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Observations on the Nests and Behavior of *Trigona* in Australia and New Guinea (Hymenoptera, Apidae)¹

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INTRODUCTION

In this paper are presented data on the comparative nest architecture of several stingless bees of the genus *Trigona* (tribe Meliponini) from Australia and New Guinea, and on some aspects of behavior of certain of these bees. In Australia, these small bees are almost universally called "native bees," while in New Guinea they are known as "sweat bees," because of the frequency with which they alight on one's skin and lap perspiration.

ARCHITECTURE

BASIC FEATURES

Any nest of a colony of *Trigona* exhibits a variety of structural features which result from the activities of thousands of worker bees. Many of the

¹ Contribution number 1076 from the Department of Entomology, the University of Kansas, Lawrence. The study here described was carried out in the Department of Entomology, University of Queensland, Brisbane, Australia, and for a brief period at the Department of Agriculture, Stock, and Fisheries, Territory of Papua and New Guinea, Port Moresby (Konedobu), Papua.

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features (e.g., cell size and arrangement) are species-typical, while others (e.g., the way in which the nest cavity is sealed) vary according to the individual nest and the particular situation occupied by it.

A study of behavioral features ordinarily requires much more time than a study of a comparable number of morphological features, and for this reason much less work has been done in comparative behavior than in comparative morphology. However, the activities of some animals produce nests or other structures. By examining the nest one can get a summation of certain activities of the animal that made it. With nests made by social animals, the summation concerns not merely numerous actions of one animal, but those of many. It seems justifiable to speak of homologous parts of nests of related species of insects and to study the comparative architecture of such nests in the hope of better understanding the relations among the species and the adaptations of the various species to their environments. Other investigators (e.g., Schmidt, 1955; Emerson, 1956) have already made important contributions using such materials.

Of course it is true that complications involving types of homologies and the meaning of the term "homology" itself are at least as numerous in connection with behavior patterns and structures resulting from them (e.g., nests) as in connection with the structures of the animals themselves. As Hubbs (1944) points out, the concept of homology is full of grave complexities. I agree with Hubbs that it would be unwise formally to subdivide homologies into types, although informally it is often convenient to think of serial homologies, general homologies, and the like. Yet in spite of its inexactitude, the idea of homology continues to be useful in all fields of comparative biology.

In the tribe Meliponini, nests have the following major structures which are presumably homologous among all the species of the tribe:

BROOD CELLS: Made of soft cerumen, in each of which a single young is reared. (Each cell is fully provisioned before egg laying with a mixture of pollen and honey, above which is usually a layer of clearer material lacking pollen; on the provisions an egg is laid by the queen; the cell is then closed. The cells are in contact with one another or connected by small pillars of soft cerumen; such pillars connect groups or layers of cells with one another and with surrounding structures.)

BROOD CHAMBER: The cavity in which the brood cells exist.

INVOLUCRUM: A sheath of one to several perforated sheets of soft cerumen surrounding the brood chamber. (The involucrum is absent in some species.)

HONEY AND POLLEN POTS: Containers made of soft cerumen built in clusters around and especially above the brood chamber, outside the involucrum.

PILLARS AND CONNECTIVES: These support all nest structures within the batumen (often they are made of soft cerumen, but close to the batumen, especially at the bottom of the nest, they are usually thickened and brittle).

BATUMEN: Made of cerumen (commonly brittle), propolis, or sometimes (outside the Australian region) of vegetable matter or of mud mixed with resin or cerumen. The batumen seals the nest cavity except for the entrance and sometimes minute ventilating perforations. In nests in hollow trees and other enclosed situations the batumen is mainly in the form of plates closing off the hollow above and below but does continue around the nest as a thin lining between the wood or other substrate and the nest cavity. This sheet is called the "lining batumen" in subsequent descriptions. In exposed nests (such as those of *T. corvina* Cockerell and *T. ruficrus* Latreille in tropical America) the batumen, which is several layers thick, is similar all around the nest.

NEST ENTRANCE: This is often continued externally as a soft or hard projecting tube, and internally far into the nest cavity as a more or less hard tube.

In one important matter the definitions given above differ from those in common use. It is usually stated that the involucrum encloses the storage pots as well as the brood chamber in some species. When it does, it is the outside wall of the nest cavity and, according to my views, is better called the "batumen." The position (separating the nest cavity from the outside world, enclosing the entire nest cavity, including the storage pots), the texture (hard, of brittle cerumen or propolis), and the protective function indicate the homology between the "involucrum" of species making exposed nests and the batumen plates of most species. Nests in cavities (e.g., of *T. iridipennis*) occasionally have two or three parallel sheets of batumen, thus approaching the laminated batumen of species nesting in the open. A nest of *T. iridipennis* found in New Guinea was in an artificial cavity much larger than cavities ordinarily used. Instead of closing off only one or both ends of a long cavity (hollow tree) with batumen plates, about 50 per cent of the nest wall was of batumen free from the wall of the cavity. In most places this was two or three layers thick, thus approaching the laminated condition of the batumen of species with exposed nests. In some nests of *T. carbonaria* there is a distinctly laminated batumen in some areas of the sides of the nest, very much as in the species making exposed nests (see fig. 28). Where laminate batumen and involucrum come close together as a result of the form of the nest cavity, they sometimes merge almost indistinguishably. Perhaps they could better be called "enveloping sheets" of two different types. The important point is that the terminology here proposed does not equate the inner sheets (involucrum) of some species with the outer sheets (batumen) of others, as did the previously accepted terminology. Perhaps the lamination of both involucrum and batumen serves to provide for better temperature insulation which is important in exposed or partially exposed nests but less important in those situated in cavities in wood or soil.

The following is a glossary of the main structures of nests of Meliponini:

ADVANCING EDGE: The margin of a comb that is advancing because of the addition of new cells.

ADVANCING FRONT: The surface or surfaces in the cell cluster which advance because of the addition of new cells.

BATUMEN: A protective layer of propolis or hard cerumen (sometimes vegetable matter, mud, or various mixtures) enclosing the nest cavity. Most commonly it consists of *batumen plates* closing off portions of a natural cavity from the nest cavity, and *lining batumen* which is a thin layer of propolis or brittle cerumen on the walls of the nest cavity. Exposed and partly exposed nests are entirely or partly surrounded by *exposed batumen*. *Laminate batumen* consists of several layers, with spaces between them in which bees can move about. Laminate batumen is usually exposed. (Batumen is a Brazilian word meaning "wall," used by von Ihering and subsequent authors, chiefly for the batumen plates.)

CELLS: Brood cells made of soft cerumen, in each of which a single young is reared.

CERUMEN: A brown mixture of wax and propolis used for construction. Newly made cerumen is soft, while old cerumen is often brittle.

CLUSTER (OF CELLS OR COCOONS): A group of brood cells or cocoons irregularly arranged, not in combs.

COCOON: Silk structure spun after defecation by the mature larva around the inner wall of its cell. The worker bees remove and re-use the cerumen of which the cell was constructed, leaving the cocoon largely exposed during the prepupal and pupal periods.

COMB (OF CELLS OR COCOONS): A layer of brood cells or cocoons crowded together.

ENTRANCE: The external opening of the nest for coming and going of the bees. It is often continued outside the nest cavity as an *external entrance tube*. It is also often continued inside the nest cavity, usually along the inner wall of the cavity, as an *internal entrance tube*.

INVOLUCRUM: A sheath of soft cerumen surrounding the brood chamber. A *laminate involucrum* consists of several layers with spaces between them in which bees can move about.

PILLARS: More or less vertical columns of cerumen (soft or brittle) within the nest. When more or less horizontal, such columns may be called "connectives." There is no real distinction in kind between pillars and connectives.

PROPOLIS: Resins and waxes collected by the bees in the field and brought to the nest for construction purposes.

STORAGE POTS: Containers made of soft cerumen for the storage of honey (honey pots) or pollen (pollen pots).

WAX: White material secreted by the bees and mixed with other substances to make cerumen. Dr. Paulo Nogueira-Neto (*in litt.*, February 5, 1960) writes: "As far as I know, pure wax is never used by meliponines except sometimes in the outermost part of the entrance tube" (as in *Trigona schrottkyi* Friese and others).

SPECIES ACCOUNTS

Trigona (Plebeia) australis Friese¹

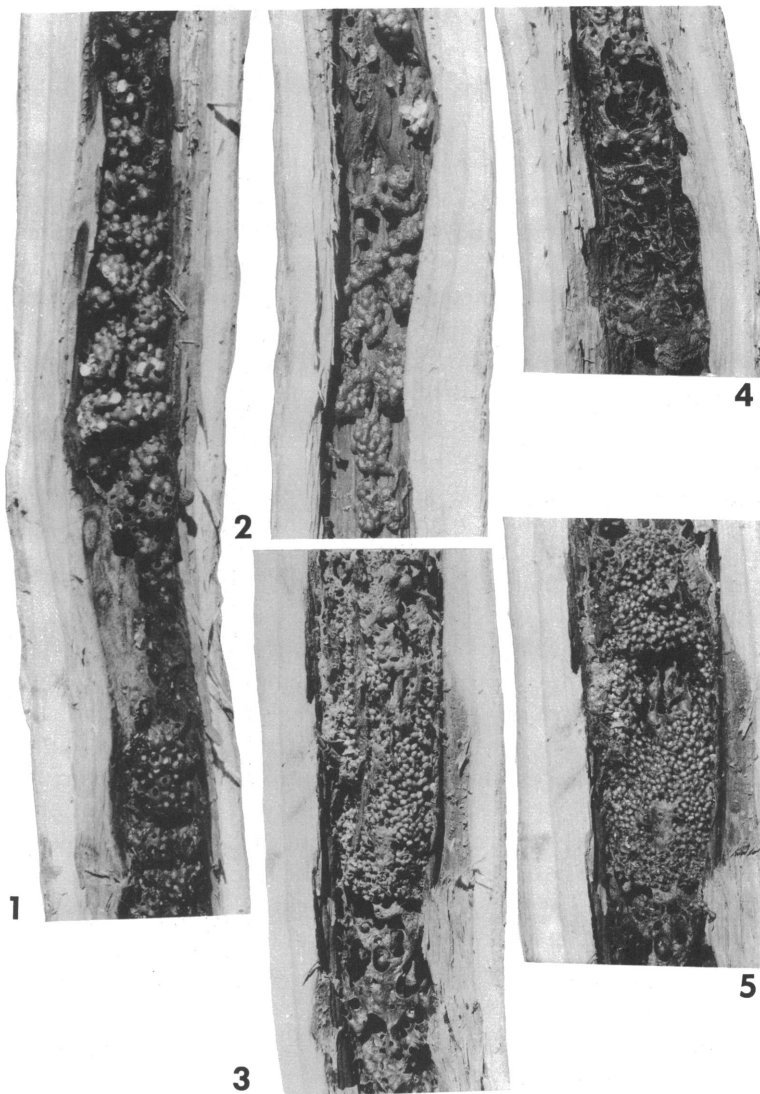
This is the common *Trigona* of south and central Queensland west of the coastal strip, although it also extends to the coast. It was perhaps by error that Hockings (1884) attributes this species (under the aboriginal name *kootchar*) to the coast. I obtained it at the following localities, nests having been opened for study at those marked with asterisks: Capalaba, Condamine, 27 miles east of Condamine, Dalby, 17 miles south of Dalby,* Glenmorgan, Helidon, 7 miles southwest of Ipswich, Jimboomba, Moggill (near Brisbane), Mutdapilly, Tamborine, Tibrogargen (near Beerwah), 4 and 13 miles south of Warwick, Yarriman.* These localities are all in open savanna.

Nests of this species are especially common in trunks of small living trees where they typically occupy long hollows. For example, one nest from 17 miles south of Dalby in a *Eucalyptus* tree about 20 cm. in diameter occupied a hollow 5 to 8 cm. in diameter. Batumen plates closed off a space 300 cm. long which was occupied by the nest. This long "pipe" was divisible into six sections from top to bottom as follows: 30 cm., empty; 80 cm., largely empty but containing some empty pots, some of which were supported on long pillars; 22 cm., largely full of clusters of pollen pots; 113 cm. of clusters of honey pots, with some rather large open spaces among them; 20 cm. of brood chamber; 35 cm. full of perforated cerumen sheets, some empty storage pots, pillars, and so on. Figures 1 to 4 illustrate the nest from the level of the pollen pots downward, as it was exposed by splitting the tree trunk.

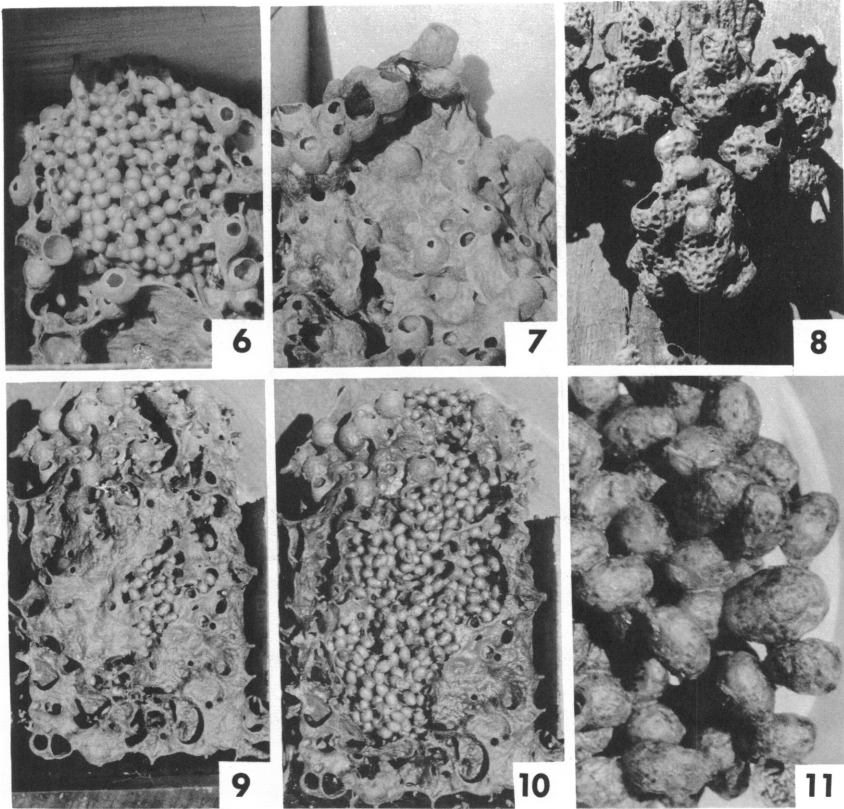
The entrance was at a knothole 35 cm. below the top of the nest cavity and was continued as the internal entrance tube 12 to 15 mm. in diameter, made of cerumen about 1.5 mm. in thickness and pitted on the outer surface (as are the pots shown in fig. 8). This tube extended down on the inside wall of the nest cavity for a distance of 44 cm., where it opened into the nest cavity.

