona* (*Scaura*) *latitarsis*. The exploring bees soon took possession of the empty termite nest and began the work of sealing all the fissures, cracks, and holes. Two days later the mother nest was found at 110 m away. On the third day the new nest was in good condition and already had a typical entrance of *Trigona cupira*. On April 6 several hundred bees, mostly males, arrived in the nest and we assumed that the queen had arrived with the group. The next day many bees started to transport pollen from the field to the new colony. The males disappeared completely by April 14.

The average time spent by the bees flying between nests (110 m) was 31.7 sec. At the end of June a small corn field, about 25 X 40 m, was planted close to the mother nest. On August 22 the plants were 4 m high, increasing the average flight time between nests to 49.3 sec.

The average time for loading material in the mother nest was 12.54 min; for unloading in the daughter colony the average was 3.78 min. Loading, therefore, took more than three times longer than unloading. A bee that spent 2 min unloading had a rather small load, while one that spent 6 min had a very large load. Although our studies of *Trigona cupira* largely agree with those of other authors, we found a few important differences. The most important in our opinion was that, while dependence on the mother nest was not as strong as suspected, it was the longest connection recorded for any stingless bee (6 months). It was quite obvious, even from the beginning,

that the bees at the new site were also collecting material elsewhere. The dependence of the daughter colony was less than 50% at its highest; sometimes it was even less than 10% of the total material being brought to the daughter nest by workers.

From the start, *Trigona cupira* bees transported all the pollen from the field. We are not sure whether they also carried pollen in liquid suspension in the crop, as do other species; the few dissections did not show any pollen in their crops. However, three months later, some bees started to carry pollen on the hind tibiae to the new nest from the mother nest.

The little information about mating has been reviewed by Michener (23). Swarms of males about nest entrances, commonly seen in species such as *Trigona jaty*, must relate to mating. Probably, young queens that go to new nests are virgin and make mating flights after reaching their new locations. While mating is usually in flight, males sometimes mate with gravid flightless queens, at least when the nest is disturbed. Whether this ever happens in an undisturbed nest is unknown.

Population of Nests, Longevity of Colonies, and Flight Range

Colony size of stingless bees has been exaggerated, particularly for those belonging to the subgenus *Trigona*. It is not unusual to read in certain papers statements like the following: "In the Rio Claro-Piracicaba region, colonies usually contain about the following number of bees," which is followed by a list of species, with a minimum and a maximum population for each. For instance, in the case of *Trigona* (*Trigona*) *spinipes* numbers have been given as 5,000 to 180,000 (see also 23). Claims of populations of 100,000 or more seem unlikely. The largest number of cells and cocoons observed by Michener (21) was 82,000 in a nest of *Trigona* (*Trigona*) *corvina*. Wille & Michener (47) offered a list of populations of several species based on counts or careful estimates: *Meliplebeia nebulata komiensis* 195–2,000 (5); *Trigona* (*Plebeia*) *schrottkyi* 300 (11); *T. (P.) mosquito* 1,175 (11); *T. (P.) frontalis* 1,900 (47); *T. (P.)* n. sp. 5,058 (47), *T. (Hypotrigona)* *braunsi* 400–750 (1, 30); *T. (H.) araujoi* 2,500 (22); *T. (Nogueirapis)* *mirandula* 2,281–4,076 (47); *T. (Trigonisca)* *atomaria* 500 (47); *T. (T.) buyssoni* 136 (47), *T. (Scaura)* *latitarsis* 393 (47); *T. (Partamona)* *cupira* 2,900 (21), 3,125 (48); *T. (Scaptotrigona)* *xanthotricha* 24–423 (10, 11); *T. (Tetragona)* *iridipennis* 2,550 (34); *T. (T.) buchwaldi* 1,326, 2,979 (47); *T. (Trigona)* *corvina* 7,200 (21); *T. (T.) spinipes* 5,500 (10, 11); *Melipona marginata marginata* 243 (10, 11), 160–170 (33); *M. marginata carrikeri* 210 (47); *M. anthidioides* 894 (10, 11); *M. fasciata melanopleura* 2,000 (47). The maximum colony size listed above is 7,200; colonies of some species may exceed 10,000, but the large sizes reported earlier need verification.

Little is known about the longevity of the colonies of stingless bees. Not long ago the known maxima reported were about 10 years. However, I obtained and have kept a colony of *Trigona* (*Tetragona*) *jaty* since 1960. As of 1981 it was still in good condition and was 21 years old, without counting the time before I obtained it. This colony survived attacks of the robber bee *Lestrimelitta limao* for one week and also suffered the eruptions of the Irazú Volcano from 1963 to 1965. During that time the nest was kept in the laboratory, close to a window with a hole through which bees had access to the field. They were also fed artificially with honey of the domestic bee during the fallout of volcanic dust.

