

## Notes on a primitive stingless bee, *Trigona* (*Nogueirapis*) *mirandula*

by

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This paper is a preliminary study of the nest and habits, and a description of the male, queen, and a melanic form, of the stingless bee, *Trigona* (*Nogueirapis*) *mirandula* Cockerell.

DISCOVERING AND ESTABLISHING THE SPECIES. *Trigona mirandula* was collected for the first time on June 15, 1902, by M. A. Carriker, an ornithologist, in Pozo Azul de Pirrís, Costa Rica, located in the pocket-like area formed by the union of the rivers Candelaria and Pirrís (Parrita), on the Pacific slope, at an altitude of 82 to 200 m. In 1917 the bee was described and named by COCKERELL (2); it is not until 1957-1959 that we have further news of *T. mirandula*. At this time, Professor Padre J. S. Moure, of the University of Paraná, Brasil, studying the Neotropical Apoidea, examined the type material in the U. S. National Museum, and found one worker specimen of *T. mirandula* (U.S.N.M. 23168) also from Pozo Azul. After a preliminary study it was obvious that the bee belonged to the group *Nogueirapis*, erected by MOURE (7) as a subgenus of *Partamona* to include Friese's *Trigona butteli*, a rare species from Perú, Bolivia and Brasil. At the British Museum he found again specimens of *T. mirandula* in Cheesman's material, collected in the island of Gorgona, Colombia. He proved also that what CHEESMAN (1) misidentified as *Trigona mosquito* var. *variicolor* was actually *T. mirandula*. While Moure was examining the types, I described (12) a new fossil *Nogueirapis* from the amber of Chiapas, Mexico. Just then Moure informed me of finding *T. mirandula* and of its position in *Nogueirapis*. Its close relation to a fossil bee from the Middle Miocene makes it an important bee for study.

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IN SEARCH OF SPECIMENS. The first expedition to search for specimens and for reconnaissance of the general environment of *T. mirandula* was made early in September, 1961. With Mr. William Ramírez, I visited the type locality, Pozo Azul de Pirris, where we stayed for 11 days. In spite of the very rainy weather and floods we were able to collect 24 species of stingless bees, including 10 specimens of *T. mirandula*, which were found on the last day of our stay. The reason for obtaining so few specimens and so late is itself an illustration of some of the general habits of *T. mirandula*. After several days collecting bees from flowers in the open fields of Pozo Azul, and failing completely to find *T. mirandula*, we decided to try the forest. There we found it attracted to sap escaping from broken and stripped woody vines on a fallen tree. In other words, *T. mirandula* appears to be restricted to the jungle, and therefore it is difficult to collect from flowers. Tropical forest flowers are for the most part very high and inconspicuous. If we were able to collect any specimens, it was because these bees were attracted to sap. This fact suggested that bees could be attracted by artificial means, and a very simple technique was devised to collect them under forest conditions (WILLE, 14). This technique consists of a 1:1 honey-water mixture, which is sprayed as a mist of fine droplets on leaves. This technique was very successful and we secured large series of *T. mirandula* during other expeditions to Pozo Azul.

When we found our first bees, I was not quite sure that they were *T. mirandula*. At first I thought so, but under a hand lens they appeared to have a narrow depression along the posterior border of the inner surface of the hind tibia, and I assumed them to be a *Plebeia*. When, at home, I examined again the supposed *Plebeia* under a microscope, I realized that they were in fact *T. mirandula*: the hairs of the inner surface of the hind tibia are uniformly distributed posteriorly, leaving just a very narrow margin glabrous, which appears as a narrow depression under the hand lens.

IN SEARCH OF NESTS: Two other expeditions to Pozo Azul (December, 1961, and May, 1962) were made, mainly to look for the nest of *T. mirandula*. The logical place to look for the nest seemed to be in a tree cavity, on the assumption that the jungle soil would be rather humid for a nest of stingless bees, and an exposed nest should be readily known by the local people of the area. Many days were spent carefully combing the trees in a well defined area of the forest where the bee was particularly abundant. In order to gain a general estimate of the proximity of the nests, bees of *T. mirandula* were marked with different colors when arriving at the baits. Certain marked bees, for instance, took one minute to leave the bait when full of honey, take it to the nest, and return again. This showed how close we were to their nest. The bees were also followed by sight when leaving the bait but the forest is too dark and the bees too small to make it possible to follow them. Threads of very fine white silk were also glued on the bees, in order to be able to follow them when returning to their nests. However, in the most successful attempts the bees were able to fly only a few meters, and then dropped to the ground.

In August, 1962 a trip was made to the mountains of Dota, where

specimens of *T. mirandula* were collected at an altitude of 200 meters (14.5 Km North of Quepos and 12 Km from the original Pozo Azul site). Since in this place *T. mirandula* was abundant, other trips were made. In January, 1963 a very interesting subterranean nest was found in the same area of Dota, in the jungle. It was 35 cm from the surface. The entire nest with the whole live population, was taken to the University in San José. The bees were black and they appeared to be an undescribed species of *Plebeia*.

It was not until September, 1963 that I had the chance to study these specimens. Under the microscope, they proved to be a beautiful new form of *Nogueirapis*, in fact, very similar to *T. mirandula*, but much darker. This indicated that *T. mirandula* probably also had its nest in the ground. This also explained why we had been unsuccessful in finding the nest previously.

In February, 1964, just before describing the supposed new species of *Nogueirapis*, I went again to Dota, accompanied this time by Dr. Stephen Wood. My main purpose was to find additional information about the supposed new species of *Nogueirapis* and to look for the nest of *T. mirandula*. On February 19, one of the local men showed me a ground nest that he had seen as much as four years previously. The most striking thing about the nest was that it contained both *T. mirandula* bees and the undescribed dark form. This unexpected fact demonstrated that actually the so-called new species was instead a melanic form of *T. (Nogueirapis) mirandula*.

## RELATIONSHIPS OF *T. (NOGUEIRAPIS) MIRANDULA*

**AFFINITIES OF *Nogueirapis*:** Although the following points have already been discussed elsewhere (WILLE, 13), it is necessary to repeat them here in order to keep the continuity of discussion. The exact position of *Nogueirapis* is still uncertain. Indications are that this subgenus is a primitive group. This is shown by its long geological history and by its unspecialized general morphology. On the basis of its unspecialized morphology and general appearance, the subgenus *Plebeia* appears close to *Nogueirapis*. However, *Plebeia* differs by the possession of a narrow depression along the posterior border of the inner surface of the hind tibia. The similarities of *Nogueirapis* and *Plebeia* are so striking that if the former had the narrow depression in the hind tibia there would be little hesitation by a bee specialist in placing the bees that are now grouped as *Nogueirapis* in the subgenus *Plebeia*. Moure has placed great emphasis on the nature of the inner surface of the hind tibia, and has distributed phylogenetically all the stingless bees in three major groups: (1) bees having the inner surface of the hind tibia normal, without any type of depression, (2) bees with a narrow depression along the posterior border of the inner surface of the hind tibia, and (3) bees with a wide depression along posterior area of the inner surface of the hind tibia which widens at its apex. Since the hind tibia of most stingless bees has another small depression or face anteriorly, the bees of this third group appear to have a median elevation along the whole length of the tibia. Since *Nogueirapis* belongs to the first group and *Plebeia*