¹ This is the species that has usually been called *Trigona cassiae* Cockerell. Cockerell (1930) separated *australis* from *cassiae* by the yellow mandibles and red-brown clypeus described by Friese (1898) for *australis*. However, a cotype from the type locality (Central Australia, von Müller, 1893) kindly lent by the late Mr. H. F. Schwarz of the American Museum of Natural History has dark mandibles and agrees well with specimens of *cassiae* from Brisbane. Mandibular color seems variable, for a few specimens from the latter locality have yellow mandibles. The clypeus is red-brown in some individuals from many localities.

Under the name *kootchar*, Hockings (1884) gave an excellent general account of this species. Important parts of this account were repeated later (in Cockerell, 1929b).



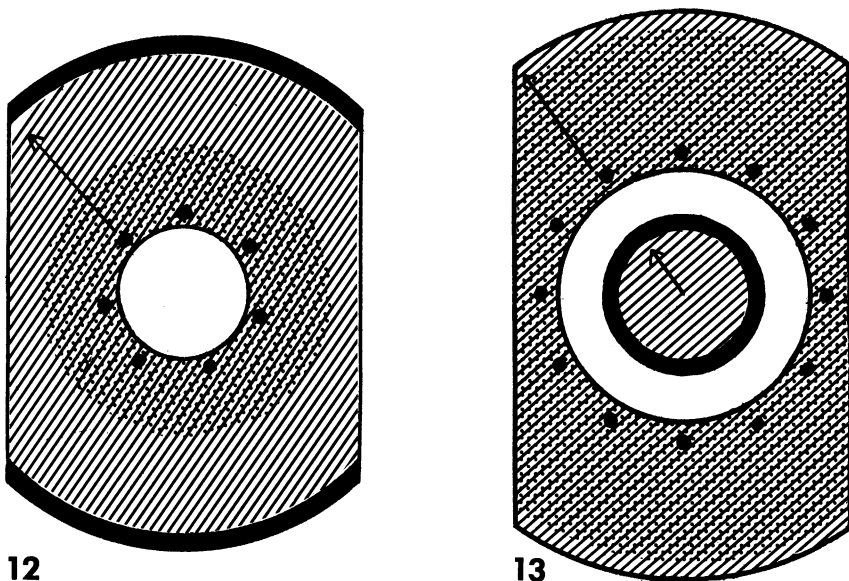
FIGS. 1-5. Portions of single nest of *Trigona australis* exposed by splitting a living *Eucalyptus* tree 17 miles south of Dalby, Queensland. 1. Mostly pollen pots (some opened, showing pale pollen, upper half of figure). 2. Mostly honey pots. 3. Brood chamber undisturbed except for removal of most of involucrum. 4. Bottom of nest, batumen plate visible near lower end of figure. The sequence 1 to 4 is from top to bottom of nest; segments of nest omitted between photographs except between 3 and 4. 5. Brood chamber of same nest, from which nearly half of cells and cocoons have been removed, exposing central hollow containing irregular sheets of cerumen supporting a few empty pots.



FIGS. 6-11. *Trigona australis*. 6. Top of cell cluster when no involucrum covered it. Note involucrum and honey pots at sides and new cells opening in various directions. 7. Newly made honey pots in box. 8. Old honey pots with pitted walls. Note that caps are not pitted. 9. Side view of brood chamber in box, showing incomplete involucrum, honey pots at top. 10. Same, with most of involucrum removed. The visible contents of brood chamber are cocoons, except at extreme top where cells can be seen. 11. Cocoons, including one of a queen.

Other nests opened were basically similar although varying, of course, according to the shape of the nest cavity.

The brood chamber in the nest described above (figs. 3 and 5) was cylindrical and consisted of a cluster of irregularly arranged cells, or, internally, cocoons. New cells were being constructed at both upper and lower surfaces but not around the lateral surface, because the entire width of the cavity had been filled with cells earlier, and there was no room for new ones at the sides. Thus there were two advancing fronts, one pro-

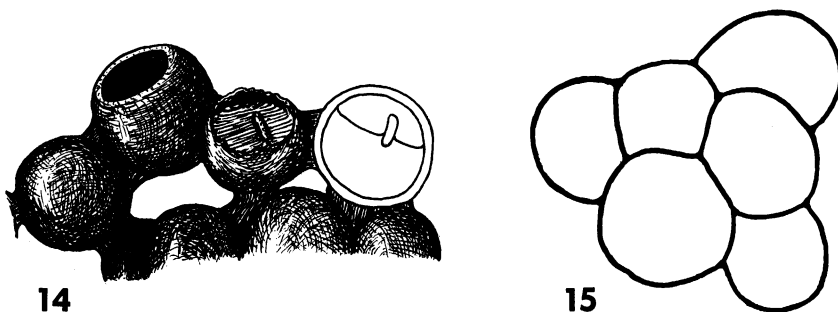


FIGS. 12, 13. Diagrammatic vertical sections through brood of *Trigona australis*. The advancing front is shown in black; the brood is shaded, cocoons being present in the stippled areas. Small black circles mark the layer where adults are emerging from cocoons. Each arrow shows progression from older to younger within the brood.

gressing upward, the other downward. In smaller nests or in nests in which the brood chamber was wide enough for enlargement, it was spherical, with the advancing front covering the entire periphery. The cells and cocoons became older towards the center of the cluster, and in the nest described above enough adults had emerged from the center to make an empty space 4 to 4.5 cm. in diameter and containing some newly constructed, loosely spaced, empty pots supported by pillars from the surrounding cocoons (fig. 5). In nests in boxes new cells were often constructed for a time mainly or entirely at the top of the cluster, perhaps because of lack of space at the bottom. When the central cavity resulting from emergence of adults reaches a certain size, new cells are started in it. Such a brood cluster, which consisted of an outer layer of cocoons (oldest ones on the inside), surrounding a space, in the center of which was a small ball of cells, is shown diagrammatically in figure 13. New cells were being made on the outer surface of this ball. The central ball of cells was supported more or less in the center of the cluster by masses of cocoons and cells. There may be a greater tendency for new cells to

develop in an upward direction than downward. The basic features of development and renewal of the cluster of cells are shown diagrammatically in figures 12 and 13.

The cells are irregularly associated in the cluster, contiguous or sometimes connected by short pillars of wax, with spaces between them, allowing bees to enter the cluster rather freely (fig. 6). The cells are spherical. The dimensions of cells and cocoons are shown in table 1. The walls of the



FIGS. 14, 15. *Trigona australis*. 14. Some cells in advancing front. The one farthest to the left is complete; next to it is one ready to receive provisions; next, a completed cell opened to show egg standing on provisions; at right is a cell seen in section showing provisions and egg. Drawing by the author. 15. Horizontal section through a small group of pollen pots.

cells are 0.10 to 0.13 mm. in thickness. New cells are constructed with openings directed away from the center of the cluster (fig. 6). The walls of open cells are not or scarcely continued beyond the level at which cells will be closed, so that open cells are little if any elongated. As shown in figure 14, the liquid provisions largely fill the cells. The viscosity and surface tension of the provisions, however, allow them to remain in position, even in cells that do not open upward, and to hold the egg (which is 0.88 mm. long) in an erect position in each cell.¹

When the curled mature larva straightens before forming the prepupa, it must elongate its cell, and as a result the cocoon which it spins is oval

¹ Rayment (1932, 1935) reports that the eggs are in contact with the provisions at both ends, and I have seen them in this position lying on the provisions in both *T. australis* and *T. carbonaria*. However, each time that cells were taken from the nest and opened under the microscope, with a minimum of jarring and disturbance, the eggs were erect, with one end entirely free from the provisions. With slight jarring they lose this position and fall down on the surface of the provisions.

TABLE 1
DIMENSIONS (IN MILLIMETERS) OF SOME NEST STRUCTURES

	<i>australis</i>	<i>cincta</i>	<i>carbonaria</i>	<i>hockingsi</i>	<i>iridipennis</i>	<i>wybenica</i>
Brood cells						
Height	3.5	2.7	3.7 -3.8	4	3.6-4	2.5 -3.5
Width	3.5	2.7	2.4 -2.6	3	3	2 -2.5
Cocoons						
Length	4-5	3.5-3.75	3.75-4.3	4.5	4	3 -3.5
Width	2.75-3	2.5	2.4 -2.5	2.75	2.5-2.8	2.25-2.5
Pots						
Height	7-11	7-9	9-20	10-13	10-25	7-9
Width	6-10	7-9	8-23	7-12	8-18	5-7
Entrance tube						
Inside diameter	8	7-15	8-16	?	10-14	10-12
Outside length	3-10	20-80	0	?	10-50	6-20

rather than spherical. The majority of the cocoons are elongated in a more or less horizontal direction (fig. 10), perhaps because the younger larvae are usually curled in a horizontal plane and therefore tend to straighten horizontally rather than vertically. The removal of most of the cerumen from the cocoons leaves them slightly spotted (fig. 11) and attached to one another by cerumen at the points of contact.

The involucrum is a single sheet of soft cerumen, often with large holes in it (fig. 9). Commonly it is absent over areas of the cluster which are rapidly growing by new cell construction (fig. 6, showing top of rapidly growing cluster). In a cavity of rather small diameter (figs. 1 to 5, 9, 10), in which the cell cluster is limited in its lateral growth, the involucrum is supported by connectives at a distance of 3 to 7 mm. from the sides of the nest cavity. Around a small cluster or a cluster in a large box, storage pots are usually constructed on the involucrum which becomes nearly unrecognizable. Once a nest, which had previously had a distinct involucrum, was found to lack it, the cell cluster being largely visible when the box was opened. Nonetheless, the involucrum is a normal feature of nests of this species and has been reported by each author studying them (Hockings, 1884; Rayment, 1935).

Newly made storage pots are shown in figures 6 and 7. They are light brown and rather smooth. Even old pollen pots retain this appearance. Honey pots, however, soon become dark brown (except for the light caps) and ultimately, probably because of the addition of strengthening materials, develop reticulated or pitted outer surfaces (fig. 8) similar to the

outer surface of the internal entrance tube. The honey is viscous and sweet, with a very pleasant taste.

The storage pots occur in irregular clusters supported by contact with surrounding structures or by short connectives allowing passage space around the clusters. New pots are added to the outside of a cluster, new walls being started on the surfaces of pre-existing pots. The result is that, while the exposed walls of pots are nicely convex, inner walls are often angulate as shown in figure 15.

The external entrance tubes seen were of thin, light brown material, made of adhering granules of soft cerumen (fig. 16), some with holes between them. The entrances are closed with plugs of rather similar material in winter, and *T. australis*, unlike *T. carbonaria*, is not found on flowers on warm winter days. At night, nests of *T. australis* are usually also closed, often by perforated sticky material (fig. 17).

Trigona (Plebeia) cincta Mocsáry¹

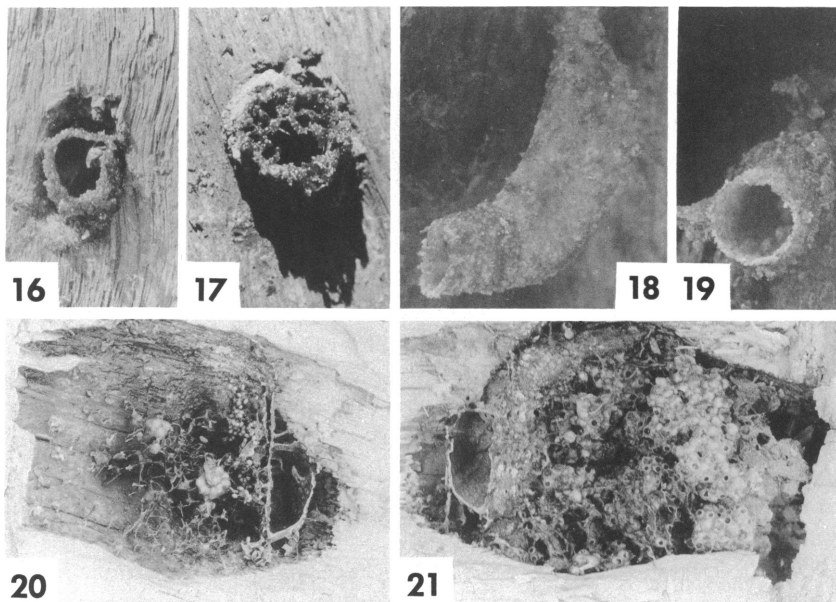
Specimens were obtained at the following localities in New Guinea, nests having been found at localities marked with asterisks: Kerema (Gulf District), Port Moresby* and Kapagere* (Central District), Papua; Buba near Lae, Northeast New Guinea. These localities are in openings in forested country, except for Port Moresby which is in *Eucalyptus* savanna. Nests at the latter locality, however, were in trunks of large, introduced, leguminous trees in the town area and may not occur in the surrounding savanna.