Dr. Kerr (16) and I have made several investigations of the flight ranges of stingless bees. Unfortunately, not many species have been studied. However, there are some obvious correlations between flight range and size. For this reason I present the data in relation to the size of the bee, although admittedly this representation could be somewhat erroneous, since we do not have enough records. 1. Small bees like those of the subgenus *Plebeia* (3 to 4 mm) have a flight range of about 300 m. 2. Medium sized bees, as in the subgenus *Trigona* (5 mm), have a flight range of about 600 m. 3. Large bees (10 mm) like *Trigona* (*Trigona*) *silvestriana* have a flight range of about 800 m; *Melipona marginata* and *Melipona fulvipes* are included in this group. 4. Very large bees (13 to 15 mm), i.e. *Melipona fuliginosa* (= *nigra* = *flavipennis*), have a flight range of about 2000 m (45). Unfortunately we lack information about the flight ranges of minute stingless bees like *Trigona* (*Trigonisca*) *atomaria* that measures only 2 mm in length. D.W. Roubik (personal communication) reports flight ranges of 2 km for *Trigona* (*Cephalotrigona*) *capitata* and >3 km for *Melipona* spp., but he believes that the normal range in the forest is <1 km.

Communication

Many species of stingless bees are able to communicate the location of a food source. Since *Trigona* (*Scaptotrigona*) *postica* is one of the better studied bees from that point of view, I will use it as an example, and then mention the variations in the communication systems. When a foraging worker of *T. postica* finds a good source of food, it makes several normal collecting flights between the nest and the site. In this way it apparently makes sure that the find is worthwhile. It then uses its mandibular gland secretion to mark a path between the food and the colony. To do this it stops approximately every two meters and leaves scented spots: on a leaf, a branch, a pebble, or even a clump of earth. When it arrives at its colony, other bees leave the nest and begin to follow the odor trail outward. Cruz-Landim & Ferreira (3) found that in *T. postica* the young bees are not able to communicate, lacking full mandibular glands. Only middle-aged bees

about 43 days old have full glands and are able to function as scout bees and to communicate. This ability is lost after about 54 days. According to Hebling et al (9) the workers of *T. (Scaptotrigona) xanthotricha* become field bees at the age of over 52 days, and communication is effected when they are over 52 days old. Some authors (3) believe that in *T. postica* the forager can act as a guide bee by leading the others in a group back and forth for several trips.

Distances between two scent marks vary considerably according to the species. For instance, in *Trigona (Trigona) trinidadensis* (7) the average distance is 10 to 30 m; in *T. (Trigona) spinipes*, it is greater than 7 m, while in *T. (Scaptotrigona) bipunctata* it is about 2 m or less (20). The same authors indicated that the scent near the food source is heavier.

According to Kerr & Esch (18) the most primitive communication was found in *Trigona (Tetragona) silvestrii*. In this species the foragers are only able to alert the members of their colonies to go to an artificial syrup source if a perfume is added to the food. They also observed the production of a weak sound when the foragers enter the hive and pass nectar to receiving bees.

Other primitive types of communication were found in several small species, such as *Trigona (Tetragona) jaty*, *T. (Trigonisca) muelleri*, *T. (Plebeia) droryana*, and *T. (Hypotrigona) araujoi*. In these species the returning foragers alert their associates by strong sounds and zigzag running, frequently striking other bees.

In *Axestotrigona ferruginea* and *Trigona (Nannotrigona) testaceicornis* the returning foragers not only alert their associates by sounds and running, as in the case discussed above, but also the nearby bees repeat their sounds; in less than one minute the whole colony buzzes and the responsive bees leave to forage.

The effectiveness of the scent marks is retained for 8 to 19 min; the strongest odor emitted by a bee was found in *Trigona (Partamona) cupira*. Kerr (17) believes that the release of this strong odor in maximal quantities into the air can form an aerial odor trail; this could function only in the calm of tropical forests.

Communication in the genus *Melipona* is quite different from that of all other stingless bees and may be considered intermediate between that of other Meliponini and the subfamily Apinae. It includes the following aspects (some studied for only one species) (45).

1. The communication system indicates distance and direction without using chemical trails and without the need for a guide to lead foragers all the way to the food site.