to the second one, Moure has not placed *Nogueirapis* close to *Plebeia*, in spite of the fact that they are similar in other respects. Unfortunately, most bees of this group (*Partamona*, *Paratrigona*, *Scaptotrigona*, and *Nannotrigona*) are, in spite of the unspecialized inner surfaces of the hind tibia, highly specialized in many other respects. *Partamona*, however, is less specialized than *Paratrigona*, *Scaptotrigona* and *Nannotrigona*. This is the reason why Moure has placed *Nogueirapis* close to *Partamona*, as a subgenus of it. But since there are some important differences between *Nogueirapis* and *Partamona*, there seems little justification for placing them together, except, of course, if we accept Moure's classification, by regarding most subgenera as genera and placing *Nogueirapis* as a subgenus of *Partamona*. In this way we still keep *Nogueirapis* as a natural group. *Partamona* differs from *Nogueirapis* mainly in the epistomal suture, the lateral portions of which are subparallel over their basal halves or more and then diverge abruptly apically; in the propodeum, in which the basal area is covered with hairs; in the spoon-shaped hind tibia; and in the large corbicula and malar space. All these characters are presumably specializations, not found in *Nogueirapis*. But if we accept modification of the inner surface of the hind tibia as one of the main phylogenetic trends in the stingless bees, then the group *Nogueirapis* is at the very bottom of the series of bees with normal inner surfaces of the hind tibiae. Similarly *Plebeia* seems to be at the bottom of the series of bees with a narrow depression along the posterior border of the hind tibia. This situation may explain why *Plebeia* and *Nogueirapis* are morphologically similar, even if they are not in the same line of evolution. For a discussion of the possible evolution of *Nogueirapis*, see WILLE (13).

**AFFINITIES OF *T. mirandula*:** COCKERELL (2) noted in the original description the relationship of *T. mirandula* to *T. zonata*. In 1948 SCHWARZ (11), although aware of the latter's relationship to *Partamona*, erected a new subgenus *Parapartamona* to include it, mainly on the basis of the finely granulose, dull cuticular surface and the long propodeum. In my opinion, the differences in question are not significant enough to justify subgeneric recognition within *Trigona*; *T. zonata* should remain in the subgenus *Partamona*. *Nogueirapis*, on the other hand, represents a natural group which should be maintained as a valid subgenus.

Although *T. mirandula* is actually related to *T. zonata* and other species of *Partamona*, its closest relative is *Trigona butteli*. Not only are they morphologically similar, but the color and general distribution of the dark and yellow marks are almost identical. A comparison of the two species gives the general impression that the color of *T. butteli* is slightly more faded. *T. mirandula* is also closely related to the fossil form *T. silacea*. Although both *T. mirandula* and *T. butteli* are similar to the fossil species, there is a larger gap between the latter and the living forms than between the two living species. On the other hand, of the two living species, *T. mirandula* is more closely related to the fossil form.

For further information see WILLE (13). Figures 1, 2, and 3, give a gen-

eral comparison of the anterior views of the heads of the three known species of *Nogueirapis*.

### DISTRIBUTION OF *T. MIRANDULA*

We still need more distributional data on *T. mirandula*. At present its known localities are Costa Rica and Gorgona Island, Colombia. In Costa Rica it is distributed throughout the tropical moist forest of the Pacific slope, starting approximately from the Pozo Azul area, southeast to the Panamenian border. The southernmost locality in Costa Rica where it has been collected is between Golfito and Kilómetro 33, not too far from Panamá. So far, all efforts to find it on the Atlantic slope of Costa Rica have failed. The second area known is the island of Gorgona, at present a penal colony. This island is located close to the Pacific coast of Colombia, South of Chaco Bay. It is logical to think that it should occur also in Panamá and at least along the Pacific slope of Colombia.

### DIMORPHISM IN *T. MIRANDULA*

As has been mentioned before, in January of 1963 a nest of *T. mirandula* was found inhabited entirely by a melanic population. In February, 1964 another nest was found, this time containing both the melanic form and the conventional ferruginous type. The total population of this nest was 2281, of which 1034 were melanic and 1247 ferruginous, giving therefore a proportion of about 1:1. By using the baiting technique it is easy to get a general estimate of the frequency of the two forms in the population. In the mountains of Dota, where the two nests were found, several counts were made at different places. The results were about 50 percent melanic and 50 percent ferruginous. On the other hand, at Pozo Azul the frequency of the melanic form is very low. For instance, during my last trip I collected 319 specimens of *T. mirandula*, of which 279 were ferruginous and 40 melanic (13%). The presence of intermediates between typical ferruginous and melanic forms was suspected at first. However, those supposed intermediate forms which were found in the second nest could more appropriately be interpreted as young individuals whose color was not well defined as yet.

It would be rather interesting to find out about the selective advantages or disadvantages of the two forms, since it is likely that the ferruginous and melanic conditions are not neutral as regards survival value. Further studies are needed in order to investigate the possible selective factors involved. Although the jungles at both places (Pozo Azul and Damas in the mountains of Dota) are almost identical there is one important difference between the two areas. In Pozo Azul the jungle covered the whole area (at least, until last year, when most of the forest was cut down) and the open places were relatively far from it, while at Damas, in the area where both nests were found, much cutting of the jungle had been done. In spite of the temptation to speculate as to the possible importance

of these obvious differences, the selective factors, if any, are probably not as obvious as one would wish them to be.

Although more nests are needed in order to find out if the two forms of *T. mirandula* are due to the simple action of a pair of alleles, it is possible to speculate that this is so. Since the ferruginous form is apparently the conventional type, it is probably the dominant form, while the melanic is the recessive one. If this is so, then the population of the first nest would be homozygous recessive, while in the second nest, the queen (which was ferruginous) should be an heterozygote which had mated with a recessive male.

## DESCRIPTIVE ACCOUNTS

The descriptions which follow include a melanic worker and male, plus a ferruginous queen. This is the first time that a male and a queen of *T. mirandula* have been described. Since the first nest, which was maintained in an artificial hive for about a year, was killed by the action of the ashes and sand thrown by the recent activity of the Irazú volcano, it was not possible to study the melanic queen. Fortunately, however, a few melanic males were secured before the population finally died off. For the descriptions some suggestions made by Moure (personal communication) have been followed. For complete explanation of measurements see HURD and MOURE (4) and for the description of the ferruginous worker form see WILLE (13).

### 1) Melanic worker form of *T. mirandula*

SIZE: Length 4.30 to 5 mm; length of forewing 4.5 mm.

COLOR: General color black brown. *The following parts yellow*: paraocular areas, which below are subparallel to eye, up to level of antennal sockets, where they become abruptly wider and with an irregular outline, ending at level of middle ocellus; a narrow stripe along frontal line, becoming wider below; supraclypeal area with an inverted V-shaped maculation although in younger forms the whole area is yellow and continuous with stripe along frontal line; a narrow premarginal band on clypeus, sometimes (mostly in younger forms) becomes an anchor-like maculation on anterior portion of clypeus, with lateral extremities of transverse bar "anchor" somewhat expanded, and vertical shaft of "anchor" (ending one third before epistomal suture) much wider than transverse bar (Fig. 4); basal two thirds (one half in immature specimen) of mandible, except small black portion at very base; a narrow genal stripe (wider apicad) along posterior margin of eye; labrum; basal extremity of scape; basal half of pronotum, medially interrupted in the mature specimens, and not reaching the notal lobes; a narrow stripe (abbreviated anteriorly) along lateral margins of mesoscutum, and continuous with axillae; a narrow marginal band on scutellum, sometimes discontinuous in the middle (in most specimens); pronatal lobes with a yellow spot. A yellow to yellowish anteroventral band on mesepisternum, slightly discontinuous at middle. Metepisternum yellow to yellowish except for a very small band on anterior and upper part. *The following parts ferruginous* (although sometimes blending into a very dark brown): ventral side of flagellum; genal area, except for the narrow band just behind the eye; distal one third of mandible, except reddish distal border; coxae; trochanters, posterior lobe of pronotum; ventral side of abdomen. Sometimes basal portion of abdominal terga ferruginous to very dark brown, contrasting with distal black portion

of terga, thus giving a faint indication of being banded. Tegula brownish translucent. Wings slightly darker at apex, never dark brownish.