The four nests found were in living or recently dead tree trunks 35 cm. in diameter or larger. One nest from Kapagere was in a roughly spherical space about 20 cm. in diameter in the bole of a tree. As shown in figures 20 and 21, batumen plates, variously duplicated, reduced a larger cavity to those dimensions. Pillars connected the roof of the nest cavity (fig. 20) to large numbers of storage pots (fig. 21). The brood chamber, below most of the storage pots, was 7 cm. high and 4.5 cm. in diameter. The entrance tube resembled that of *T. australis* but projected farther from the tree (table 1, figs. 18 and 19).

Brood chambers of only two nests were examined; they were basically alike and markedly different from any nest of *T. australis* examined. Both

¹ Because Friese (1898) published Mocsáry's description, there has been confusion as to the authorship of this name. The description is apparently in Mocsáry's wording and attributed to him; the correct original reference would appear to be *T. cincta* Mocsáry, in Friese (1898, Termész. Füzet., vol. 21, p. 431). I have made no study of geographical variation in this species, but the form here dealt with should be *T. cincta cincta*, not the subspecies *percincta* Cockerell from northern Australia.

were small, as in the nest described above, but size may not be a specific character. Seen from the outside, the clusters seemed to be made up of cells closely joined together by a great deal of soft cerumen, so that there were few openings among them (figs. 22 and 24). The sides and upper parts of the clusters examined were made of irregular concentric layers that might almost be called hemispherical combs, one cell thick, with

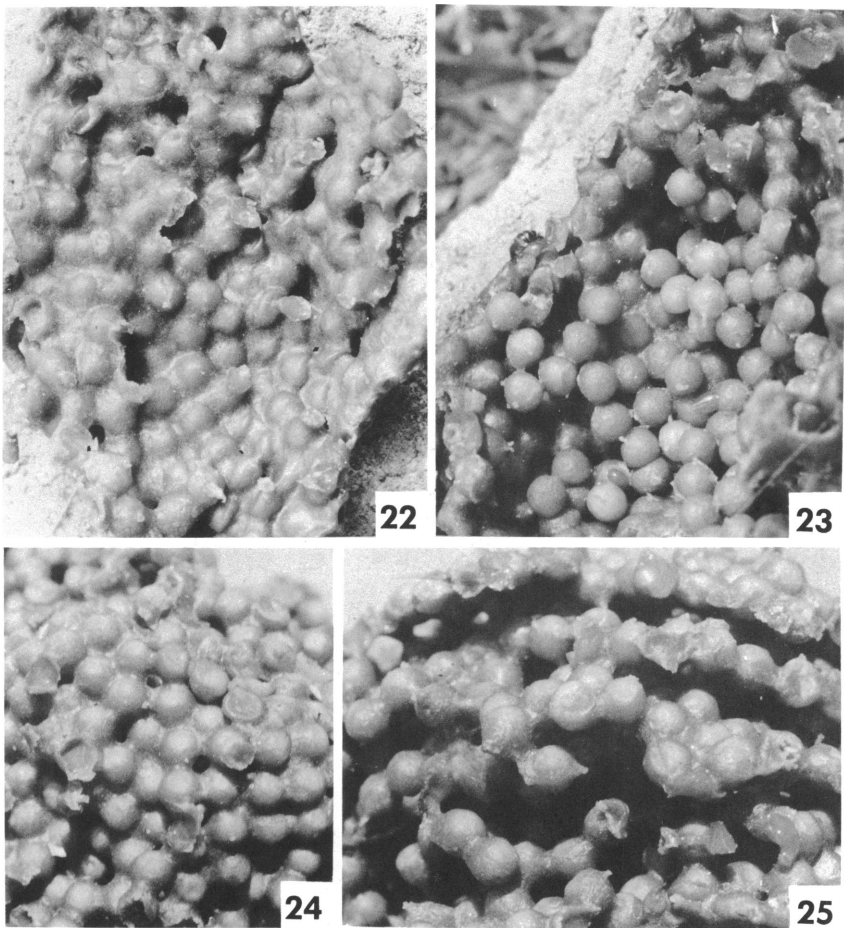


FIGS. 16, 17. *Trigona australis*, entrance of a nest from Yarriman, Queensland. 16. Open. 17. Partly closed.

FIGS. 18, 19. *Trigona cincta*, nest entrances.

FIGS. 20, 21. Nest of *Trigona cincta*. 20. Inside view of top of nest. 21. Nest seen from above, top (shown in fig. 20) removed.

spaces between them in which bees can move about (figs. 25, 26). The layers were connected by a few connectives and pillars, and the spaces between the layers were connected by a few openings. New cells, which opened upward to outward and were spherical, were constructed on the surface of the cluster (top and sides) and connected to form new layers as added cells were made. In the two clusters studied, new cells were not being made on the lower surfaces. In *T. australis* also, downward expansion of the cluster is often not evident. Inside and beneath several layers of cells like those described above, the cells (containing large larvae) are



FIGS. 22-25. *Trigona cincta*, nests from Kapagere, Papua. 22. A layer of cells from the brood chamber. 23. Cells containing large larvae, from which much cerumen has been removed. Note cells, still connected in layers by much cerumen, in upper, right-hand, and deep central parts of photograph. 24. Outside of brood chamber, showing layer of cells in side view. 25. View upward into broken cluster (marginal portion), showing arrangement of cells in irregular layers.

separated owing to the removal of much of the cerumen which joins them into layers. Often they are then connected by small points of contact much as in *T. australis*. Some, however, are completely free and lie in piles (fig. 23). The organization into layers therefore disappears. Presumably removal of the excess cerumen is necessary in order to allow the mature

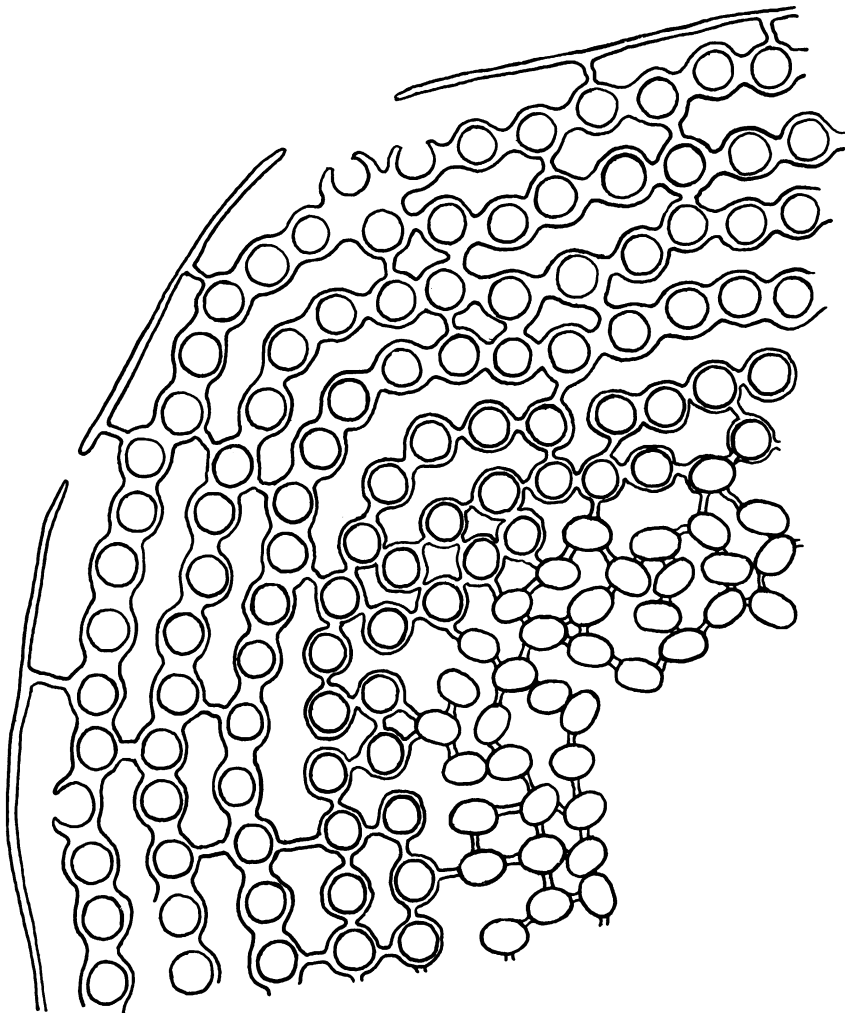


FIG. 26. Vertical section through upper part of cell cluster of *Trigona cincta*, showing involucrum (left and above), layers of cells, cocoons, and empty central space (lower right).

larvae to straighten out, elongating the originally spherical cells. The cocoons are oval as in *T. australis*, and cerumen is removed from them as in that and other species. The cocoons are connected by small bits of cerumen as in *T. australis*. In the centers of the clusters studied were open spaces resulting from emergence of adults. Presumably new cell construction would ultimately begin in these spaces, as it does in *T. australis*. Fig-

ure 26 shows diagrammatically the structure of a segment of the cell cluster.

A somewhat comparable arrangement of the cells into concentric layers has been described for *T. (Hypotrigona) araujo* Michener (under the name *T. gribodoi* form *brussuso* or *landula*) by Portugal-Araújo (1955a, 1955b). However, the cells appear to be vertically elongated in that species.

The cell cluster in *T. cincta* is surrounded by an involucre (often incomplete) consisting of a single sheet of soft cerumen, just as in *T. australis*.

The storage pots were essentially like those of *T. australis*. Old pitted honey pots, like those common in nests of *T. australis*, were not observed. The honey was viscous and sweet.

Nest entrances are of thin, delicate, yellowish or pale brown, soft cerumen, often with perforations in the distal parts of the external tube (figs. 18 and 19). At night they are closed by perforated or reticulated wax or cerumen.

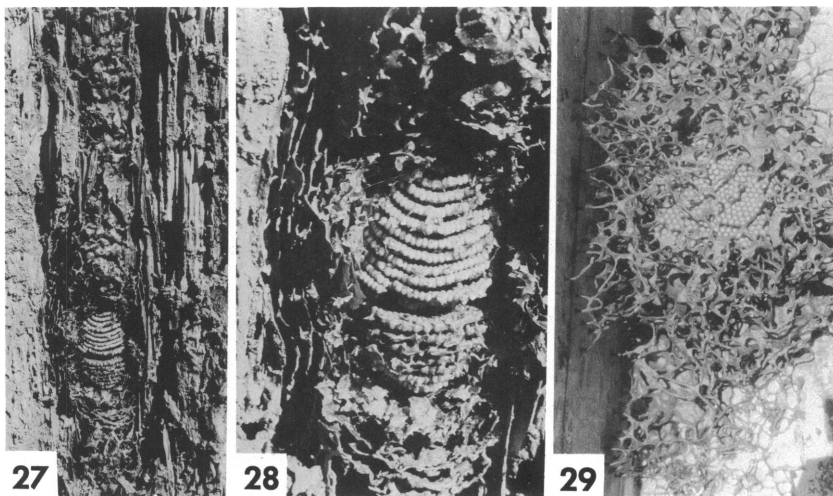
Trigona (Tetragona) carbonaria Smith

This *Trigona* is very common in coastal Queensland and extends as far south as Sydney, New South Wales. Contrary to Hockings (1884), I found it far less common in the interior where it is replaced as the dominant *Trigona* by *T. australis*. I have obtained *T. carbonaria* at the following localities in Queensland, nests having been opened for study at those marked with an asterisk: Beenleigh, Beerwah, Binna Burra (near Lamington National Park), Brisbane,* Bundaberg, Caboolture, Caloundra, Capalaba, Mount Edwards, Gladstone, Ipswich, Jimboomba, Mackay, Maroochydore,* Moggill (near Brisbane), Noosa, Petrie, Rockhampton, Sarina, Tamborine, Tibrogargen (near Beerwah), Yaamba, Yarriman.* Some were found at the edges of rain forest, but most of the localities were in *Eucalyptus* savanna.

Smith (1863) briefly described a nest of this species. A fuller account of its biology was given by Hockings (1884) under the aboriginal name *karbi*, the important points being later repeated by the same observer (in Cockerell, 1929b).