2. The sounds produced in the hive by the returning foragers vary proportionally to the distance of the food source (as in the case of *Apis*). For this

reason the sounds probably serve for more elaborate communication and do not merely stimulate responsive bees to leave and forage.

3. The forager acts as a guide by leading its associates partway towards the food source. According to the observations of Esch (8) this is done after several repetitions. The forager indicates the direction of the food site; for example, in *Melipona seminigra*, according to Kerr & Esch (18), the forager guides its recruits toward the food source for only 10 to 20 m. This suggests that a progressive abbreviation of the flight of the guide could lead, by ritualization, to the straight run of the waggle dance of *Apis*, which on horizontal surfaces is also a movement towards the food. In summary, the direction of the flight of the forager indicates the direction to the food source.

During my studies in Corcovado National Park, the largest rain forest area of Costa Rica, I recognized the adaptation of the communication system of the stingless bees to the rain forest. Since an odor trail can lead to any height in the forest, these bees can take advantage of food sources in the high trees. As is well known, contrary to the situation in northern forests, most trees of tropical rain forests are not pollinated by wind, and bees play a major role in their pollination. With powerful binoculars I could verify that stingless bees were visiting flowers of the high trees. I am convinced that without the Meliponinae, tropical rain forest tree communities would be much modified.

Necrophagous Trigona

I have seen several species of the subgenus *Trigona* chewing bits from freshly dead animals. Some authors have considered this behavior as actual consumption of animal flesh (35), but I have thought that these bees collect pieces of meat in order to mix them with resin, wax, and perhaps other materials for construction of their exposed nests. Recently, however, Roubik (personal communication) has found a really necrophagous *Trigona*, *T. (Trigona) hypogea*. According to Roubik, dead animals are its sole protein source. These bees deposit trail pheromones between the nest and dead animals and thus recruit quite rapidly to a fresh animal carcass; for instance, one colony recruited several hundred foragers in two hours. This permitted bees to keep away dipteran competitors; the flies seeking oviposition sites were chased away by the bees. The bees were seen on carcasses of monkeys, snakes, fishes, birds, toads, and frogs. A frog, 4 cm long, was reduced by the the bees to a skeleton within six hours. According to Roubik, the bees masticate and consume flesh at the feeding site; they do not carry flesh in the corbiculae. Indeed, the corbiculae of this species are reduced and probably could not effectively carry pollen. Presumably, liquified flesh is transferred by trophallaxis to other workers in the nest, which in turn convert it into a glandular secretion. The nests lack stores of pollen, but a presum-

ably glandular product as well as honey is stored. Pollen collection by this species has not been seen.

Trigona hypogea, like other species of its subgenus, has large mandibular teeth. Probably other species use flesh occasionally, when pollen is scarce, but only *T. hypogea* has a specialized dependency on flesh, perhaps acquired because it is a wet forest bee occurring in areas where there are long seasons with little flowering.

Division of Labor

Social life in the stingless bees, as in other social insects, involves division of labor. Only the females are divided into castes, which are queens and workers. According to Kerr & Santos Neto (19), division of labor in the stingless bee is similar to that found in honey bees, as was later confirmed by Bassindale (1).

The different tasks among the workers are not rigidly established but rather they reflect tendencies toward certain tasks at certain ages. The sequence of activities in the workers can be divided into five or six stages. The duration of each stage depends on the species and on the condition of the colony. These stages are as follows: (a) self-grooming (during the first hours after emergence from the pupae); (b) incubation and repairs in the brood chamber; (c) construction and provisioning of cells, cleaning of the nest, and feeding young adults and the queen; (d) further cleaning of the nest, reconstruction of the involucre, reception of nectar, and guard duty at the entrance of the nest; (e) collection of pollen, nectar, and propolis.

Simões & Bego (36) studied division of labor of *Trigona (Scaptotrigona) postica* in a normal colony (with a physogastric queen) and in another colony with virgin queens. They observed that, as in *Apis*, the activities of the workers were modified according to age and also in relation to the needs of the colony. The task sequence with aging was the same in the two colonies, but some activities progressed more rapidly in the colony containing virgin queens. The workers' mean life span was longer in normal colonies than in the one with virgin queens.

The longevity of the workers is longer than that of tropical *Apis*. According to Darchen (7), studying the workers of *Trigona (Scaptotrigona) xanthotricha*, in "the 80th day, all the bees marked for this work, were alive; at the 94th day all of them were dead." Roubik (personal communication) found average life spans for *Melipona favosa* and *fulva* to range from 24 to 50 days, depending on level of worker activity and foraging.