**PUBESCENCE:** Very short, longer on scutellum and on ventral part. It is pale brown, becoming whitish ventrally.

**PUNCTATION:** Very fine (minute) and sparse, slightly granulate, interspaces several times (about four) width of punctation. Punctuation of mesoscutum as that of front, scutellum with interspaces slightly microrugose. Mesepisternum with middle portion as dense as mesoscutum, and with punctures becoming denser anteriorly and sparser posteriorly and ventral. Basal portion of propodeum rugose, with rugosity recurved.

**STRUCTURE:** Head slightly broader than width of abdomen; length of eye 2.8 times breadth; inner orbits concave, with very faint convergence below; interorbital distance shorter than eye length (80: 60: 76: 59 = length of eye and upper, median and lower interorbital distances respectively<sup>1</sup>); malar area linear (2.5), its length less than half width of flagellum; clypeus slightly longer than half its width, but much shorter than clypeocellar distance (28 × 51: 58 = length and width of clypeus and clypeocellar distance respectively), clypeus gently convex; interalveolar distance slightly greater than transverse diameter of antennal sockets, and much shorter than alveolar distance (13: 17:  $\emptyset$  12 = interalveolar and alveolar distance, and transverse diameter of antennal socket respectively); frons slightly depressed along median line, ending in a short carina below; vertex slightly convex, without postocellar carina; interocellar distance almost twice ocellorbital distance, the latter slightly shorter than transverse diameter of median ocellus (18: 10.5:  $\emptyset$  11 = interocellar and ocellorbital distance, and transverse diameter of median ocellus respectively); posterior margin of head strongly concave; ocelloccipital distance shorter than diameter of ocelli, and about three fifths of the orbitoccipital distance (9.5: 15 = ocelloccipital and orbitoccipital distance respectively), without preoccipital carina; scape shorter than alveolar distance (40:50) and shorter than half length of pedicel and flagellum (90); proportional length of first four flagellar segments as follows: 6: 6: 7: 7; diameter of fourth flagellar segment 9; anterior border of pronotum slightly concave, almost straight; scutellum slightly projected and paraboloid in contour (19 × 43 = length and width of scutellum respectively); distance between lower metapleural suture and second coxa one fourth width of flagellum; length of propodeal spiracle 3.9 times its width (measure from inner border of atrial rim); middle basitarsus about two thirds tibial length (60:43); shape of hind tibia subtriangular with posterior distal extremity slightly angulated; length of hind tibia 2.5 times its width (89:36) with a discal corbicular hair, almost as long as length of scape (there is another long hair, but much shorter than discal corbicular hair and closer to hind border of tibia); rastellum composed of 8 strong bristles, as long as width of flagellum, and restricted to median area of distal border of tibia; hairs of inner surface of hind tibia uniformly distributed posteriorly, leaving just a very narrow margin glabrous; hind basitarsus two times longer than broad (43 × 21), with distal half of posterior margin parallel to anterior margin, obliquely truncated; vein separating first and second submarginal cells (Rs) relatively well indicated, that separating second and third (1 r-m) virtually absent; length of marginal cell 3.75 times its width; submarginal angle (basal angle of first R<sub>1</sub> cell) a right angle; base of first median cell non-petiololed (with vein separating first cubital and median cells transversally placed).

**VARIATION:** The main variation found is in the length of the narrow yellowish stripe around the frontal line, which usually reaches the anterior ocellus. In some of the specimens, however, the stripe does not extend as far as the anterior ocellus, and can be separated from it by a width equal to that of flagellum, although sometimes less or more than width of flagellum. More rarely the stripe around the frontal line disappears

1 To convert the measurements into millimeters, each unit or scale interval = 0.017 mm.

completely. Other variations are found mostly in younger forms, and they have been already indicated in the general description.

## 2) Melanic male form of *T. mirandula*

SIZE: Length 4.70 to 5 mm; length of forewing 4.30 mm.

COLOR: Very similar to that of the melanic worker, with the following differences: yellow paraocular areas slightly narrower; yellow stripe around frontal line absent (Fig. 5); scape with a yellowish stripe in front; small portion at very base of mandible dark, not black; narrow yellow genal stripe along posterior margin of eye better defined; metepisternum slightly yellowish to light brown; ventral side of abdomen almost as dark as dorsal side.

PUBESCENCE AND PUNCTATION: As in the worker, except that pubescence is very short on ventral surface.

STRUCTURE: Besides the usual male characters, like the number of antennal and abdominal segments, simple hind tibia, and genitalia, there are certain structural differences from the worker: wider eyes, length of eye 2.3 times breadth; low margin of eye almost touching clypeus (77:51:60:44 length of eye and upper, median and lower interorbital distances respectively); clypeus much longer than half its width (39 × 45); interalveolar distance slightly greater than alveolorbital distance (13:11), the latter equal to transverse diameter of antennal sockets; proportional length of first four flagellar segments as follows 5:10:10:10; middle basitarsus slightly more than three fourths tibial length (60:50); length of hind tibia slightly more than three times its width (83 × 26); hind basitarsus almost three times longer than broad (43 × 15); length of marginal cell four times its width; submarginal angle (basal angle of first  $R_1$  cell) slightly more than 90°; sixth sternite with a long and stout median spine of 0.37 mm in length by 0.085 mm wide (at the widest).

GENITALIA: Penis valves (= sagittae) long and claw-like, bend at right angles toward the sides, like those of *T. pallida* (= *pallens*) and *T. compressa*, see SCHWARZ (11).

## 3) Ferruginous queen of *T. mirandula*

(Gravid and preserved in Dietrich's fixative)

SIZE: Length 10 mm; length of forewing 3.7 mm.

COLOR: General color ferruginous. The following parts dark brown: A large bilobed spot on upper part of head (Fig. 6)<sup>2</sup> covering vertex and extending anteriorly about two thirds of alveolacellar distance (to lateral ocelli); dorsal surface of scape and pedicel; posterior articulation of mandible; around epistomal suture; mesoscutum, except a narrow yellowish stripe along its lateral margins; scutellum; metanotum, except its dorso-lateral area; outer side of posterior (one third) and distal (one fifth) border of hind tibia; outer side of hind basitarsus; narrow distal border of first five abdominal terga. Sutures and most borders of thorax marked off with dark pigmentation.

PUBESCENCE: Very short, longer on vertex, scutellum and on last two abdominal terga. It is pale brown.

PUNCTATION: Similar to that of worker, but basal portion of propodeum not rugose.