Nests of this species are especially common in trunks of large, dead, standing trees, although they also occur in cavities in living trees. The following is a description of a typical nest found in the trunk of a dead *Eucalyptus* about 35 cm. in diameter near Maroochydore (fig. 27). The nest was in a central hollow, 13 to 15 cm. in diameter, in the trunk; a portion of this cavity 81 cm. long was occupied by the nest. A horizon-

tal batumen plate, 5 to 15 mm. thick, made of brittle, dark gray material, with black nodules on its upper surface, closed the lower end of the nest cavity. Anastomosing pillars of similar material, the largest ones hollow and up to 5 mm. in diameter (most not over 2.5 mm. in diameter), arose from the plate and supported the structures above it (figs. 30 and

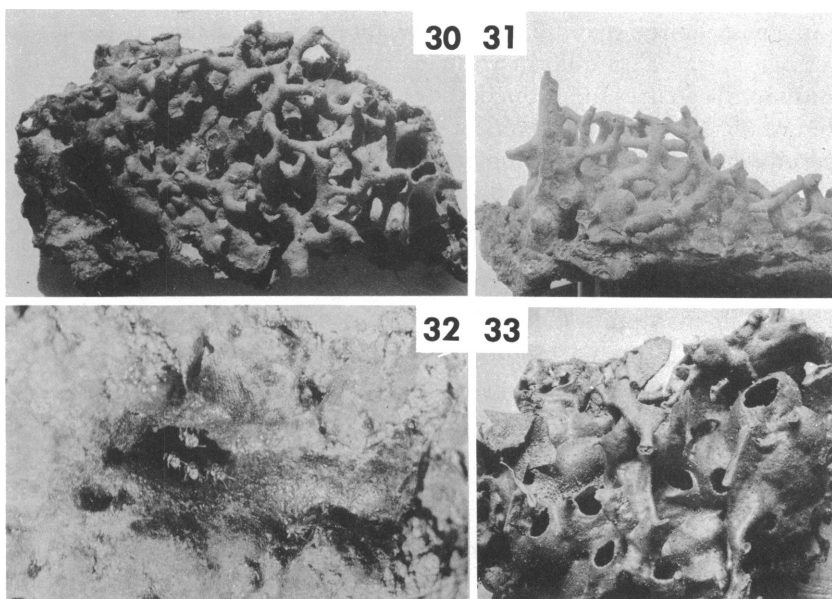


FIGS. 27–29. *Trigona carbonaria*. 27. Nest in dead *Eucalyptus* from Maroochydore, Queensland. The nest cavity extended 10 cm. above, and 2 cm. below, photograph; portion shown, 69 cm. in height. Storage pots can be seen among laminae of wood and batumen from brood chamber to top of photograph. 28. Brood chamber of same nest. Note soft layers of involucrum pushed aside to show brood on both sides below, and above, brood chamber; also several layers of brittle batumen to left of brood chamber. Gap in combs just below middle of brood chamber results from emergence of adults; the advancing front of new cells is just below this gap; above gap, all the brood was in cocoons, and two layers of cocoons can be seen at bottom of brood chamber; cells made of cerumen form the layers from the latter cocoons to the advancing front. 29. Top view of nest from Brisbane, Queensland, in large box. Note enormous number of pillars and connectives, some of which are expanded to form a very incomplete involucrum.

31). At the upper end of the cavity there was no batumen plate (although it occurs in some nests), but the cavity was closed by the thin, dark, lining batumen, mostly 0.25 to 1.0 mm. thick, which coated the inner wall of the nest cavity. Sheets of wood extended into the cavity from all sides, so that it was quite irregular in shape. The upper 55 cm. of the nest cavity contained storage pots. Next came the brood chamber, 10 cm. high, below

which was 16 cm. of irregular cerumen sheets and pillars, with a few storage pots immediately below the brood chamber (fig. 27). The nest entrance was in a crack through the side wall of the trunk.

Other nests were similar in basic organization, varying, as indicated below, according to the shape of the nest cavity.



FIGS. 30-33. *Trigona carbonaria*. 30. Top view of part of lower batumen plate of nest from Maroochydore, Queensland, showing hard brittle pillars arising from it. Note that largest pillar (at right) was hollow. 31. Side view of same. 32. Nest entrance, Brisbane, Queensland. 33. Old honey pots, nest from Maroochydore, Queensland. Note how entire group has stretched, probably in summer heat, on axis from upper right to lower left.

The brood chamber in the nest described above was 10 cm. in height and about 6 cm. in diameter (fig. 28). One was found as small as 6 cm. in height and 4 cm. in diameter, but this was in a nest occupying a small cavity and was probably unusual. The cells and cocoons are arranged in essentially horizontal layers. In some, as shown in figure 28, these layers are distinctly concave on their upper surfaces, while in other nests (fig. 37) there is only a weak tendency towards such concavity. On more careful examination, it can be seen that the layers of cells and cocoons are not separate combs but form a single spiral. Such was the arrangement in all

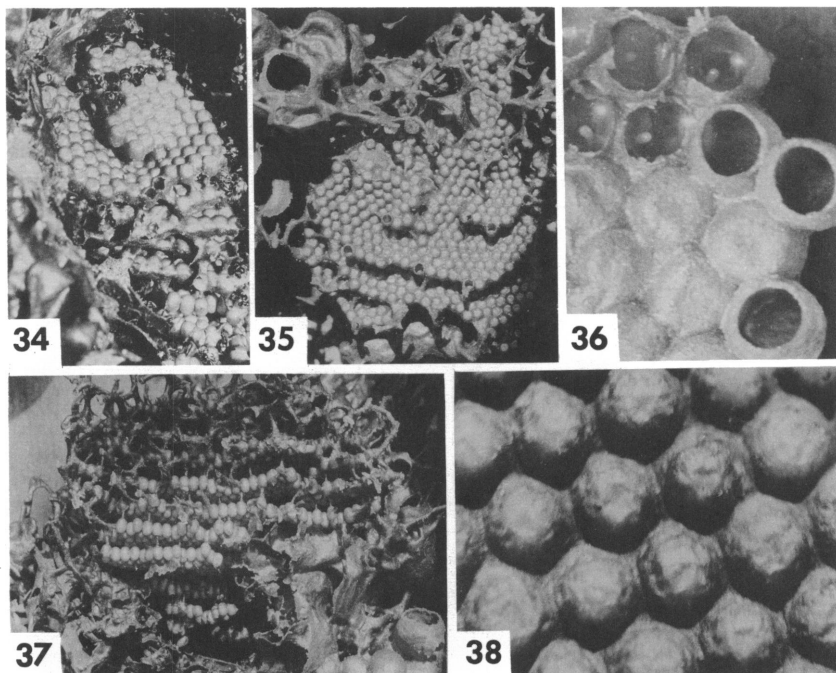
nests examined. The summit and growing point of such a spiral is shown in figure 34. Figure 35 shows an unusual condition in which a double spiral seemed to be developing, but this probably was a result of damage caused when I opened the nest a few weeks before. This figure is of interest primarily in connection with *T. hockingsi*, discussed below, which has numerous small, advancing patches of cells. Later examination of the same nest showed that it had somehow returned to the normal pattern of a single spiral. The uniform arrangement of cells in a comb is shown not only in the figures mentioned above but also by the cocoons shown in figure 38. Between the layers of cells or cocoons are vertical pillars of cerumen (fig. 37), 2.5 to 3 mm. in length and 0.5 to 1.0 mm. in diameter.

New cells are constructed at the advancing edges of the comb, as shown in figures 35 and 36.¹ As the summit advances spiral fashion, the outer margins of the upper two or three turns of the spiral advance outward as new cells are added along the margins. Each turn of the spiral reaches its maximum diameter in this way, and new cells are rarely if ever added to the margin of the comb more than two or three turns below the advancing summit of the spiral. The advancing face of the brood thus involves cells at two or three levels on the comb, the face itself being convex (figs. 39 and 40). Cells become younger towards the summit of the spiral and towards the margin of any one portion of the spiral.

The cells are made of soft brown cerumen, and the combs are connected, as indicated above, by numerous pillars of similar cerumen. As shown in figure 37, the pillars are reduced in number and thickness when the cerumen of the cells is removed after cocoon formation. Depending on the speed of reproduction, there are usually from three to five levels of cells, below which are layers of cocoons. Figure 38 shows the extent of removal of cerumen from around the cocoons; the ends of the cocoons are left nearly free of cerumen, but the sides adjacent to one another are held together by the original cell walls as shown in figure 41; exposed sides of cells on the margins of the combs are cleaned of cerumen, showing the pale brown cocoons (fig. 37).

The emergence of adults occurs first, of course, among the oldest cocoons and then towards progressively younger ones. It follows that adults appear first in the center of the lowest level of the brood and progressively outward and upward. The result is that the lower turns of the spiral be-

¹ Rayment's statements that cells of this species (1935, p. 525) and others of the genus (1930) open downward as do queen cells of *Apis* are, of course, erroneous.

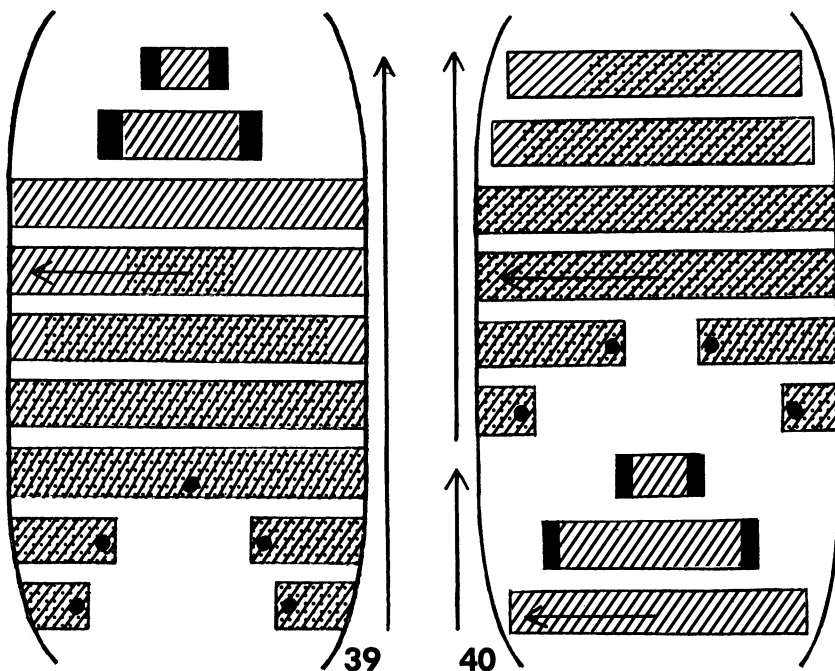


FIGS. 34-38. *Trigona carbonaria*, nest from Maroochydore photographed at various times in box in Brisbane. 34. Advancing front of comb showing formation of spiral. Exposed cocoons can be seen in lower right. 35. Advancing front of comb when a double spiral was forming. This was soon abandoned for the normal single spiral. It was not necessary to remove the involucrum to make this photograph, although at other times the brood chamber of the same nest was covered by involucrum. At the upper left are a few honey pots; the irregular shape of the closed one developed after the pot was closed. New open brood cells can be seen along the advancing edges of the comb. 36. Advancing edge of brood comb showing three open empty cells; other cells have been opened to show eggs standing in provisions. 37. Side view of brood chamber exposed by removal of involucrum; large cavity (only partly visible) at bottom results from emergence of adults from cocoons; advancing front is at top of photograph. 38. Top view of cocoons.

come first mere rings, with a cavity (resulting from removal of abandoned cocoons) inside, and then disappear as the cavity grows outward and upward into the centers of higher levels. That new supporting pillars are constructed as needed is well shown by the scattered cells often seen attached to the involucrum and indicating the location of a layer of comb otherwise entirely gone. Such cells are often supported by two or three

little pillars, although there is much less than one pillar per cell or per cocoon in the original construction. It is only as the surviving cocoons become isolated as a result of emergence of their neighbors that additional supports are built.

Thus far growth of the combs has been discussed as though it continued perpetually upward. Such, of course, is not the case. Slumping of layers of cocoons does sometimes occur so that spaces between them are reduced,

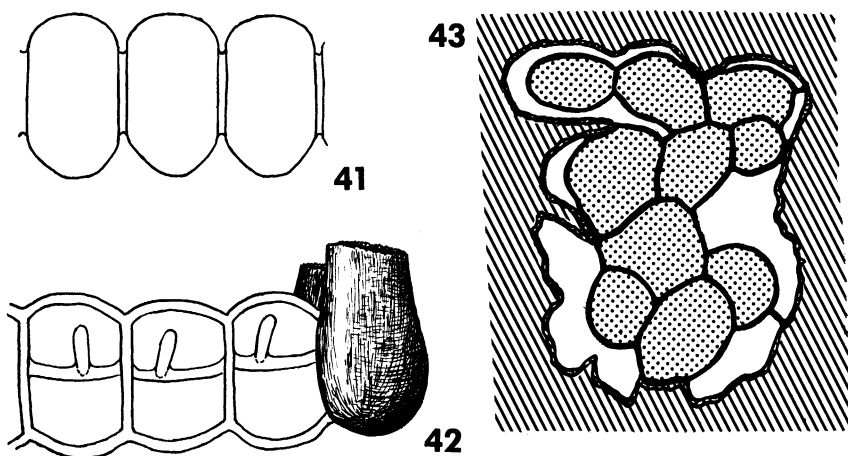


FIGS. 39, 40. Diagrammatic vertical sections through brood of *Trigona carbonaria*. The explanation of symbols is the same as for figures 12 and 13.

but this lowering never involves the advancing summit of the spiral, and therefore continuous upward growth is not possible. When the cavity at the bottom of the cluster reaches a certain size, a comb is started there and grows upward as the bees emerge from layers above it, making room for new growth below. The diagrams (figs. 39 and 40) illustrate the manner in which the advancing front of new cells moves to the top of the cell cluster and starts again at the bottom to repeat its rise. No brood chamber was found with more than one advancing front, except that for a short time in one nest new cells were still being constructed on the uppermost

layers while a new comb was being started in the cavity at the bottom. The queen must have had to go back and forth to deposit her eggs in both areas.

The dimensions of the cells and cocoons are given in table 1. Figure 42 shows cells with eggs and a new cell ready to be provisioned. The rim of such a cell stands 1.0 mm. above the tops of adjacent closed cells, and its opening is about 2.0 mm. in diameter. The total depth of provisions



FIGS. 41-43. *Trigona carbonaria*. 41. Side view of group of cocoons showing the wax remaining between them after the bees have removed as much as possible of the wax from which the cells were constructed. 42. Side view of a group of cells showing three in sectional view, eggs standing, clear fluid surface layer of provisions. At right is a cell ready to receive provisions. 43. Horizontal section through group of honey pots near top of nest from Maroochydore, Queensland. The shape of the cavity, lined by a thin layer of batumen, is shown, as is the way in which the pots (stippled) are supported in some cases by connectives, in others by broad contact.

in cells is about 2.25 mm., of which the top 0.25 mm. is clear material not mixed with pollen. The eggs are white, 0.80 mm. long and 0.27 to 0.28 mm. wide, and stand on end in the provisions supported by the viscosity and surface tension of the fluid. The eggs are consistently acentric in their positions in the cells, as shown in figure 36.