Queen Behavior and Oviposition

Oviposition and queen behavior have been studied by Sakagami and his associates for 18 species of stingless bees, and their papers are listed by Michener (23). One of the best studied species is *Melipona quadrifasciata*.

When a cell is ready, a concentration of workers is noted in the vicinity, every worker inserting its head, one after another, into the cell. Apparently in response to this activity, the queen approaches the cells and takes up a fixed position at its side. The workers insert their heads in the cell with increasing excitement, perhaps because the queen now touches the workers with the antennae and anterior feet. After a few minutes workers start regurgitating honey, pollen, and salivary secretion (larval food) into the cell. Only 4 to 5 discharges of food by different workers into the cell are sufficient to provision it. According to Sakagami and associates the workers regurgitate larval food into the cell in response to the queen's fixed location. Toward the end of the provisioning one or more workers frequently lay trophic eggs in the cell. The queen approaches the cell, inspects it, then eats any worker's eggs found in it as well as some of the larval food. After this the queen deposits her own egg in the center of the cell, on the food; then a worker closes the cell, using the cell rim material to form the closure. In *Melipona*, while the workers provisioning the cell leave it relatively slowly, the queen retreats quickly from the cell.

There are many variations in the details of oviposition and queen behavior. For instance, in the Neotropical subgenera *Trigona* and *Hypotrigona* (17) several cells are simultaneously constructed. Cell provisioning may be completely synchronized, as in the subgenera *Nannotrigona* and *Plebeia*. In others, such as *Scaptotrigona*, it is only partially synchronized. As mentioned before, in *Melipona* only one cell is constructed at a time, and the bees gather about it; this is also true of the African genus *Meliponula*, except that in the latter the queen does not maintain a fixed position before laying.

In contrast to *Melipona*, in the majority of species of *Trigona* the workers leave the cell very rapidly after provisioning it, even falling from the combs; in an extreme case, as in the subgenus *Partamona*, the workers fly, apparently to get away from the cell and the queen.

The laying of trophic eggs by the workers also varies. In various minute species of *Trigona* and in all Old World *Trigona* studied (50), no such eggs are found, since the ovaries of these workers are not enlarged. According to Darchen (5), the African *Meliplebeia nebulata komiensis* also lacks trophic eggs. On the other hand, in most Neotropical stingless bees and the African genus *Meliponula*, trophic eggs are laid. While in *Melipona* and *Meliponula* the eggs laid by the workers are small, in most Neotropical *Trigona* species the trophic eggs are as large as or longer than eggs of the queens. In contrast to the genus *Melipona*, in which the workers lay eggs that stand on end in the middle of the surface of the provisions in the same way as those of the queen, the trophic eggs of *Trigona* are placed on the rim of the cell.

Another interesting behavior, found in several species of *Trigona* (12, 26, 29), is imprisonment of virgin queens. According to Juliani, in *Trigona* (*Tetragona*) *jaty* and *T. (Plebeia) remota*, the workers make a complete small chamber enclosing the queen (12). Sometimes she tries to break the chamber walls and run away, but the workers chase her until she is caught and imprisoned again. In *T. jaty* and *T. (Plebeia) droryana* the workers generally place some propolis at one side of the chamber. These species kill the prisoner queen when necessary, by smearing her body with propolis. Sometimes the virgin queen of *T. droryana* hides in an empty and unfinished food pot, where the workers imprison her by closing up the pot as a chamber. *T. jaty*, *T. (Plebeia) julianii* and *T. remota* construct the imprisonment chambers close to the food pots. The chambers of *T. droryana* are usually made in the involucre.

The imprisonment chambers for the virgin queens of *T. jaty*, *T. remota*, and *T. droryana* have a small opening through which the workers can feed the prisoner queens. At other times the small hole is closed and the queen remains alone. What is the meaning of this behavior? The maintenance of imprisoned virgin queens is a guarantee against being orphaned. In *T. jaty* and in *T. (Plebeia) droryana* the colony generally kills the prisoner virgin queens when the nest has mature royal cells. The old nest of *T. jaty* mentioned in relation to the longevity of colonies probably has changed queens more than once.

Theft, Pillage, and Honey

Theft and pillage are not exclusively human traits; they are also common among animals. Stingless bees are examples of animals that rob and plunder for several reasons.

Bees that rob for no apparent reason do so more frequently when colonies are clustered together, probably since the smell of the honey from a neighboring colony incites pillage. Although the possible relationship between the quality of honey and robbery has not been studied, Table 2 summarizes some known characteristic of honeys.