STRUCTURE: Length of eye 3.2 times breadth (65 × 20; inner orbits subparallel ventrally, with slight convergence above; interorbital distance larger than eye length (65:64:75:70); malar area long, its length greater than width of flagellum (12 × 9);

2 Very similar to that of the fossil form *T. silacea* (Fig. 1).



length of clypeus half its width, and much shorter than clypeocellar distance ( $26 \times 53:59$ ), clypeus gently convex; interalveolar distance slightly greater than transverse diameter of antennal sockets, and much shorter than alveolar distance ( $14:20:\varnothing 13$ ); interalveolar area gently convex; frons slightly depressed along median line; vertex slightly convex, without postocellar carina; interocellar distance slightly greater than ocellorbital distance, the latter almost twice than transverse diameter of median ocellus ( $17:15:\varnothing 8.5$ ); posterior margin of head strongly concave; ocelloccipital distance greater than diameter of ocelli, and half orbitocipital distance ( $10:20$ ); without preoccipital carina; scape longer than alveolocellar distance ( $50:46$ ) and one third length of pedicel and flagellum ( $150$ ); proportional length of first four flagellar segments as follow:  $9:7:7:8$ ; diameter of fourth flagellar segment 9; anterior border of pronotum slightly concave, almost straight; scutellum semicircular in contour ( $23 \times 48$ ); distance between lower metapleural suture and second coxa one fourth width of flagellum; length of propodeal spiracle 2.3 times its width; middle basitarsus about two thirds tibial length ( $65:45$ ); length of hind tibia three times its width ( $105 \times 35$ ); hairs of inner surface of hind tibia uniformly distributed posteriorly, leaving just a very narrow margin glabrous; hind basitarsus three times longer than broad ( $47 \times 15$ ); vein separating first and second submarginal cells (Rs) well indicated, that separating second and third (1 r-m) absent; length of marginal cell about 3.4 times its width (distal ends of wings of specimens are torn of old age); submarginal angle (basal angle of first  $R_1$  cell) slightly more than  $90^\circ$ ; base of first median cell non-petiolated (with vein separating first cubital and median cells transversally placed).

## THE NEST

*Trigona mirandula* is a ground nesting species. Species that build their nests underground are relatively few among the stingless bees. It is significant that the greatest number known to be subterranean belong to the most primitive groups, *Plebeia* (*s. lat.*) and *Nogueirapis*. The specialized groups which have ground nesting species are *Melipona* and the subgenera *Trigona*, *Tetragona*, and *Paratrigona*; *Melipona schencki picadensis* Strand and *Trigona* (*Trigona*) *fulviventris* Guérin nest preferentially among the roots of trees. *Trigona* (*Tetragona*) *mombuca*<sup>3</sup> and *T.* (*Paratrigona*) *lineata nuda* Schwarz 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* Moure (= *petropolis* Schwarz) makes its nest in soft soil and usually less than one meter deep.

Among the more primitive ground nesting species known, five belong to the subgenus *Plebeia* (*s. lat.*), and all, excepting *Trigona quadripunctata* (Lepeletier)<sup>4</sup>, which installs its nest in deserted *Atta* nests, are African species<sup>5</sup>.

<sup>3</sup> This species has been taken as the genotype of another group, *Geotrigona*, by MOURE.

<sup>4</sup> Placed by MOURE (6) in a separate group: *Schwarziana*.

<sup>5</sup> The African *Plebeia* species have also been given several different generic or subgeneric names by MOURE (9), such as *Plebeiella*, *Plebeina*, and *Meliplebeia*. In the author's opinion, only the latter name should be kept as a subgenus, since it is actually a rather specialized side branch of the *Plebeia* stock.

These are as follows: *Trigona beccarii* Gribodo, *T. tanganyikae medionigra* Cockerell, *T. lendliana* Friese, and *T. denoiti* Vachal, the latter usually found in termite nests. It is interesting to point out that the other relative of *Nogueirapis*, the subgenus *Partamona*, still preserves some of the subterranean habits. This is illustrated specifically by *Trigona (Partamona) cupira* Smith; this species nests in a variety of situations: Occasionally it can make an aerial or exposed nest, but more frequently its nest is semi-exposed, usually under some protection, or its nest is built inside of vertical ground walls or roadside banks, or less frequently in horizontally level ground, sometimes using nests of *Atta*.

Although only the nest of *T. mirandula* is known in *Nogueirapis*, it is highly probable that the nest of *T. butteli* is also subterranean. If this is the case, then the whole subgenus *Nogueirapis* is typically a ground nesting group. For the following description of the nest of *T. mirandula*, the terminology used by MICHENER (5) has been adopted here. However, since laminate batumen and involucre are sometimes difficult to distinguish from each other, they have been called here enveloping sheets of two different types, as Michener has also suggested as an alternative. In certain cases, when the enveloping sheets are apparently of one kind, the difficulty is to determine which of the two types is present. Such is the case with the nest of *T. mirandula*: the enveloping sheets around the brood chamber are dark and somewhat brittle, and have been interpreted as involucre by Michener (when observing the nest at the University in San José). On the other hand, the enveloping sheets were regarded by me as laminate batumen in the second nest. The reason for this discrepancy was that the second nest had a very soft, brown sheet that partially surrounded the combs; there were also the same type of soft sheets in certain spaces between the combs. These light colored and soft sheets were interpreted as the true involucre, the dark and more brittle sheets as the laminate batumen. We still need more information to be able to homologize these two types of sheets, meanwhile it is better to use the general term of enveloping sheets.

**GENERAL ARRANGEMENT OF THE NEST** (Fig. 8): The nest cavity is found from 30 to 35 cm. from the surface of the ground, with the entrance burrow either vertical or inclined. The nest proper, which is almost black in color, is spherical and protected by a hard lining of batumen; it has a diameter of about 20 cm. The brood chamber, including several enveloping sheets, is suspended by means of pillars to the hard batumen layer which surrounds the nest cavity, leaving in this way an empty space between the outermost enveloping sheet and the nest cavity. This space is much larger below, where the food pots are found.

**THE ENTRANCE BURROW:** In one of the nests the entrance burrow was vertical and 35 cm deep, while in the other nest the burrow was slanting, with an inclination of about 25°, and 58 cm in length (Fig. 9). The entrance burrow protrudes above the soil surface forming a small and delicate turret one centimeter in height. This turret is made of light brown waxy material, and is thin and with numerous small perforations (Fig. 13). The diameter of the turret varies from 6 to 8 mm, and it is slightly oval rather than completely

round. The burrow is irregular in shape and size: in one of the nests, for instance, the diameter of the burrow varied from 15 to 12 mm (at 3 cm depth) to 30 to 25 mm (at 20 cm depth). In the other nest the main variations were as follows:  $13 \times 10$  mm;  $20 \times 12$  mm and  $9 \times 7$  mm. The burrow is lined with dark brown cerumen of 0.5 to 1 mm in thickness, sometimes (at least in one of the nests) it has concentric thin layers in the outermost portion of the wall. These layers are apparently old wood; if this is so, then the bees may use holes formed by rotting of roots to start their nests. The entrance burrow penetrates the nest cavity at one side, it ends after entering slightly the enveloping sheets of the brood chamber (Fig. 8).

**THE NEST CAVITY:** The nest cavity is completely lined by a thin batumen layer of 1 to 2 mm in thickness, in some areas thicker. Although this layer is thin, it is hard and brittle, giving a good protection to the nest. This lining batumen is almost black in color, with some tinge of dark brown. The whole cavity is rounded, about 29 cm in diameter, but slightly flatter at the bottom, where sometimes the entrances of short blind and vertical burrows are found which are also lined with batumen (Fig. 8). These blind projections were absent in one nest, while the other nest had three of them. Two of the projections measured 4 cm in length, the other one only 2 cm; they were wide at the base (about 20 mm), becoming progressively narrower at their distal ends. It is interesting to point out that similar but single and much longer blind burrows (30 to 95 cm) were found by PORTUGAL-ARAUJO (10) in two African *Plebeia* nests (*T. langanyikae medionigra* and *T. lendliana*); these burrows were sometimes absent in at least one of the species. According to Portugal-Araujo these blind burrows are used for draining the excess moisture. Although there is good evidence that this is the case for the African species, it is questionable that the burrows have the same use in *T. mirandula*. The blind burrows in this nest are too short and they are sealed with batumen.