The involucrem is laminated, consisting of several sheets of soft cerumen, with perforations allowing access to spaces between them. In figure 28 the smashed and bent sheets of cerumen, visible beneath and immediately to the left of the brood chamber, are the involucrem. In some nests, at least in those in artificial containers, the involucrem may be incom-

plete (fig. 29). The nest from Maroochydore was placed in a Nogueira-Neto hive and soon built an involucrum similar to that which it had had in nature. At a later date, however, the involucrum was largely gone, and still later it was reconstructed. The removal and subsequent reconstruction may have been related to rapid expansion of the brood chamber. Sometimes in nature the summit only of the brood chamber is without an involucrum, perhaps in connection with the upward growth of the brood chamber. The combs are, of course, supported within the involucrum by pillars and connectives of cerumen.

Outside the involucrum and brood chamber, nests of *T. carbonaria* are characterized by an abundance of long pillars and connectives of cerumen. These are especially noteworthy where a nest occupies a disproportionately large box or hollow (fig. 29). They support storage pots, the involucrum, and the brood. Old pillars are often enlarged and strengthened and become brittle cerumen, at least near their connections to the batumen.

The storage pots are constructed in clusters (fig. 33). They are made of thin, soft, dark brown cerumen sometimes only about 0.13 mm. thick, but often as much as 0.65 mm. thick. Usually the pots of any one cluster all contain honey or all contain pollen. While most of the pots are normally above the brood chamber, as in figure 27, some are often beside or below the brood. Newly constructed pots (fig. 37, lower right) are of the usual shape, and pollen pots retain this shape. Honey pots, however, because of the fluidity of their contents, slump down (fig. 35, upper left) and become irregular and often very low and broad. The honey is fluid and sour. The pots, as are those of *T. australis*, are built one upon another, so that the convex surfaces of older pots form concavities in newer ones, as in figure 15. In clusters of honey pots, however, the pressure of the liquid contents straightens these convexities (fig. 43). The great variation in pot size shown in table 1 can be found in a single nest.

The batumen has already been described for the nest from Maroochydore, except to note that, as shown in figure 28, there were several layers of hard brittle cerumen in some areas of the sides of the nest. That they were not involucrum was shown not only by their texture but by the fact that they paralleled the walls of the cavity rather than curving around the brood chamber. Such laminated batumen was found in only one other nest of the species; usually batumen is limited to batumen plates and the lining batumen and, in boxes or small hollows, to the latter alone. The external entrance of the nest consists of hard, black cerumen or propolis spread out (to a diameter of 7 cm.) on the surface of the tree trunk about the opening, with no projecting tube (fig. 32). The internal en-

trance tube of rather hard, dark brown cerumen extends for several centimeters to the vicinity of the storage pots or brood. The entrance is not closed at night or in winter, and unlike *T. australis*, workers fly about and often visit flowers on warm winter days in Brisbane and its vicinity.

Trigona (Tetragona) genalis Friese¹

Only a single nest of this species was seen and it had been considerably damaged by Papuan natives before I was able to examine it. It was in deep rain forest on the Murua River near Kerema, Gulf District, Papua. It occupied a cavity in the trunk of a living tree about 40 cm. in diameter. The entrance tube was said to have projected but little from the trunk and was about 2 meters above the ground.

The cells and cocoons formed a beautiful spiral comb, similar to that of *T. carbonaria*, with a diameter of about 9 cm. There was no obvious involucre, but it might have been destroyed by natives. The cocoons were 5 mm. in height and 2.5 mm. in width. The storage pots, which were not numerous, were above the brood chamber, and were 12 to 15 mm. in diameter. The honey was even more fluid and less pleasant than that of *T. carbonaria*.

Trigona (Tetragona) hockingsi Cockerell²

A single nest of this species was sent by J. R. Wassell from Silver Plains, near Coen, north Queensland. It was established in Brisbane, and observations were made on it from time to time until the bees became moribund or died in June, presumably as a result of cold (0° C.) winter weather. (Of course the local species, *carbonaria* and *australis*, were not so much affected by cold.) The nest was in a hollow tree trunk 15 to 18 cm. in diameter, and occupied a hollow 7 to 10 cm. in diameter and over 60 cm. in length (the upper extremity of the nest hollow was not sent; therefore its full length cannot be given). Approximately the upper half of the nest was nearly packed with storage pots. Below this was the enormous brood chamber, about 37 cm. long (figs. 44, 45). Below the brood chamber was a mass of anastomosing heavy pillars arising from the lining batumen and especially from the batumen plate which was 9 cm. below the bottom of the brood chamber. Especially the lowermost of these pillars were of hard, brittle cerumen.

¹ I am indebted to Padre J. S. Moure for the identification of this species.

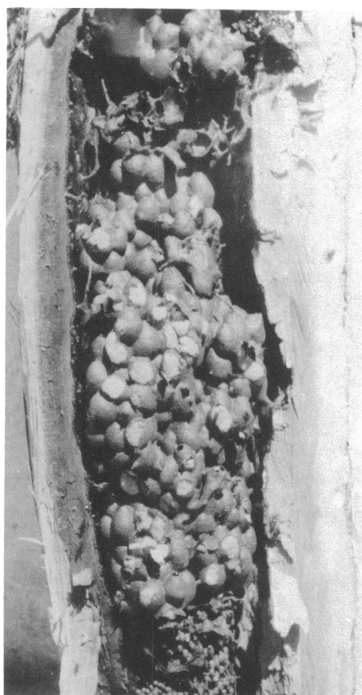
² This name was first published by Cockerell (1929a) and was republished more conspicuously a few months later (1929b). The species is morphologically very similar to *T. carbonaria*, of which it was regarded as a subspecies. However, Padre J. S. Moure and I independently concluded that it is specifically distinct.

The arrangement of the cells and cocoons in this species is intermediate between the "cluster" and the "comb" arrangement characteristic of *T. carbonaria* and others.¹ An advancing front of new cells slopes somewhat, as can be seen from figure 48, which is a nearly horizontal view of such a front. Across such a front numerous small patches of horizontal comb are constructed. These small combs advance laterally at their edges from the high side of the front (tops of figs. 50 and 51) towards the low side. The patches of comb are connected by inclined groups of cells and, where one overlaps another, by vertical pillars such as those that connect layers of cells of *T. carbonaria*. A rapidly advancing front (fig. 50), with numerous new cells, slopes more and has more layers exposed and hence more advancing edges than a slowly advancing front like that shown in figure 51. A short distance below the front, where the cells are slightly older, much more cerumen is added to them, some of this taking the form of coarse vertical and oblique pillars. The result is that away from the vicinity of the front cells seem irregular, darkened, and the appearance of horizontal combs sometimes vanishes (fig. 47) but after the cocoons are spun and the cerumen is removed from them the appearance of irregular horizontal combs returns (fig. 46).

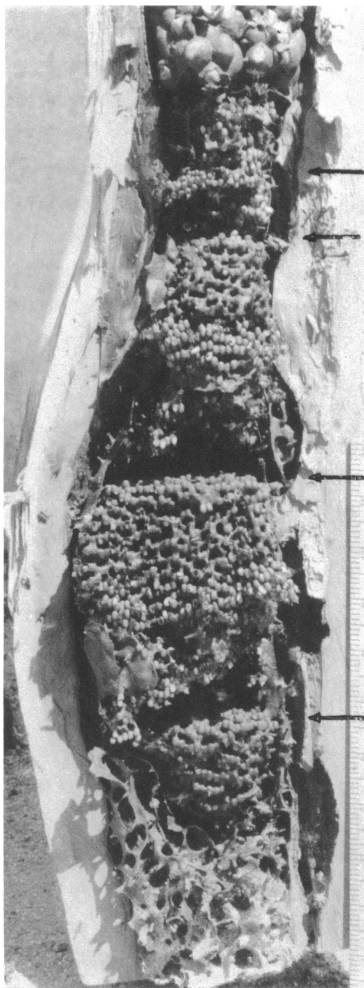
Another species in which the combs are irregular is the African *T. (Meliponula) bocandei* Spinola (see Portugal-Araújo, 1955a, 1955b). However, the type of irregularity seems to be quite different from that of *T. hockingsi*, irregularly arranged clumps of cells being particularly common around the margins of the combs. *Trigona (Plebeia) schrottkyi* Friese from South America, while having a helicoidal comb, also has small independent combs, groups of cells and sometimes isolated cells, so that it, too, seems to stand to a degree between comb-makers and cluster-makers (Nogueira-Neto, *in litt.*, February 5, 1960).

As shown in figure 45, the nest of *T. hockingsi*, when found, had four advancing fronts of cells, each with an empty space above it resulting from the emergence of adults from cocoons and the removal of the cocoons by worker bees. That multiple fronts are usual in this species is probable, for at no time after the nest was installed in a box for observation were there fewer than two advancing fronts of new cells in the brood chamber. Figure 52 illustrates the situation diagrammatically. I never lo-

¹ Hockings (*in* Cockerell, 1929b) states that the comb is spiral as in *T. carbonaria*. Both Padre J. S. Moure and I have examined type material of *hockingsi* and find no differences between my specimens and paratypes of *hockingsi* in the Queensland Museum and the British Museum. It is possible that Hockings' statement was an error or that there is variation in comb construction in this species.



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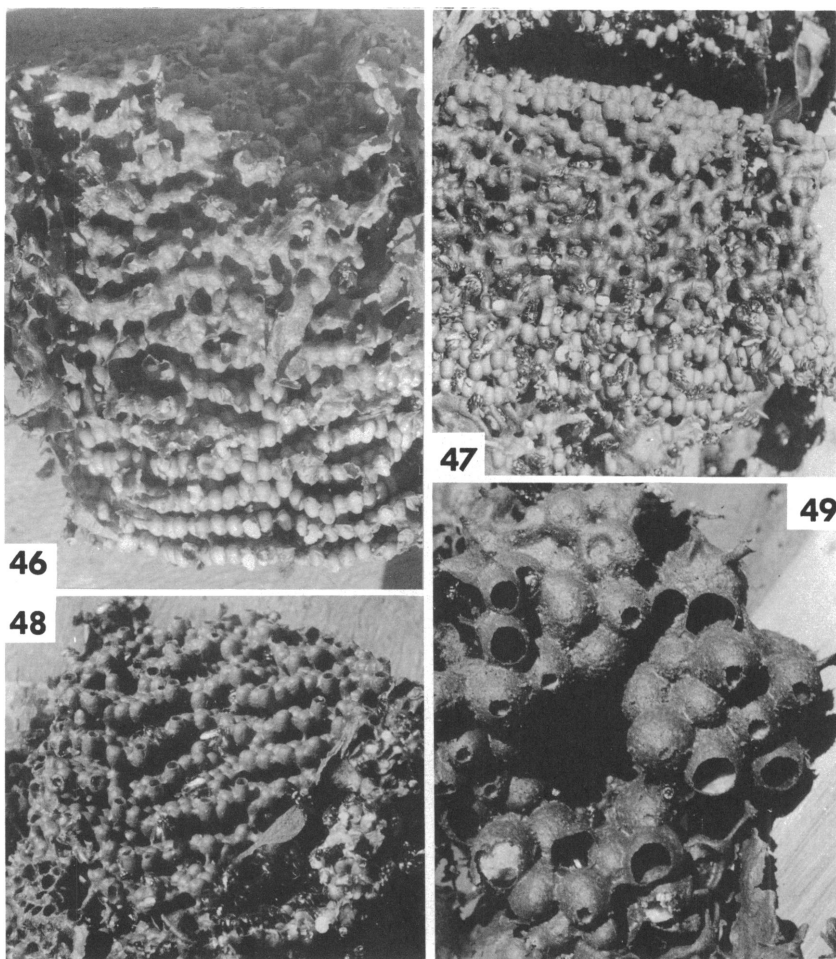


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FIGS. 44, 45. Nest of *Trigona hockingsi* from near Coen, north Queensland (taken by J. R. Wassell). Line at lower left represents 12.5 cm. in length. 44. Upper portion, showing pollen pots and upper extremity of brood chamber. 45. Brood chamber and lower part of nest, including batumen plate (just at level where tree was cut). As shown by marks at the side, there were four advancing fronts of new cells, above each of which was a cavity resulting from emergence of adults from cocoons.

cated the queen, but presumably she travels up and down to lay eggs in each front as new cells are provisioned.

As in *T. carbonaria*, new cells are constructed at advancing edges of combs, and the rim of a new cell, before it is closed, stands well above the



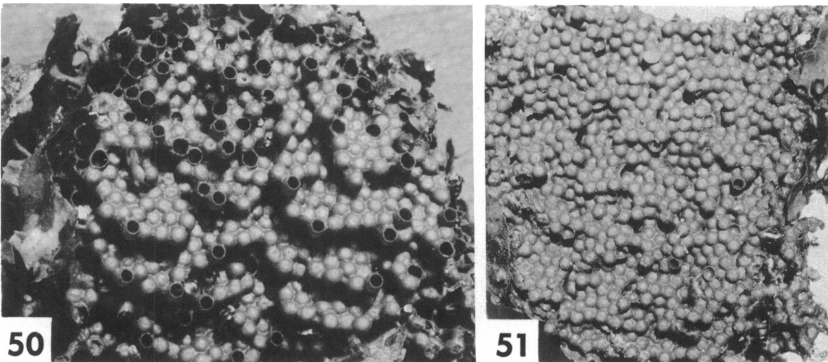
FIGS. 46-49. *Trigona hockingsi*. 46. Part of brood, showing irregular horizontal combs; pupae in cocoons below, new cells above. Note sloping and slightly concave advancing front in shadow above. 47. Part of brood, showing region where combs are very irregular. At top, cocoons from which adults are emerging; next, space resulting from emergence of adults; next, advancing front where a few layers of cells are not heavily covered with cerumen, below which cells are joined by abundance of cerumen; finally, cocoons again exposed (lower part). 48. Slightly oblique view of sloping advancing front (such as is shown in fig. 50), showing new cells being constructed at advancing edge of combs. 49. Pollen pots, some empty, some open but full, others closed and full.

caps of adjacent closed cells. Provisions, eggs, color of cells, and the like are as in *T. carbonaria*. The dimensions of cells are shown in table 1.