In my experience, the taste of most of the honey of the bees mentioned in Table 2 is constant among various colonies of each species. Since these bees visit a wide variety of flowers for food, it seems probable that the specific differences in taste are at least partly due to different treatments or additives by bees.

Another reason for robbery could be confusion of nests, not only because of their proximity, but also because of similar appearance and orientation of entrances, and perhaps because of the similar odor of their provisions. This can be easily verified if two similar colonies are placed next to each other with entrances oriented in the same direction; pillage soon

Table 2 Observations on honey of some Costa Rican Meliponinae

<i>Trigona frontalis</i>	Sweet, rather acid, pleasant
<i>T. pseudojatiiformis</i>	Sweet, slightly acid, yellowish, good
<i>T. tica</i>	Sweet, slightly acid, viscous, good
<i>T. mirandula</i>	Sweet, slightly acid, viscous, good or acid, bitter, fluid, not pleasant
<i>T. (Plebeia) n. sp.</i>	Very bitter
<i>T. latitarsis</i>	Sweet, pleasant, viscous
<i>T. guatemalensis</i>	Sweet, rather watery, good
<i>T. ornateiceps</i>	Sweet, scarcely sour, good
<i>T. p. peltata</i>	Sweet, not sour, viscous, good
<i>T. mexicana sub-obscuripennis</i>	Sweet, slightly acid, fluid
<i>T. mellaria</i>	Very watery, acid (like lemonade)
<i>T. testaceicornis perilampoides</i>	Sweet, viscous, neither acid nor bitter
<i>T. capitata zexmeniae</i>	Sweet, rather acid, viscous, good
<i>T. tataira mellicolor</i>	Acid to sweet, moderately viscous
<i>T. buchwaldi</i>	Acid, watery
<i>T. dorsalis</i>	Very acid
<i>T. j. jaty</i>	Sweet to somewhat acid, viscous, good
<i>T. nigra paupera</i>	Sour, bitter, watery
<i>T. perangulata</i>	Sour, watery
<i>T. corvina</i>	Sour, sometimes slightly bitter, watery
<i>T. f. fulviventris</i>	Sweet, viscous, slightly acid, good
<i>T. fuscipennis</i>	Sour, watery, worse than that of <i>T. corvina</i>
<i>T. nigerrima</i>	Bad tasting, not sour or viscous, salty and bitter
<i>Lestrimelitta limao</i>	Mixed with pollen
<i>Melipona f. fasciata</i>	Sweet, slightly acid, watery
<i>M. fasciata melano-pleura</i>	Sweet, watery
<i>M. marginata carrikeri</i>	Sweet, not sour, viscous, good

develops. On the other hand, if these two colonies are placed with their entrances in different directions, or if the entrances are painted in different colors, the tendency toward pillage is reduced. Pillage can be either slight or devastating. In the first case, the plundered colony can resume its normal activities. In the second case, the colony is razed and occasionally occupied by the attackers. An attack can last a few hours or a few days and even in several observed instances combats have lasted almost a month. There have been examples where one colony was attacked by three others or where one colony attacked two others; even the plundered colony can change its role of victim for that of robber. Two-way pillage has also been observed between colonies. The materials most frequently taken are propolis, wax, and other construction materials, in addition to pollen and honey. The attackers, to steal the pollen, first soften it with a liquid they secrete,

swallow it, and then transport it in their crops, not on the hind legs as when it is collected from flowers.

Bees that obligately rob other nests for subsistence are perhaps the most interesting. In Central America there is only one of these species, the "lemon bee" or "robber bee" (*Lestrimelitta limao*). The workers have no corbiculae or similar structures for carrying pollen, and therefore must attack and rob other colonies to survive. The robbers' strategy consists of the use of enlarged mandibular glands that secrete a strong lemony smell, from which they derive their common and scientific names. With this odor they suppress the typical odor of the attacked colony. Guard bees of a colony do not permit the entrance of strange bees, which they recognize by the characteristic smell of the hive. A few (or even one) of the lemon bees force their way into the nest to be plundered, and although they may be killed in this venture, they spread their strong, peculiar odor. Once the attacked colony has lost the ability to perceive its proper scent, the attackers can come and go as they please. At the same time, the strong lemon odor released by the first few attackers helps the others locate their objective. In the Botanical Garden of the University of Costa Rica, I have observed an attack on a colony of *Trigona* (*Tetragona*) *jaty*. Once the lemon odor was dispersed inside the attacked nest, a band of robbers took possession of the entrance and would not let any of the victims out nor could any of the returning workers enter. The latter were received by the attackers with open jaws, although they were not harmed. Meanwhile the other robbers removed their booty uncontested. This went on for several hours during the first day and was continued the next day, and sporadically for almost a week (41).