**THE BROOD CHAMBER AND ENVELOPING SHEETS:** The brood chamber and its protective sheets of cerumen occupy most of the nest cavity, except for the lower area where the food pots are found. This whole, composed of the enveloping sheets with the brood chamber inside, is round, although it may be slightly flat at the bottom, and it has a diameter of about 15 cm. The whole unit is suspended and supported by pillars to the hard batumen layer which surrounds the nest cavity. These pillars are of different diameters, from 1 to 4 mm. A few of them are obviously small roots that have been coated with cerumen. Sometimes the pillars are flat, forming just thin but wide and resistant supports. The space which is left between the enveloping sheets and the batumen covering varies. Thus, around the upper parts the space is usually small, about one centimeter, while around the lower parts the space is much larger, sometimes from 2.5 to 5 cm. in thickness. In these large spaces are located the food pots, some of which are connected to the enveloping sheet by pillars.

The enveloping material which surrounds and protects the brood chamber consists of numerous brownish-black paper-thin sheets, most of them somewhat brittle. Sometimes the brood chamber is partially surrounded by a

soft and light brown sheet. In general, the enveloping layer is thicker and with thicker and harder sheets below (6 cm wide and with about 10 sheets in one of the nests). Above and at the sides it is usually thinner and with fewer sheets (2 cm wide and with about 5 sheets in one of the nests). There are small pillars 2 to 3 mm in length between the sheets. The sheets are for the most part not well differentiated individually into concentric units, but there is a tendency to form an irregular framework, which makes it difficult to determine the exact number of sheets forming the enveloping layer.

The brood chamber proper measured 8 cm in diameter by 5 cm in height in one nest, and 10 × 7 cm in the other. The cells and cocoons are arranged in essentially horizontal layers or combs. These combs, however, are rather irregular, with some areas slanting at about 20° from the horizontal, and with some of them joining in a spiral manner. Layers of cells in clusters are also found (Fig. 15). The brood chamber contains cocoons and cells in curious arrangement. In one nest, for instance, the cells and cocoons were distributed in two separate sets of combs (Figs. 14 and 15). In one set (with 6 combs) there were only cells with eggs and young larvae, while the other set (with 8 combs) consisted of cocoons, most of which contained pupae. The other nest had three sets of combs, 2 of them cocoons and the rest cells. They were as follows: 1st set) with four combs, all cells with eggs and advancing edges, 2nd set) with four combs, all prepupae in cocoons, 3rd set) with five combs, all pupae in cocoons, many of them already emerged as adults. The sets are separated from each other by small gaps, with some of the combs almost touching each other. However, in the nest with three sets there was a larger gap (4 cm) between two of the sets, this gap was filled with light-brown and soft paper-thin sheets, placed in an irregular manner. Several cocoons were found attached irregularly on these sheets. Although there are small pillars between the cell layers, there are none between the cocoon layers, in which case the combs are supported by marginal pillars.

The cells are vertically elongated, about 4.5 mm high by 2.75 to 3 mm wide.

**THE FOOD POTS:** These are all located below in the nest cavity, partially under the enveloping sheets (Fig. 14). They are almost black, with thin walls (less than 1 mm) and soft texture. Although the individual pots are essentially distinct, there is fusion of their walls. There are differences in sizes among the pots; the diameter varies from 12 to 15 mm and the height from 20 to 30 mm. The honey and pollen pots are more or less separated; the pollen pots are located under the enveloping sheets of the brood chamber, while the honey pots are in a separate group, just in front of the pollen pots, but not under the enveloping sheets. The honey and pollen pots are alike. The honey is rather good in taste, light yellowish in color, and low in viscosity, but penetrating in sweetness, and with a slight acid taste. However, the honey from the nest kept at the University in San José, in an artificial hive, was rather unpleasant in taste.

**ADDITIONAL REMARKS:** Several shiny black and more or less rough rounded masses of firm sticky material (18 × 15 mm and 5 mm high) were found

in the lower parts of the nests and between the enveloping sheets and the batumen layer (Fig. 18). This material becomes very viscous with slight heat. The same type of sticky material has been found by Michener and the author in other nests of stingless bees (unpublished). Something similar has also been reported by PORTUGAL - ARAUJO (10) under the name of resin and gum deposits, in the nests of *T. lendliana* and *T. tanganykae*. It is possible that these masses are stores of waterproofing for use in lining batumen.

It is interesting that these subterranean nests can be maintained in artificial hives. Other ground species have been also maintained in boxes (PORTUGAL - ARAUJO, 10 and MOURE, 8). A nest of *T. mirandula* was kept in a wood box of 16 × 16 × 37 cm on the inside. The bees never did line the wood surfaces with batumen, and all the empty spaces left in the interior of the box were filled with numerous brownish-black, paper-thin sheets. These sheets were rather soft and most of them placed along the length of the box, as if they were hanging from the top (Fig. 17).

## HABITAT

*Trigona mirandula* is typically a tropical jungle species. That it is essentially a forest bee is suggested not only by its having been collected solely in that type of environment, but also by the curious fact that when a nest is artificially exposed, by cutting the forest down, the typical entrance turret of the nest, which is made of wax, melts easily in the heat of the sun, and the bees have to remake it again late in the afternoon, when the heat of the day is over. This behavior is repeated day after day, showing that the bees are not well adapted to an exposed environment.

*Trigona mirandula* lives in the tropical moist forest of the Pacific slope of Costa Rica, including the small tropical wet forest area around Golfito [cf. HOLDRIGE'S (3) classification of the Middle American vegetation]. These two life-zone formations, the Tropical Moist Forest and the Tropical Wet Forest, have an annual average rainfall of 2000-4000 mm and 4000-8000 mm, respectively, with a normal distribution, and a maximum dry season of two to three months. The region where *T. mirandula* lives is bounded by the mean annual isotherm of 24°C. The forest is tall, with the canopy almost completely closed, and with an average height of 30 to 40 meters. The big trees are usually spaced well apart, and their tops are often hidden by the crowns of the smaller ones (from 15 to 25 meters high). In this way two upper strata are formed, which, however, are not well differentiated. Close to the forest floor there is another stratum, composed mainly of herbs and seedlings, such as the dwarf palms of the genus *Asterogyne*, small Heliconias, and many piperaceous and melastomaceous plants. Among the large trees, the following are some of the genera: *Pithecolobium*, *Pterocarpus*, *Swartzia*, *Cynometra*, *Hymenaea*, *Anacardium*, *Spondias*, *Brosimum*, *Ficus*, *Carapa*, *Cedrela*, *Ceiba*, *Hura*, *Sterculia*, *Virola*, and *Calophyllum*. Among the shrubs and medium-sized trees, which are part of the second stratum, are found several species of palms, such as *Iriartea*, *Socratea*, *Welfia*, *Bactris* and *Astrocaryum*.

Other trees in this statum are *Cordia*, *Ocotea*, etc. Vines and epiphytes are frequent and occur at all heights on the trees. There are very few tree ferns, but small ferns on the tree trunks and on the forest floor are not uncommon. A general view of the type of forest where *T. mirandula* lives is shown in figure 21. Since these bees occur from underground probably to high levels in the forest, their habitat actually forms a continuum in which all the three-dimensional space is occupied by them. We do not know as yet how high the bees fly in the forest but in order to obtain pollen, they probably go to or near the main canopy.