A laminated involucre of several perforated sheets of wax surrounds the brood chamber.

Storage pots (figs. 44 and 49) are constructed in the usual clusters; in the nest examined, many contained pollen, and relatively few contained honey. They were made of soft, dark brown cerumen as are those of *T. carbonaria*.

The entrance tube of the nest studied was said to project but little from the tree trunk. Hockings (*in* Cockerell, 1929b) says that this species builds "a large cellular excrescence over the hive entrance" and that the bees traverse its passages to enter the hive. In a box in Brisbane, the bees made an external entrance tube about 17 mm. in diameter and 10 mm. in



FIGS. 50, 51. *Trigona hockingsi*. 50. Top view of advancing front of cells, showing new cells constructed at margins of advancing combs. Photograph taken in fall, when activity had largely stopped. 51. Same, photograph taken during active season. (The differences between the two photographs may not result from seasonal differences.)

length. The internal entrance tube extended for about 10 cm. down the inner surface of the box. Almost the whole of the external part of the entrance tube and much of the internal part were made of paint, brought in from freshly painted surfaces on the tibiae of worker bees. All colors were brought to the nest in Brisbane, although white predominated. Colonies of *T. carbonaria* and *T. australis* showed no such behavior. It seems probable that the numerous complaints about the removal of paint by *Trigona* from newly painted objects (e.g., houses) in northern Queensland result from the activities of *T. hockingsi*.

Trigona (Tetragona) iridipennis Smith¹

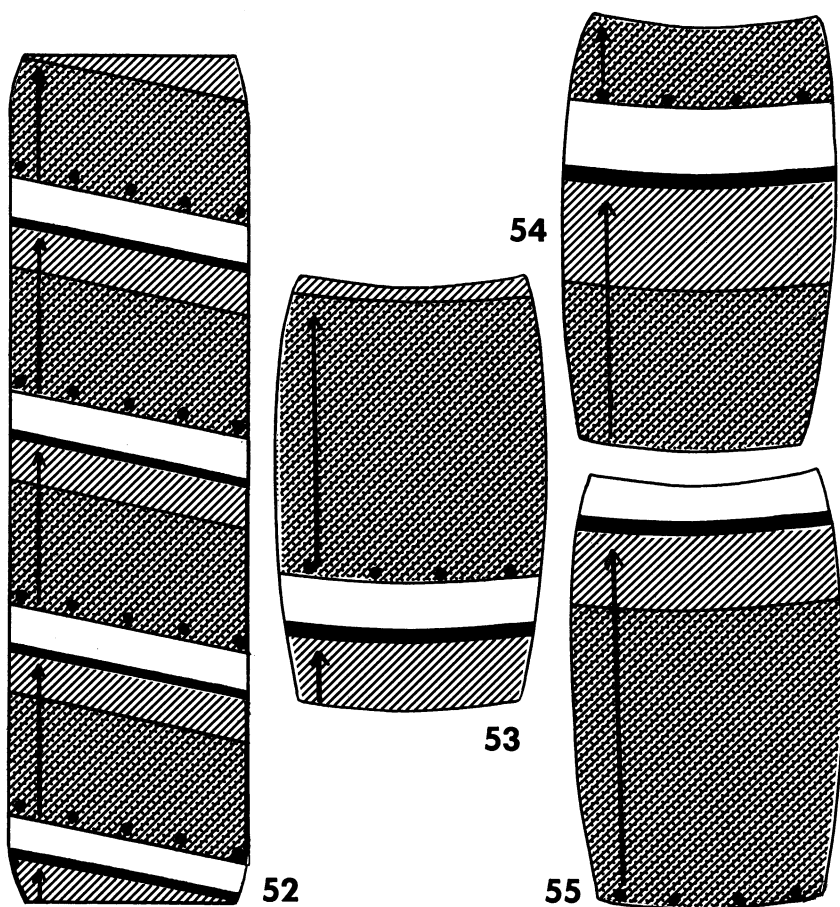
Nests of this common and widespread Indo-Malayan species were found at Port Moresby; Koitakinumu Estate, Sogeri Plateau, 1600 feet in altitude; Bisianumu, Sogeri Plateau, 1800 feet in altitude; and Kapa-gere, near Rigo; all in the Central District of Papua. Other nests were found near Bubia, vicinity of Lae, Northeast New Guinea. The nests were found in rain forest, on rubber plantations (formerly rain forest), and in trees or logs in villages and towns.

Nests were found in a wide variety of situations, ranging from hollows in trees such as are used by the species discussed above, to small hollows, boxes, and irregular spaces in masonry walls and stairways. Unlike the species already discussed, which apparently consistently make nests in tree trunks, *T. iridipennis* sometimes nests in hollows in or among roots of trees, in fallen logs, and other places at or near the ground level. One nest was in an empty tank inverted on top of the ground. Schwarz (1939) summarized the available information on nesting places of this species and notes similar adaptability, including even nests in the soil.

In the small and often irregular hollows there is no need for typical batumen plates, although perhaps they are made by this species on occasion. The nests contain relatively few pillars and connectives of cerumen. The brood chamber is below or sometimes beside the storage pots. The largest brood chamber seen was in the nest from Koitakinumu Estate; it was cylindrical, 22 cm. in length and 7 to 8 cm. in diameter. The smallest occupied a wedge-shaped space only 3 cm. in height and 6 cm. in horizontal dimension.

The cells and cocoons are in a cluster arrangement, not in combs. Unlike those of the species of *Plebeia* discussed herein, and like those of the other *Tetragona*, the advancing front of new cells is roughly horizontal and

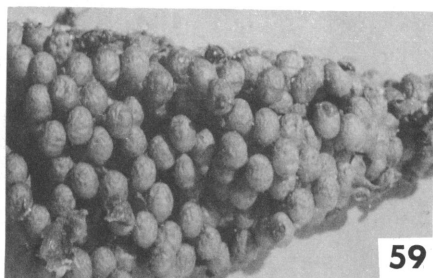
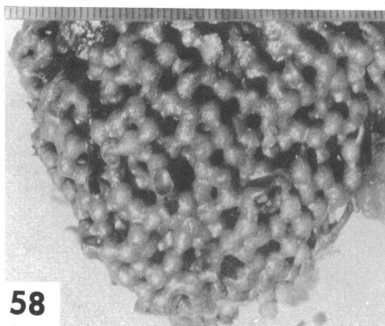
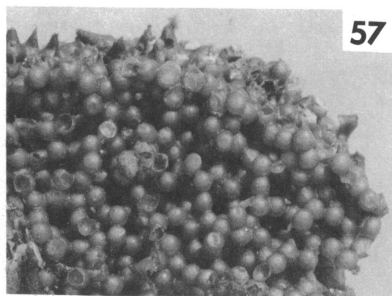
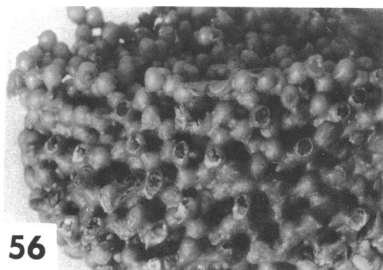
¹ This species was identified by me as *T. iridipennis* Smith, 1854. Later Padre J. S. Moure of the Universidade do Paraná, who has kindly examined some of my specimens, pointed out that my material from locations in New Guinea is slightly larger than typical *iridipennis*, although not so large as *valdezi* Cockerell. I suspect that it may be *Trigona biroi* Friese, 1898 (part). The latter was described from New Guinea specimens collected by Biró and Philippine specimens from the Mocsáry collection. The type series is likely to have been composite. Probably the holotype, if designated by Friese, was a specimen collected by Biró in New Guinea, in view of the patronymic. However, having access to Philippine cotypes only, Schwarz (1939) applied the name *biroi* to the Philippine insect. Because the species from New Guinea is at least extremely close to *iridipennis* and is probably the same as the form called *iridipennis* from the Solomon Islands, it seems best to retain that name for the moment. The nest structure seems to be similar in *iridipennis* (or its close relatives or geographical variants) all the way from Ceylon to New Guinea. (Compare photographs made in Ceylon by Lindauer, 1956, with those in the present paper.)



FIGS. 52-55. Diagrammatic vertical sections through brood. 52. *Trigona hockingsi*. 53-55. *Trigona iridipennis*. The explanation of symbols is the same as that for figures 12 and 13.

progresses upward through the brood chamber, and all new cells open upward. Diakonoff (1947) has clearly shown, for this or a related species, how new cells are constructed at the advancing front, and that, as in the Australian species discussed above, the egg stands on end supported by the liquid provisions. The cells are vertically elongated, and the cocoons are vertical. The newly constructed cells are attached at the points of contact, and sometimes three or four cells are broadly attached together (fig. 58), but there are no small combs as in *T. hockingsi*. Rarely, where the

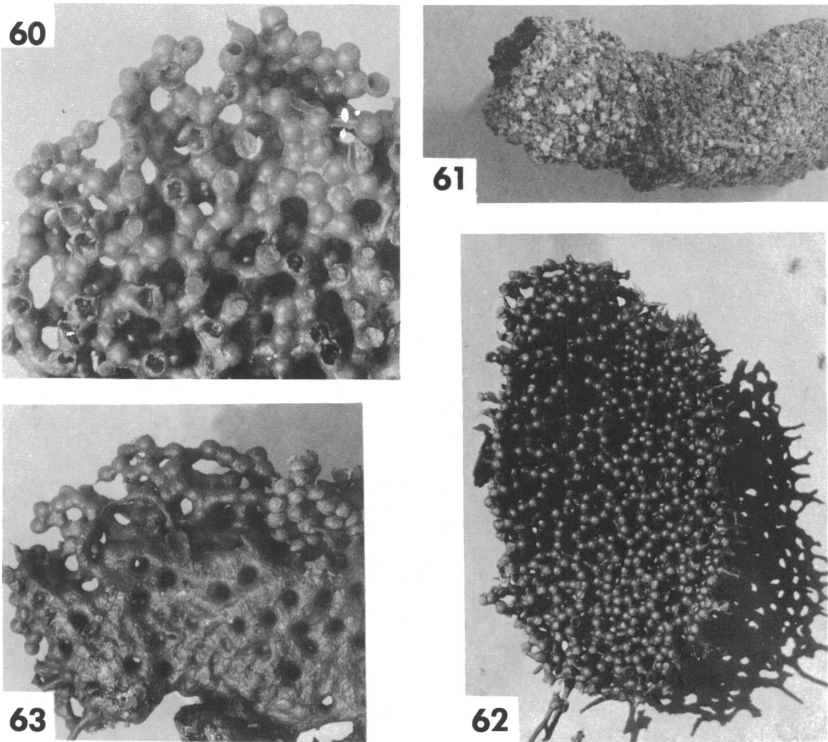
cells are crowded into a thin horizontal or sloping crevice, they form larger groups at about the same level (fig. 60) but such appears to be a result of the type of space occupied. That the species can adapt itself to such limited space seems to be a significant specific character. In nests



FIGS. 56-59. *Trigona iridipennis*. 56. Side view of part of brood cluster of nest from hollow stump at Koitakinumu Estate, Papua, showing slightly concave advancing front above, cells of front relatively free, not joined by large quantities of cerumen; slightly below, front cells are joined by quantities of dark cerumen. Broken points scattered over latter area were connectives to wall of cavity. 57. Top view of advancing front. 58. Side view of brood, showing closely joined cells; scale in millimeters. 59. Side view of mass of cocoons from nest at Bubia, New Guinea, fitted into a wedge-shaped cavity in a log.

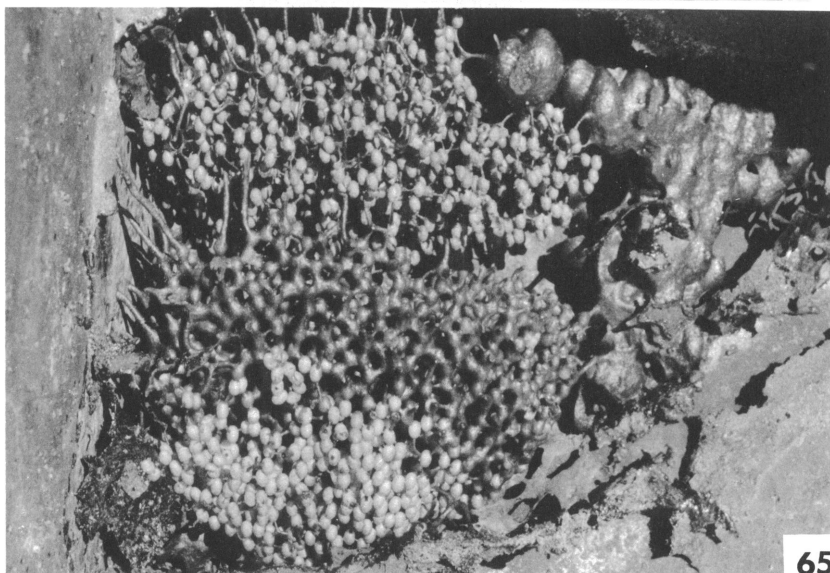
having adequate space and a more or less cylindrical cell cluster, the advancing front of cells is somewhat concave (figs. 56, 57, and 62), possibly because, as connections of cerumen among the cocoons above the front are removed, a few cocoons fall onto the advancing front and lie there, in the center, in horizontal rather than the original vertical positions, until the emergence of the bees. Such cocoons are often much more numerous than in figure 57, and would hinder the building of new cells in the center of the front.