Another rare species, *Lestrimelitta ehrhardti*, exists in South America and was studied by Sakagami & Laroca (32). The species was discovered when robbing a nest of *Melipona quadrifasciata quadrifasciata*. They observed that it is similar to *L. limao* not only in its mild disposition and strong lemon-like odor, but also in its nest architecture. *Lestrimelitta guyanensis* from French Guyana presumably has similar habits.

In Africa there is another robber bee, *Cleptotrigona cubiceps*, which has been studied by Portugal-Araújo (31). This bee invades colonies of the small species of *Trigona* (*Hypotrigona*). It lacks any obvious odor, unlike *Lestrimelitta*. When attacking a nest a few bees inspect the entrance tube and its location; then the robbers increase in number, reaching 40 to 60. First they destroy the tube entrance, while the attacked bees pour honey from the inside of their nest; they close the entrance by this method temporarily and the honey that is poured is collected by the attackers. At the end of the day the robber bees return home. During the night the entrance tube of the attacked bees is rebuilt. The following morning the *Cleptotrigona* come

again; the attacked bees pour honey again, but this time the honey flows and drips to the ground and continues to do so for many hours without stopping, not even at night. After a while the robber bees no longer seem interested in the honey that pours out. They try to open the entrance more widely and try to get inside the attacked nest. This is not always successful. After 1–3 days the honey stops pouring; then the *Cleptotrigona* and the workers from other nests of the attacked species collect all the honey close to the entrance. After this the attackers enter the nest without resistance, and soon start coming out of the nest carrying propolis and cerumen on their legs, while others have abdomens swollen with honey and brood food. While this is happening, a group of robber guards is established at the entrance, as is the case with *Lestrimelitta limao* described above. The group action of the attacking bees suggests the existence of a pheromone that triggers the response.

Defense Mechanisms

Even though the Meliponinae do not sting, most of them possess efficient means of defense. Whoever has disturbed nests of species such as *Trigona cupira*, *T. testacea musarum*, *T. guatemalensis*, *T. tataira mellicolor*, *T. corvina* and *T. fuscipennis* can testify to the efficacy of their attack. Their strategy consists of biting, becoming entangled in the intruders' hair, and getting in the nose, ears, and eyes. Alarm pheromones are clearly involved in these responses. However, not all species are so aggressive: Species such as *Trigona jaty*, *T. testaceicornis*, *T. fulviventris*, and *Melipona beecheyi* rarely attack a person. In some species of the subgenera *Plebeia* and *Tetragona* the use of sticky materials against intruders has been observed. The robber bee (*Lestrimelitta limao*) places small balls of wax at the entrance of its nest; according to some authors (32) their purpose is to repel ants. Another means of defense is the use of unpleasant odors, as is the case in *Trigona capitata* and *Melipona marginata*; *M. interrupta* emits skatol when disturbed (Roubik, personal communication).

Among the stingless bees, *Trigona (Oxytrigona) tataira* and its relatives have a unique defense mechanism. These bees have enlarged mandibular glands capable of producing enough caustic liquid to cause blisters when they bite (41). I had the opportunity to observe this behavior in Costa Rica. The effect of the substance took place very gradually as I experimented on myself. The next day after the bite I felt a slight itching in the affected part; it slowly turned reddish. As the reddish hue was intensified, I felt an increasing burning sensation that reached its maximum after 24 hr. After a few days the affected skin dried and sloughed off, as in common burns. I also observed that other people react differently, some forming blisters very quickly. All species of *Oxytrigona* have the same kind of defense.