### GENERAL BEHAVIOR

The bees are very timid and never fly at a person when their nest is opened. They are easily attracted to honey baits (Fig. 19 and 20) and apparently they are able to communicate the food source, since after the first bee arrives, the area with bait will soon be covered by a large number of them. The following observations were made mainly with a bee colony located in a clearing of the jungle, and shown to me by the owner of the area. According to him, he saw the nest for the first time some four years ago; the area was then pure jungle. He was making a trail through the forest one afternoon (about 4 o' clock), and when coming back he saw several bees flying near the ground where some leaves and small branches had fallen earlier. He then cleaned the area and found the nest entrance. In the years since, he has seen the nest often.

The bees are very active early in the morning; they start their activity about 5:45 A. M. The first bee to come to bait which was placed in the field during the predawn darkness arrived at 5:50 A. M. During the first few hours in the morning many bees were seen carrying pollen to the nest. After about 10 A. M. the activity diminishes, but even at noon bees were seen entering and leaving the nest, although none of them carried pollen. From about 10 A. M. to 2 P. M. the area becomes very warm, and not many bees were seen at the entrance. The small turret entrance was melted by the heat of the sun. After 2.30 P. M. the bees become more active, carrying pollen to the nest, and more bees were seen at the entrance. In the entrance there are usually from three to five bees (Figs. 11 and 12) which act as guards and repair the turret as necessary. On disturbance the bees close the entrance. While I was taking a close-up picture, for instance, they closed the entrance, leaving just a small slit-like opening, which they reopen about 15 minutes later. Similar behavior was observed by Michener at the nest maintained at the University in San José. When leaving the nest the bees make an orientation flight, always facing the nest entrance, and flying in concentric semicircles which are increased in size as the bee gets farther from the nest (Fig. 7). Occasionally a bee seems to simplify its orientation flight by making a very short one. The bees returning to the nest (with pollen or without it) get lost very often, and sometimes they have a difficult time finding the entrance.

Considerable activity was observed late in the afternoon (4 P.M.) and even at 5:50 P. M., when it begins to get dark, some bees are still going in and

out of the nest. At 6 P. M. however, no more bees were observed outside, not even on the bait. By this time the bees had already reconstructed the entrance turret, which melted by the heat of the sun. The reconstruction started about 3 P. M., but they worked more actively in the last hour. After 6 P. M. when it is quite dark, the bees start to close the entrance of their nest, and by 7 P. M. they have closed it completely, leaving just small perforations on the walls of the turret. The nest was checked several times during the night, and bees were detected close to the entrance each time. The nest entrance was reopened by the bees at 5:30 in the morning, just when it started to get light, and another day of outside activity began.

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### SUMMARY

A primitive stingless bee, *Trigona (Nogueirapis) mirandula* Cockerell, was studied in the following aspects: 1) historical background of the bee; 2) relationships of *T. mirandula* to *T. butteli* and the fossil form, *T. silacea*, and their general relations to the groups *Partamona* and *Plebeia*; 3) geographic distribution of the bee in Central America and Colombia; 4) The occurrence of color dimorphism in this bee: a ferruginous form, which was the only type known previously, and a melanic form, described for the first time in this paper; 5) description of the male and queen, which were unknown for the subgenus until the present; 6) a general survey of the ground nesting species of stingless bees and a description of the nest of *T. mirandula*; 7) the habitat of the bee in the Tropical Moist forest; and 8) the general behavior of the bee outside the nest.

### RESUMEN

El presente trabajo consiste en un estudio sobre una abeja Melipónida primitiva, *Trigona (Nogueirapis) mirandula* Cockerell. Se estudiaron los siguientes aspectos: 1) Antecedentes históricos del descubrimiento de esta abeja. 2) Relación de *T. mirandula* con *T. butteli* y la forma fósil *T. silacea*, y su parentesco general con los grupos *Partamona* y *Plebeia*. 3) Distribución geográfica de la abeja en Centro América y Colombia. 4) La existencia de dimorfismo en el color de esta abeja: una forma ferruginosa, el único tipo que se conocía previamente, y una forma melánica, que se describe por vez primera en el presente trabajo. 5) Descripción del macho y de la reina, hasta el presente desconocidos. 6) Reconocimiento general de las especies Melipónidas que anidan en el suelo y descripción del nido de *T. mirandula*. 7) El habitat de la abeja en la Selva Húmeda Tropical. 8) Comportamiento general de la abeja fuera de su nido.

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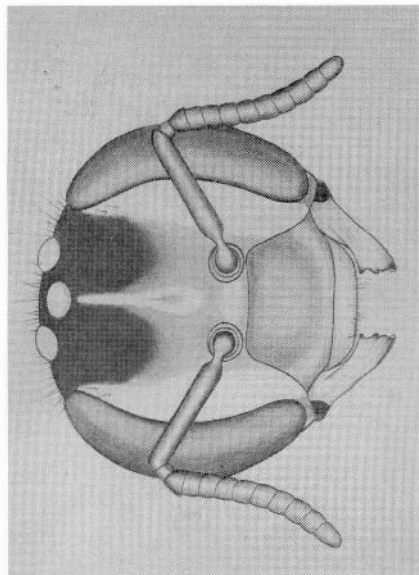
Figs. 1, 2 and 3: Heads of workers

Fig. 1. *Trigona silacea*

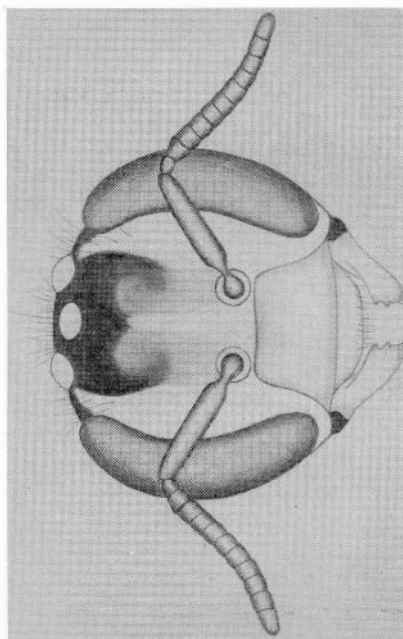
Fig. 2. *Trigona mirandula*

Fig. 3. *Trigona buteli*

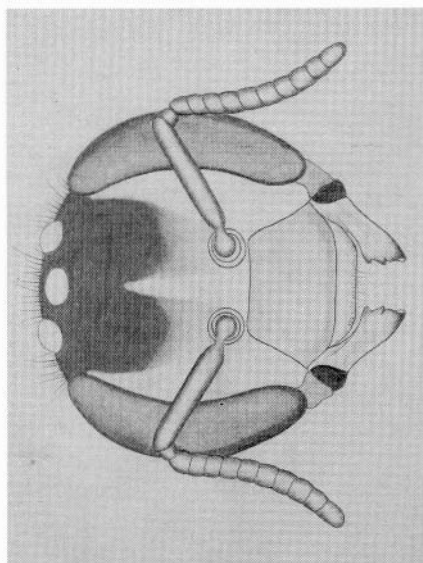




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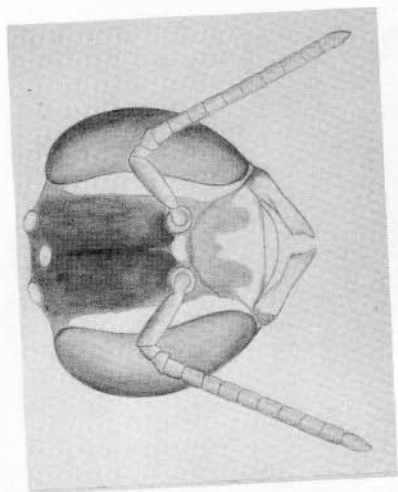
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Figs. 4, 5 and 6. Heads of *Trigona mirandula*