Some time after the cells are closed, much additional cerumen is added to them and to the connections among them. This condition is well shown in figure 56, where the upper cells next to the front are seen to be a little



FIGS. 60–63. *Trigona iridipennis*. 60. Oblique view of sheet of cells, several cells thick at lower right, tapering to one cell in thickness at advancing edge (above and left) where new cells in various stages of completion are visible. This sheet of cells penetrated a thin, subhorizontal, wedge-shaped space in a log near Bubia, New Guinea, which it nearly filled. Scattered broken places represent pillars to roof of cavity. 61. Entrance tube, nest from Bubia, New Guinea. 62. Top view of advancing front of cells. Note by shadow (upper left) that entire front was gently concave. Light spots in shadow at right show how porous the front of cells was. 63. Bottom view of sheet of cells shown in figure 60. Lower half of figure shows cells completely fused by cerumen; they were separated from the floor of the cavity only by crawling space for the bees.

paler and less fully fused together than those below. The result, as shown in figure 58 and especially figure 60, is that groups of four, eight, or more cells become broadly joined together; interstices among the cells remain,



FIGS. 64, 65. *Trigona iridipennis*, nest from Bubia, New Guinea, in a tank inverted on the ground, and isolated from most of the space within the tank by batumen sheets made by the bees; these were broken away to make the photographs. 64. Entire nest. Batumen sheets enclosed a narrow entranceway, extending to right, as shown, and ending in the entrance tube at ground level beyond and below lower right corner of photograph. 65. Main part of nest showing storage pots (right) and brood. The latter consists of cocoons above and below, cells between, with advancing front near middle of photograph. Space left by emergence of adults and destruction of cocoons visible above advancing front.

however, and allow the entrance of worker bees. The maximum degree of joining of cells by excess cerumen is seen in figure 63, which is the under side of the thin wedge of cells shown in figure 60. Here the lower layer of cells, separated only by crawling space from the lining batumen, was a nearly continuous plate of cerumen, with only a few perforations among the cells; it was necessary to break the plate to learn that it was made up of cells instead of solid cerumen.

As shown in figures 59, 64, and 65, cerumen is largely removed after the cocoons are spun, and the cocoons are then connected and supported only by small points of cerumen or, as shown in figure 65, in some cases by small pillars and connectives of cerumen.

There is only one advancing front per nest. Figures 53 to 55 illustrate diagrammatically the upward progress of the front.

The involucre is completely absent.

The storage pots are constructed in the usual way but are not numerous; the honey is extremely liquid and sour. The dimensions are shown in table 1.

The batumen is usually limited to lining batumen, although perhaps batumen plates are sometimes constructed. The nest represented by figures 64 and 65 was made in an empty tank turned upside down on the ground. The entrance was at ground level at the corner of the tank, and a tube made of brittle cerumen or propolis extended along the wall of the tank to the nest. At one point (upper right, fig. 64) a small cluster of honey pots was in an enlargement of the tube. At various places along the inside of the tube were masses of sticky material. The tube and the entire nest were enclosed by thin, dark gray, brittle batumen, in some places two layers thick, with spaces containing a few bees between the layers. This batumen was chipped away, after which the photographs shown as figures 64 and 65 were taken.

The external entrance tubes in this species are black, thick-walled, hard but not brittle, and sometimes had white particles (paint?) on the outside (fig. 61). The outer surface is rough. No internal entrance tube was found in nests of this species, although the external tube may extend some distance through the substrate or along the wall of a cavity to the nest. It should be noted that previous authors (see Schwarz, 1939) have recorded far larger and longer entrance tubes than those that I found in New Guinea. Lindauer (1957) states that the entrance is closed at night.

Trigona (Tetragona) wybenica Cockerell¹

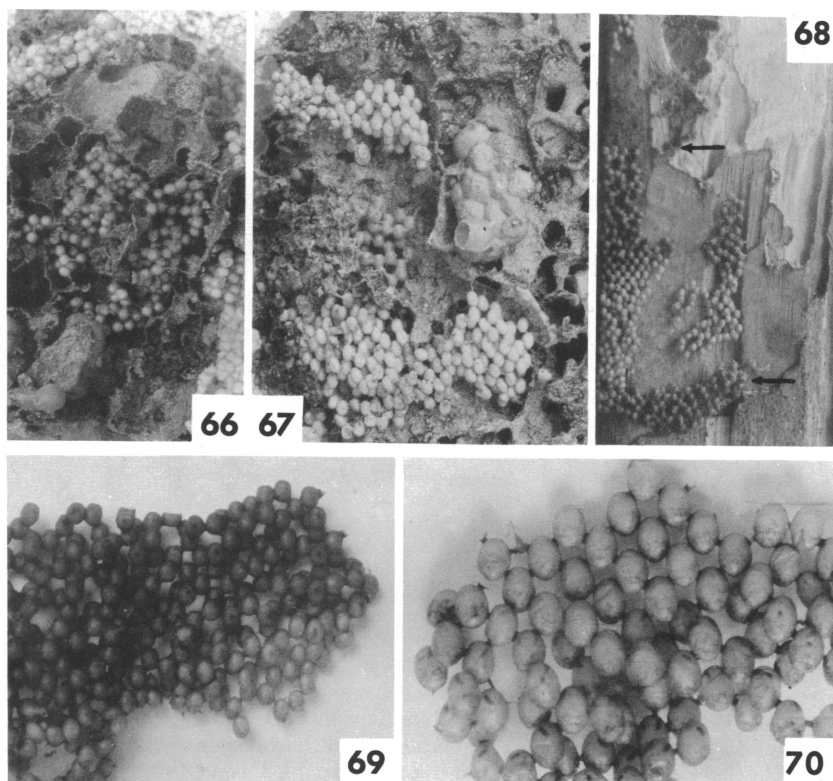
Nests of this little *Trigona* were found at Mossman, northern Queensland; and at Kerema and Port Moresby, Papua. The species was taken on flowers at Bubia, near Lae, Northeastern New Guinea. The nests were in exposed sunny situations, one in a dry rotten fence post, the others in wooden buildings. No nest was found occupying a large hollow; in all cases the nests were in thin, interconnecting, rot cavities or in crevices between boards in houses or other buildings. Similar nesting places have been recorded by Schwarz (1939) and Krombein (1950) for this or closely related species. The result is diffuse nests with groups of brood cells and storage pots scattered about wherever space is available.

The cavity of the single nest found in a rotten fence post seemed to be divided by irregular sheets of hard cerumen (figs. 66 and 67) into thin spaces for cells and pots. It therefore seems that scattering of these structures is probably an obligate rather than a facultative characteristic of nest architecture in this species.

Populations of nests of this species are small and nest cavities correspondingly so. For example, one of the larger nests in houses at Kerema was found to occupy a horizontal space 5 to 8 mm. high between two boards, and a vertical space 6 mm. thick and continuous with the horizontal one at the side of one of these boards. The horizontal space was 105 cm. long and for the most part about 7 cm. wide; the vertical portion of the nest was about 40 cm. long and 5 cm. high. These spaces or cracks were, of course, largely enclosed by the boards themselves, covered with very thin and inconspicuous lining batumen, but at some places at the edges where the spaces would have been open to the outside, small walls of batumen (black, rather brittle cerumen) closed the cracks, enclosing the nesting space. Such a wall can be seen surrounding the nesting area in figure 68, which shows part of a nest between vertical boards of a window frame.

Cells and cocoons are not arranged in combs but are in irregular arrangement and attached to one another and to the walls of the nest at points of contact or by short pillars (figs. 69 and 70). Normally crawling spaces exist on each side of the layer of cells in a crevice. Unlike *T. hock-*

¹ Both Padre J. S. Moure and I have seen type material of *T. wybenica* Cockerell, 1929 (described from Thursday Island in Torres Strait), and we agree that my specimens both from Australia and from New Guinea are *wybenica*. Padre Moure suggests that *clypearis* Friese, 1908, from New Guinea may be a prior name for the same species. To me it seems probable that *wybenica* is only a race of *T. fuscobalteata* Cameron, 1908, which is common farther north (Malaya to the Caroline Islands).



FIGS. 66–70. *Trigona wybenica*. 66. Top view of brood in nest from Mossman, north Queensland, showing how brood is separated by sheets of propolis. Note queen cocoon near top center. 67. Side view of portion of same nest, showing small group of cells and two groups of cocoons; queen cocoon below center of upper group of cocoons. A group of honey pots is at right of center; the one empty pot was made after the nest was opened and while stored for two days with left side upward. 68. Part of nest in crack between vertical boards from Kerema, Papua. The part of the crack which forms the nest is enclosed by a sinuous wall of propolis. Two advancing fronts of cells can be seen (indicated by ink marks). Cocoons are pale, in contrast to dark cells. 69. Cells and (below) cocoons from same nest. The advancing front is above, where incomplete cells can be seen. 70. Cocoons from same nest.

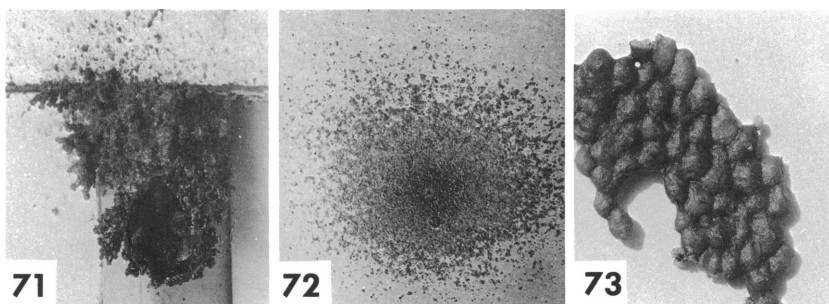
ingsi and *T. iridipennis*, added cerumen is not put on the cells after they are constructed. Both cells and cocoons are vertically elongated. The former are rather light brown, the latter straw-colored. When cells are constructed in a horizontal space, there is no distinct advancing front but in a nest in vertical spaces there may be several advancing fronts. Figure 68

shows two fronts in a single portion of a nest. As in other species, an empty space resulting from the emergence of adults and the removal of empty cocoons is above each front. Each nest studied contained one queen, which must therefore have had to move around the nests to the various advancing fronts where new cells were being made and provisioned.

There is no involucre in nests of this species.

The storage pots are small and generally in patches a single layer in thickness (fig. 73), presumably because of the flat spaces occupied by nests of this species. The dimensions are shown in table 1.

There are no large pillars of cerumen in nests of this species. The nest entrance consists of black, rather thick, stiff but not brittle cerumen. In



FIGS. 71-73. *Trigona wybenica*. 71. Nest entrance in building, Port Moresby, Papua. 72. Small opening (above nail head) in wall, around which bees have placed propolis. No nest was constructed in this location. 73. Layer of storage pots, Kerema, Papua.

some cases there is virtually no external entrance tube, but often there is a short one, usually tuberculate or with projections on the outer surface. Figure 71 shows one of the most fully developed entrance tubes of this species that were seen. The small spots of wax away from the entrance tube on the wall of the building are characteristic. There is no internal entrance tube.

DISCUSSION OF ARCHITECTURE

Table 2 summarizes the main architectural and related features of the nests of the seven species of *Trigona* that were studied. It is evident that certain characteristics (nos. 2, 3, 4, 8, 10, 12, 14) separate the two subgenera as they are represented among the seven species. These are not all subgeneric characters, for species in other areas do not in all cases

TABLE 2
SUMMARY OF THE MAIN FEATURES OF THE NESTS

	Species ^a												
	A	B	C	D	E	F	G						
1 Arrangement of cells (spiral comb, 1; many small combs, 2; cluster, 3; concentric layers, 4)	3	4	1	1	2	3	3						
2 Shape of cells (spherical, 1; vertically elongated, 2)	1	1	2	2	2	2	2						
3 Direction of opening of cells (up, 1; radial, 2)	2	2	1	1	1	1	1						
4 Shape of advancing front (spherical or hemispherical, ^b 1; convex, 2; flat or concave, 3)	1	1	2	2	3	3	3						
5 Number of advancing fronts (one, 1 ^c ; more than one, 2)	1	1	1	1	2	1	2						
6 Cerumen added to cells after closing (yes, 1; no, 2)	2	2	2	2	1	1	2						
7 Outer cerumen removed from cells before cocoon formation (yes, 1; no, 2)	2	1	2	2	2	2	2						
8 Involucrum ^c (laminated, 1; one layer, 2; absent, 3)	2	2	1	3?	1	3	3						
9 Pots (small, 1; large, 2)	1	1	2	2	2	2	1						
10 Honey (sweet, viscous, 1; sour, liquid, 2)	1	1	2	2	2	2	2						
11 Pillars and connectives ^d (fully developed, 1; rather well developed, 2; weakly developed, 3)	2	2	1	2	2	2	3						
12 Entrance at night (open, 1; closed, 2)	2	2	1	1	1	1	1?						
13 External entrance tube ^e (long, 1; short, 2; absent, 3)	2	1	3	2?	2?	1	2						
14 Walls of external entrance tube (thick, 1; thin, 2)	1	1	2	2	2	2	2						
15 Internal entrance tube (present, 1; absent, 2)	1	?	1	?	1	2	2						
16 Type of cavity (large hollow, 1; variable, 2; small space, 3)	1	1	1	1	1	1	3						

^a These species are designated as follows: A, *australis*; B, *cincta*; C, *carbonaria*; D, *genalis*; E, *hockingsi*; F, *iridipennis*; G, *wybenica*. The first two belong to the subgenus *Plebeia*; the others, to the subgenus *Tetragona*.

^b Limited space may make such a front merely convex.

^c Minor exceptions are described in the accounts in the text.

^d Depending to an important degree on the nature of the hollow occupied.