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Literature Cited

1. Bassindale, R. 1955. The biology of the stingless bee *Trigona* (*Hypotrigona*) *gribodoi* (*Meliponinae*). *Proc. Zool. Soc. London* 125:49-62
2. Cockerell, T. D. A. 1934. Some African meliponine bees. *Rev. Zool. Bot. Afr.* 26:45-62
3. Cruz-Landim, C. da, Ferreira, A. 1968. Mandibular gland development and communication in field bees of *Trigona* (*Scaptotrigona*) *postica*. *J. Kans. Entomol. Soc.* 41:474-81
4. Cruz-Landim, C. da, Rodriguez, L. 1967. Comparative anatomy and histology of alimentary canal of adult apinae. *J. Apic. Res.* 6:17-28
5. Darchen, R. 1969. Le comportement de ponte des reines des deux especes d'abeilles sans dard (*Trigones*). *Gaz. Apic.* 743:103-4
6. Darchen, R. 1969. Sur la biologie de *Trigona* (*Apotrigona*) *nebulata komiensis* Cock. I. *Rev. Biol. Gabonica* 5: 151-87
7. Darchen, R. 1969. La biologie des trigones et des melipones (Hymenopteres, Apidae) a la lumiere des travaux recents. *Ann. Biol.* 8:455-90
8. Esch, H. 1967. The sound produced by swarming honeybees. *Z. Vergl. Physiol.* 56:408-11
9. Hebling, N. J., Kerr, W. E., Kerr, F. S. 1964. Divisão de trabalho entre operárias de *Trigona* (*Scaptotrigona*) *xanthotricha* Moure. *Pap. Avulsos Dep. Zool. São Paulo* 16:115-27
10. Ihering, H. von. 1903. Biologie der stachellosen honigbieneen Brasileens. *Zool. Jahrb. Abt. Syst. Oekol. Geogr. Tiere* 19:179-287
11. Ihering, H. von. 1930. Biologie das abelhas mellíferas do Brasil. *Bol. Agric. 5-8* Secr. Agric. Ind. Commer. São Paulo. 140 pp. Transl. H. von Ihering, Ref. 10
12. Juliani, L. 1962. O aprisionamento de rainhas virgens em colonias de Trigoniini (Hymenoptera, Apoidea). *Bol. Univ. Paraná, Cons. Pesqui., Curitiba, Brasil* 20:1-11
13. Juliani, L. 1972. A descrição do ninho e alguns dados biológicos sobre a abelha *Plebeia julianii* Moure, 1962 (Hymenoptera, Apidae). *Rev. Bras. Entomol.* 12:31-58
14. Kelner-Pilau t, S. 1970. Une melipone (s.l.) de l'ambre balte (Hym. Apidae). *Ann. Soc. Entomol. Fr. (NS)* 6:437-41
15. Kerr, W. E. 1951. Bases para o estudo da genetica de populações dos Hymenoptera em geral e dos Apinae sociais em particu ar. *Anais Esc. Super. Agric. Luiz de Queiroz Univ. São Paulo* 8:219-354
16. Kerr, W. E. 1959. Bionomy of Meliponids-VI. Aspects of food gathering and processing in some stingless bees. Food gathering in Hymenoptera. *Symp. Entomol. Soc. Am., Detroit*, pp. 24-31
17. Kerr, W. E. 1969. Some aspects of the evolution of social bees. *Evol. Biol.* 3:119-75
18. Kerr, W. E., Esch, H. 1965. Comunicação entre as abelhas sociais brasileiras e sua contribuição para o entendimento da sua evolução. *Cienc. Cult. São Paulo* 17:529-38
19. Kerr, W. E., Santos Neto, G. R. 1953. Contribuição para o conhecimento da bionomia dos Meliponini. II Divisão de trabalho entre as operarias de *Melipona quadrifasciata quadrifasciata* Lep. *Cienc. Cult. São Paulo* 5:224-25
20. Kerr, W. E., Zucchi, R., Nakadaira, J. T., Butolo, J. E. 1962. Reproduction in the social bees (Hymenoptera, Apidae). *J. NY Entomol. Soc.* 10:265-76
21. Michener, C. D. 1946. Notes on the habits of some Panamanian stingless bees (Hymenoptera, Apidae). *J. NY Entomol. Soc.* 54:179-97
22. Michener, C. D. 1959. Sibling species of *Trigona* from Angola. *Am. Mus. Novit.* 1956:1-5
- 22a. Michener, C. D. 1961. Observations on the nests and behavior of *Trigona* in Australia and New Guinea. *Am. Mus. Novit.* 2026:1-46
23. Michener, C. D. 1974. *The Social Behavior of the Bees. A Comparative Study.* Cambridge, Mass: Harvard Univ. Press. 404 pp.