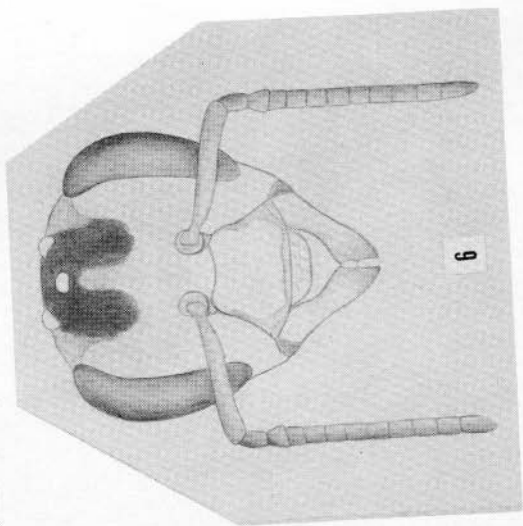
Fig. 4. Melanic worker

Fig. 5. Melanic male

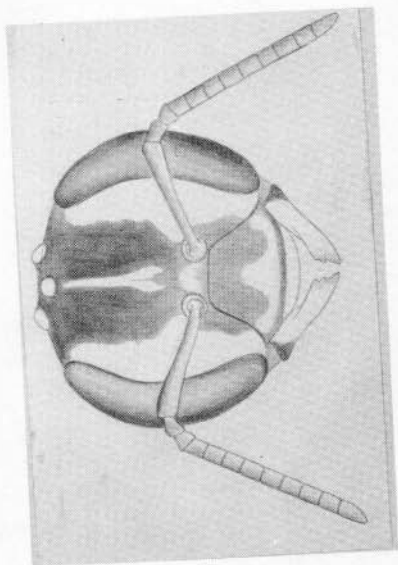
Fig. 6. Ferruginous queen



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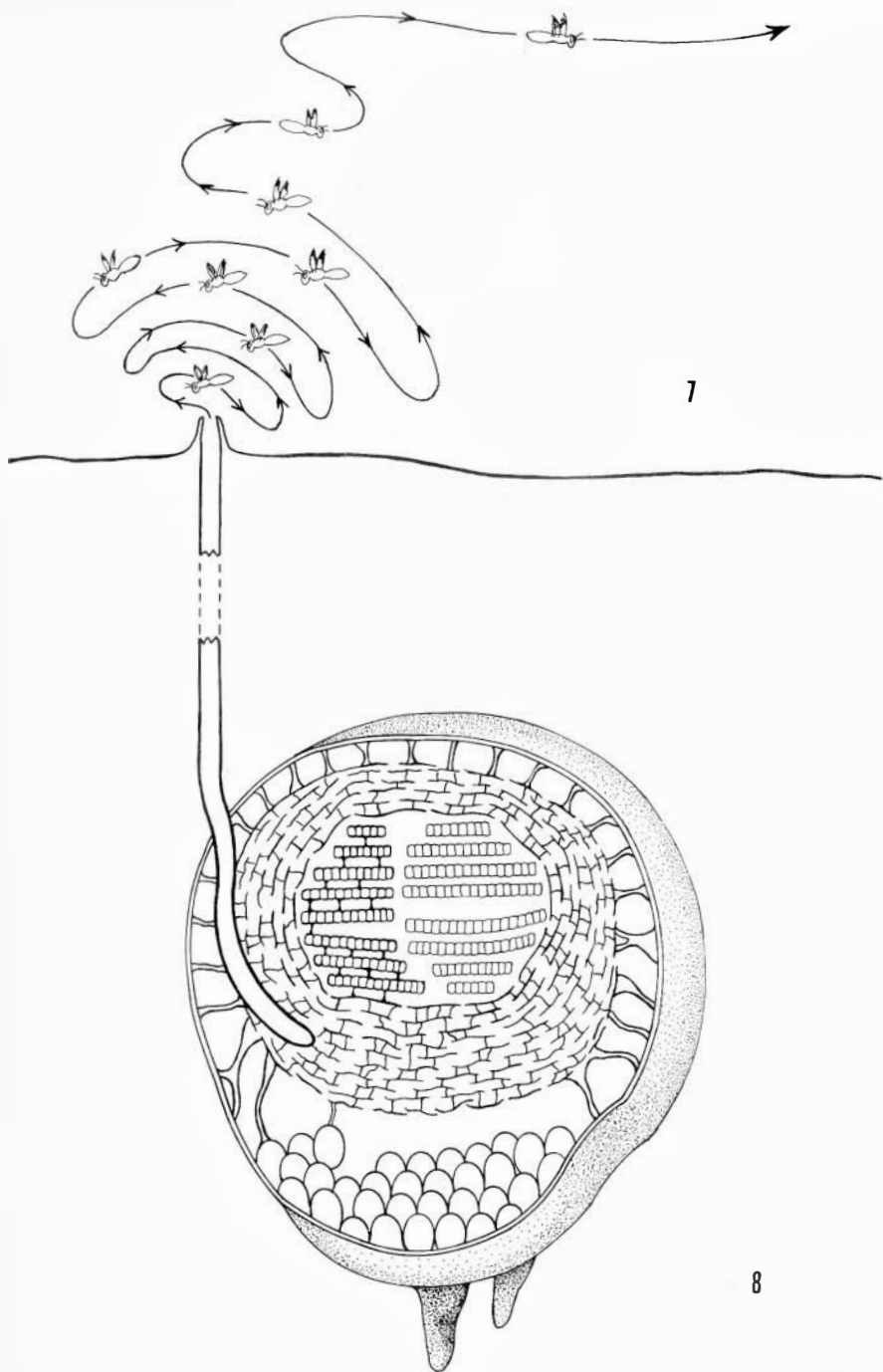
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Fig. 7. Diagram showing "orientation flight"