^e The maximum development is indicated. Short entrance tubes may be found at some nests of any ordinarily long-tubed species.

agree. The probabilities are that the characters listed above are, however, diagnostic of the species groups (phyletic lines) concerned, even though not of the entire subgenera.¹

The arrangement of the brood cells is a character that has received much attention in the past, for it has been assumed (e.g., by Kerr and Laidlaw, 1956) that the cluster arrangement is primitive and the comb specialized. It seems logical that the apparently unorganized arrangement should be more primitive than the organized one. The cluster arrangement occurs in some but not all species of the following groups of the tribe Meliponini: *Lestrimelitta*, *Plebeia*, *Tetragona*, and *Scaura*. It probably occurs in all species of *Hypotrigona*. It is clear that, if the cluster arrangement were primitive and characterized primitive species in each of these groups, combs must have arisen independently at least in the first four groups listed. The alternative, that the cluster arrangement is specialized, implies that the cluster-making behavior arose independently in several comb-making groups. To me it seems unlikely that the habit of organization of cells to form almost identical combs would arise repeatedly and independently, while it seems that disorganization of combs to produce the cluster arrangement might more easily occur independently in various phyletic lines.

I suspect that the cluster arrangement of cells such as is found in *T. wybenica* and *T. iridipennis* is an adaptation to the regular (*wybenica*) or facultative (*iridipennis*) use of small crevices or small irregular spaces for nests. Moure, Nogueira-Neto, and Kerr (1958) have indicated that lack of nesting places is an important factor limiting populations of meliponine bees. Obviously adaptation to a different type of cavity would be an important step in the evolution of these bees. It is significant that species of *Tetragona* occupying such small cavities do not construct involucra. There would be no space for involucra in the cavities used. Virtually no cluster-making species constructs an involucre.

The only known exceptions to the last statement are *T. (Plebeia) australis* and *cincta*, both of which make clusters of cells in large cavities and construct involucra. These species may be primitive in their architecture, and *T. cincta*, the cells of which are in layers and open laterally at the sides of the cluster and upward at the top, might suggest the manner of evolu-

¹ It is reasonable to suspect that all Australian *Plebeia* are rather closely related to one another and make clusters of spherical cells. However, Rayment (1930) says, in describing *T. (Plebeia) cockerelli*, that these bees make horizontal brood combs. Probably he refers to *Trigona* in general rather than this species, and, as he further says that the cells open downward, one is perhaps justified in ignoring the entire paragraph on biology.

tion towards both vertical combs with horizontal cells (as in *Dactylurina*) and horizontal combs with vertical cells (as in most *Trigona*).

If indeed the *Plebeia* of the Australian region are the most primitive of the Meliponini in the type of cell cluster, it is perhaps significant that they occupy a geographically isolated area (the nearest other species of *Plebeia* being in Africa) and that in three architectural characters (2,¹ 3, and 8 in table 2) they are, so far as I know, unique among the Meliponini.

It seems likely to me that cluster-makers other than the *Plebeia* of the Australian region arose from forms making horizontal combs. As do *T. iridipennis* and *wybenica*, they have vertically elongated cells opening upward. One reason for this arrangement in a cell cluster may be that such bees arose from forms having cells that were crowded together in horizontal combs.

It seems quite possible that most of the forms that have been stated to be primitive because they make cell clusters are in reality specialized in this very feature.

Figures 12, 13, 26, 39, 40, and 52–55 illustrate diagrammatically the organization of the brood chambers, with special reference to the advancing fronts, for several species. As can be seen, in figures 12 and 13 (*Plebeia* of the Australian region) the cluster grows in all directions (although principally upward and laterally, little downward, according to most observations), and the advancing front is convex. In figure 39, the front is also convex, if the various levels of comb are considered together. In figures 52 to 55 the fronts are flat or concave. Data on the limited fauna of the Australian region are insufficient for any conclusions to be based on the primitiveness of such characters, but it is important that this and similar characters be studied in further detail within the American and African faunas.

If the Australian *Plebeia* are primitive, their simple involucre may also be primitive; laminated involucre may have arisen later and, as suggested above, may have been lost entirely in species that make use of small and irregular nesting cavities.

An interesting point for which objective data are lacking but which is nonetheless probably true is that the amount of storage, and particularly the amount of honey stored, is much greater in cool than in warm climates. Thus *T. australis* and *T. carbonaria* in southern Queensland store large quantities of honey and were much sought after by the

¹ Paulo Nogueira-Neto of São Paulo writes that in *T. (Plebeia) schrottkyi* Friese from South America perhaps 5 per cent of the cells are spherical; the rest are somewhat elongated vertically, and all open upward.

aborigines, while the species of northern Queensland and New Guinea store but little, so little that the natives of New Guinea seem to pay little attention to their nests. Paulo Nogueira-Neto tells me, however, that in Brazil species in tropical areas sometimes store more honey than their close relatives in cooler regions.

CELL PROVISIONING AND NEST CONSTRUCTION

SUPPOSED PROGRESSIVE FEEDING

It is well known, as indicated in the reviews of meliponine biology by Schwarz (1948), Kerr and Laidlaw (1956) and Moure, Nogueira-Neto, and Kerr (1958), that in bees of this tribe each brood cell is provided with all the necessary provisions, after which the queen lays an egg in it. The usually high side walls of the open cell (fig. 42) are then reshaped by a single worker to form the cap of the cell, which is thus closed and is not opened at any time for the introduction of more food. In short, the cells are mass provisioned.

Rayment (1932, 1935, and quoted in the reviews listed in the preceding paragraph) stated that in both *T. australis* and *T. carbonaria* he had repeatedly observed that the cells were left open for as much as three days after the hatching of the egg and that "after-feeding" takes place. By "after-feeding" he clearly meant addition of food to the cell after egg laying; probably he meant after hatching. It is difficult to understand these reports. I have made observations throughout a year on nests of *T. australis* and *T. carbonaria* established in hives of the type designed by Nogueira-Neto (1948, 1953) and on a nest of *T. hockingsi* for a period of six months. In no one of these nests, nor in nests of these and other species opened in the field, was there ever noted any evidence whatever that cells were left open or reopened after egg laying. Any cells artificially opened were promptly sucked dry by worker bees. My observations covered periods of pollen shortage, nectar shortage, and both together, as well as all seasons, so that it seems improbable that any environmental conditions would induce the bees to leave the cells open after egg laying. Moreover, Hockings (1884) for *T. australis* and *T. carbonaria* and later (*in* Cockerell, 1929b) for *T. hockingsi* and *T. wybenica*, long before Rayment's publications, recorded accurately the way in which the cells are mass provisioned and sealed.

NEST CONSTRUCTION BY *Trigona carbonaria*

On September 8, 1958, and at intervals thereafter a sheet of glass was placed on top of the brood chamber of a Nogueira-Neto hive (for

design, see Nogueira-Neto, 1948, 1953, 1956, or Portugal-Araújo, 1955a). On top of the glass was placed a board so that light could not enter the nest directly, but the edges of the glass were exposed to bright light. The bees promptly started to coat the inner surface of glass with a layer of cerumen, the lining batumen. However, this material was added slowly, except where there were scratches in the glass. Light entering the margins of the glass would of course be reflected into the nest box by the irregular surfaces of the scratches; such light sources were promptly covered. Covering the margins of the glass with opaque tape changed the conditions, so that the scratches were covered but little more quickly than was the general surface of the glass. Obviously the bees respond not only to actual openings but to light sources in closing their nesting cavities.

Bees were watched on many occasions carrying cerumen for pillars (which had been destroyed in installing the glass) or for the covering being placed on the glass. Workers carried the cerumen in small strings extending backward between the legs from the mandibles, but not at all forward from the mandibles. Although usually much shorter, sometimes such a string of cerumen was as long as the bee's body. Bees carrying such cerumen wandered about, apparently rather randomly. When they reached a projecting point on top of the nest, they added their cerumen to that forming the point. First they would work the front end of the string into the cerumen of the point and then, moving the string forward, incorporate the whole of it into that already there. Growth of pillars seemed to be largely due to the tendency of bees on the top or sides of the cell cluster or storage pots to climb any high point and add cerumen to the summit. If a bee carrying cerumen happened to climb the walls of the box instead of the nest itself, the cerumen was added to the coating being placed on the glass.

These fragmentary data are presented briefly here only as an indication of the important information that could be obtained from a proper ethological investigation by persons living in areas inhabited by meliponine bees.

BEHAVIOR OUTSIDE THE NESTS

AGGRESSIVENESS

There is no satisfactory measure of aggressiveness in *Trigona*, and within any species large colonies are more likely to attack an intruder than weak ones. Nonetheless experience indicates a wide variability among species in the readiness with which the workers attack persons opening a nest. The following tabulation indicates roughly the relative aggressiveness of the forms studied:

Not aggressive	<i>australis, cincta, wybenica</i>
Moderately aggressive	<i>carbonaria, iridipennis</i>
Strongly aggressive	<i>hockingsi, genalis</i>

Those listed as not aggressive virtually never fly at a person opening the nest, while those listed as strongly aggressive do so in large numbers and crawl into one's hair, bite one's skin, and the like. Even the most aggressive listed above are not nearly so aggressive as such Neotropical species as *T. corvina* and *T. ruficrus*.

SWARMING

The manner of multiplication of colonies of South American Meliponini is now well known, thanks to the studies of Kerr (1951) and Nogueira-Neto (1954), summarized by Kerr and Laidlaw (1956) and Moure, Nogueira-Neto, and Kerr (1958). Colony multiplication has not been observed in Indo-Australian species, but all evidence points to the fact that the process is the same as in American species. Flights of numbers of bees, commonly males but sometimes workers, about nest entrances are well known in the Indo-Australian region (Schwarz, 1948; Pagden, 1957).

A few hundred males of *T. carbonaria* were seen flying in the vicinity of a nest of this species in Brisbane daily except in bad weather from February 27 to the end of April. They appeared in good weather, about 9:00 A.M., and continued until about 4:30 P.M. Sometimes some of them could be seen resting on a tree trunk or on the outside of the hive instead of flying. They formed a loose aggregation in the air 2 to 6 feet above the ground. Sometimes it was around the shaded nest box itself, but most of the time it was in partial sun up to 15 feet from the nest, and sometimes it was divided and dispersed so that bees could be seen flying about many places in an area up to 20 feet in diameter. It is interesting that most of these flying males had small masses of cerumen attached to the outer surfaces of the hind tibiae.

Many swarms of *T. wybenica* were seen about the government buildings in the suburb of Konedobu, Port Moresby. In the walls of these buildings were numerous nests of this species. In addition there were far more numerous places, mostly around cracks, nail holes, and the like, which opened into larger cavities inside, where the bees, presumably in the initial stages of establishing new colonies, had surrounded a hole with propolis or cerumen. Sometimes a small, and to the human observer obviously inadequate, hole had a considerable amount of such material around it. Ordinarily a small cavity had only a few spots of propolis or cerumen at the entrance, while larger and more suitable ones had

more or were completely surrounded by this material. Figure 72 shows a hole that opened into a satisfactory cavity, but the opening itself was far smaller than is normally used by this species. It had been extensively surrounded by propolis or cerumen, and a few bees were seen going in and out of it over a period of six weeks (mid-April through May, my entire stay in New Guinea). Some of the other cavities where preparations for a colony of bees had begun were also being visited at least occasionally by bees, while others seemed completely abandoned.

Rather small dense flights of 10 to 100 males were seen around the entrances of several established nests. In one case at about 10:00 A.M. a young queen (at least not physogastric) came out of a nest entrance that was surrounded by a large flight of males. Unfortunately she was grasped by an ant and fell to the ground and was lost, so that subsequent behavior could not be observed. Similar flights of males were sometimes seen about entrances of unoccupied sites, and once a flight was seen around a place that could never be occupied because of the small size of the cavity inside. All these sites, however, had considerable propolis or cerumen around the entrances, although in no case was an external entrance tube formed.

The occurrence of flights of males at such new sites indicates that, as Nogueira-Neto and Kerr have found, young queens arrive there from the old nests unmated. The numerous flights around established nests suggest that mating may sometimes occur before the young queen leaves to go to a new site, for it seems improbable that there would be as many replacement queens being produced as there were swarms about established nests.

Small flights of workers were also observed about certain potential nesting places which had been well plastered with propolis. Pagden (1957) also noted flights of workers. Perhaps they are associated with the actual movement of part of a colony to a new nesting place.

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SUMMARY AND CONCLUSIONS

The nests of meliponine bees exhibit many features of phyletic and adaptive significance. These characters, which of course result from the behavior of the numerous workers in the colonies, should be considered in conjunction with morphological features and other behavioral ones in assessing the relationships of species of this tribe. Homologies of nest parts are discussed, and a terminology for them is presented. Failure to formalize such matters in the past has resulted in the confused use of the word "involucrum" for two different structures in different species.

The nests of seven species of *Trigona* from Australia and New Guinea are described. The nests of those species of the subgenus *Plebeia* that were studied (*australis* and *cincta*) differ from other known meliponine nests in having spherical cells which open in various directions, not necessarily upward; from those of other species in which the cells are arranged in clusters, these differ in the presence of an involucrum consisting of a single cerumen sheet. Possibly these features are primitive. It seems reasonably clear that the cluster arrangement of cells found in other species, and considered primitive by previous authors, is in reality an adaptation (associated with loss of the involucrum) making possible the use of small and irregular cavities for nesting places. One species (*T. hockingsi*) arranges its cells in a manner intermediate between combs and clusters. Reports that two species of Australian *Trigona* (*australis* and *carbonaria*) leave the brood cells open and add provisions to them until as much as three days after hatching of the larvae could not be verified and presumably have no basis in fact. These Australian bees, as do all other *Trigona* species, mass provision their cells.

The establishment of new colonies was not observed, but flights of

males and other activities indicate that it must be similar to that of South American stingless bees.

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