24. Moure, J. S. 1951. Notas sobre Meliponinae (Hymenoptera, Apoidea). *Dusenía* 2:25-70
25. Moure, J. S. 1961. A preliminary supra-specific classification of the Old World Meliponinae bees (Hym. Apoidea). *Stud. Entomol. Rio de Janeiro* 4:181-242
26. Moure, J. S., Nogueira-Neto, P., Kerr, W. E. 1958. Evolutionary problems among Meliponinae. *Proc. 10th Int. Congr. Entomol., Montreal* 2:481-93
27. Nogueira-Neto, P. 1948. Notas bionômicas Sôbre meliponíneos. I-Sobre o ventilação dos ninhos e as construções com ela relacionadas. *Rev. Bras. Biol.* 8:465-88
28. Nogueira-Neto, P. 1954. Notas bionômicas sôbre meliponíneos. III-Sôbre a enameagem. *Arg. Mus. Nac. Rio de Janeiro* 42:219-452
29. Nogueira-Neto, P. 1958. Rainhas prisioneiras. *Chácaras e Quintais São Paulo* 97:477
30. Pooley, A. C., Michener, C. D. 1969. Observations on nests of stingless bees in Natal (Hymenoptera: Apidae). *J. Entomol. Soc. South. Afr.* 32:423-30
31. Portugal-Araújo, V. de. 1958. A contribution to the bionomics of *Lestrimelitta cubiceps*. *J. Kans. Entomol. Soc.* 31:203-11
- 31a. Roubik, D. W. 1981. A natural mixed colony of *Melipona*. *J. Kans. Entomol. Soc.* 54:263-68
32. Sakagami, S. F., Laroca, S. 1963. Additional observations on the habits of the cleptobiotic stingless bees, the genus *Lestrimelitta* Friese (Hymenoptera, Apoidea). *J. Fac. Sci. Hokkaido Univ., Ser. 6 Zool.* 15:319-39
33. Schulz, W. A. 1905. Neue Beobachtungen an süßbrasilianischen Meliponiden-Nestern. *Z. Wiss. Insektenbiol.* 1:199-204, 250-54
34. Schulz, W. A. 1909. Ein javanischen Nest von *Trigona canifrons* F. Sm. in einem Bambusstabe. *Z. Wiss. Insektenbiol.* 5:338-41
35. Schwarz, H. F. 1948. The stingless bees (Meliponinae) of the Western Hemisphere. *Bull. Am. Mus. Nat. Hist.* 90:1-546
36. Simões, D., Bego, L. R. 1979. Estudo da regulação social em *Nannotrigona (Scaptotrigona) postica* Latreille, em duas colonias (normal e com reinhas virgens) com especial referencia ao polietismo etario (Hym., Apidae, Meliponinae). *Bol. Zool. Univ. São Paulo* 4:89-98
37. Smith, F. G. 1952. Bee-keeping observations in Tanganyika. *East Afr. Agric. J.* 18:1-3
38. Spinola, M. 1840. Observations sur les apiaries meliponides. *Ann. Sci. Nat., Zool.* 13:116-40
39. Wille, A. 1959. A comparative study of the dorsal vessels of bees. *Ann. Entomol. Soc. Am.* 51:538-46
40. Wille, A. 1961. Evolutionary trends in the ventral nerve cord of the stingless bees (Meliponini). *Rev. Biol. Trop.* 9:117-29
41. Wille, A. 1961. Las abejas jicotes de Costa Rica. *Rev. Univ. Costa Rica* 22:1-30
42. Wille, A. 1963. Phylogenetic significance of an unusual African stingless bee, *Meliponula bocandei* (Spinola). *Rev. Biol. Trop.* 11:25-45
43. Wille, A. 1966. Notes on two species of ground nesting stingless bees (*Trigona mirandula* and *T. buchwaldi*) from the Pacific rain forest of Costa Rica. *Rev. Biol. Trop.* 14:251-77
44. Wille, A. 1969. A new species of stingless bee *Trigona (Plebeia)* from Costa Rica, with descriptions of its general behavior and cluster-type nest. *Rev. Biol. Trop.* 15:299-313
45. Wille, A. 1975. Las abejas jicotes del género *Melipona* (Apidae, Meliponini) de Costa Rica. *Rev. Biol. Trop.* 24:123-47
46. Wille, A. 1979. Phylogeny and relationships among the genera and subgenera of the stingless bees (Meliponinae) of the world. *Rev. Biol. Trop.* 27:241-77
47. Wille, A., Michener, C. D. 1973. The nest architecture of the stingless bees with special reference to those of Costa Rica. *Rev. Biol. Trop.* 21: Suppl. 1, pp. 1-278
48. Wille, A., Orozco, E. 1974. Observations on the founding of a new colony of *Trigona cupira* (Hymenoptera, Apidae) in Costa Rica. *Rev. Biol. Trop.* 22:253-87
49. Winston, M. L., Michener, C. D., 1977. Dual origin of highly social behavior among bees. *Proc. Natl. Acad. Sci. USA* 74:1135-37
50. Yoshikawa, K., Ohgushi, R., Sakagami, S. F. 1969. Preliminary reports on entomology of the Osaka City University 5th scientific expedition to Southeast Asia 1966. *Nat. Life SE Asia* 6:153-81



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