Fig. 8. Diagram of nest



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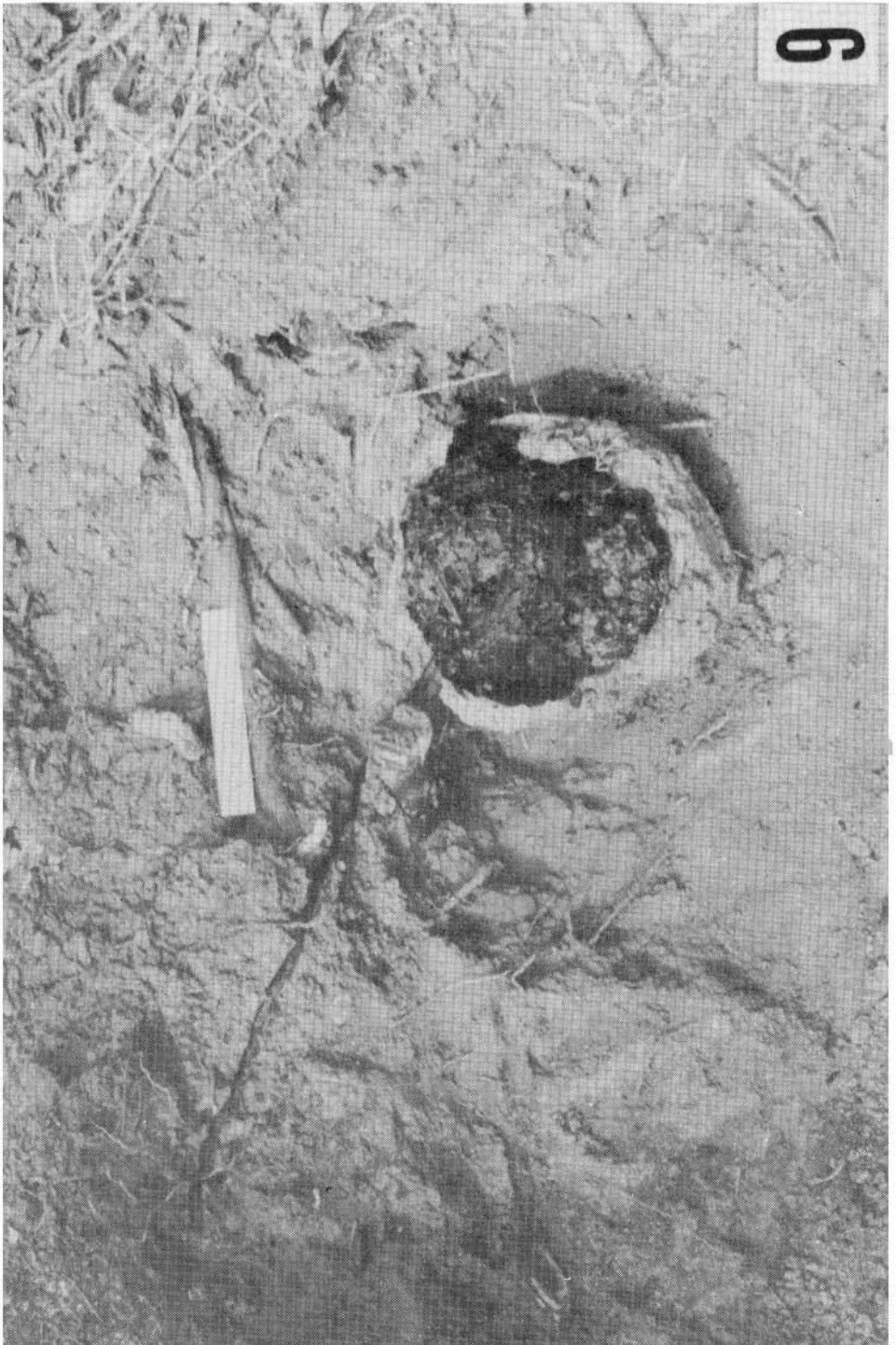


Fig. 10. Nest entrance

Fig. 11. Nest entrance (from artificial hive) showing three guard bees



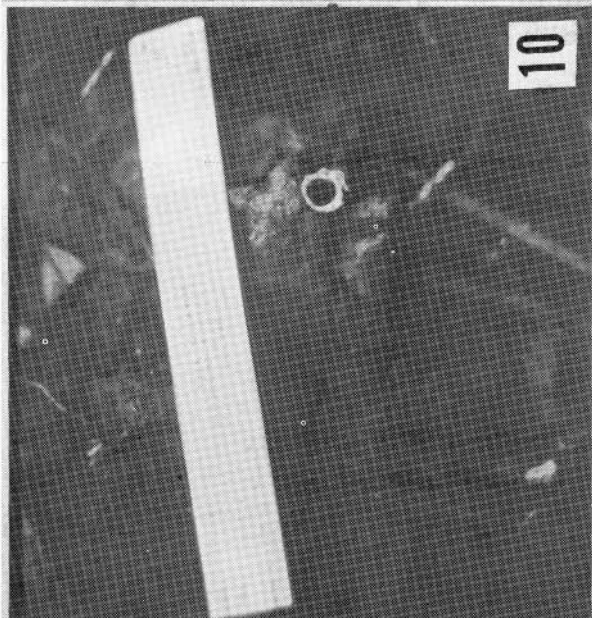
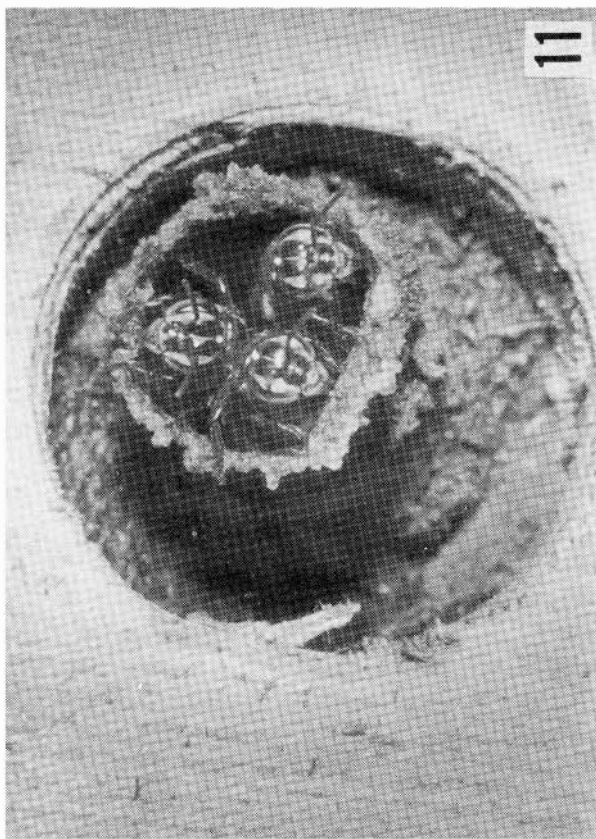


Fig. 12. Nest entrance (from artificial hive) showing a bee ready to fly

Fig. 13. Nest entrance (from artificial hive) showing turret with small perforations

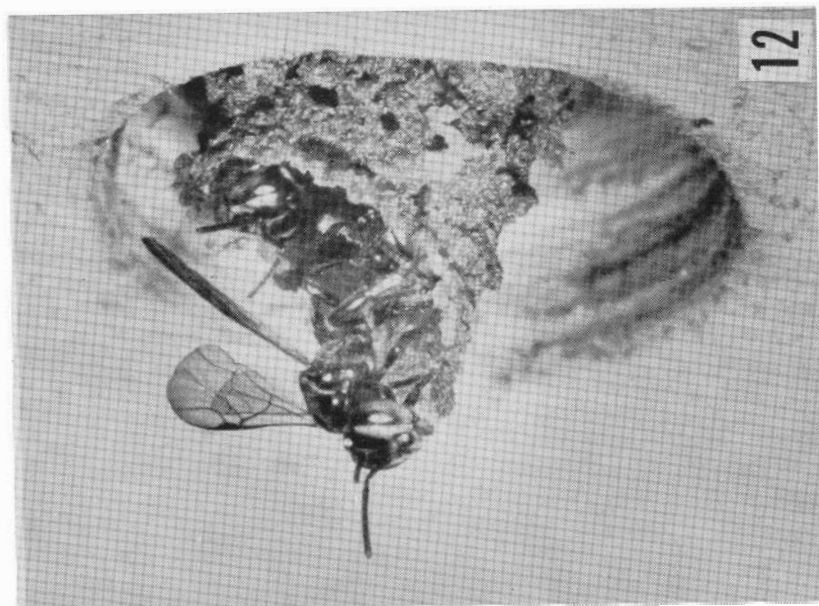


Fig. 14. Nest showing brood combs, enveloping sheets, and food pots. Note that the brood chamber shows two separate sets of combs: To the left only cells while at right the combs consist of cocoons.

Fig. 15. Brood chamber showing few cells in cluster

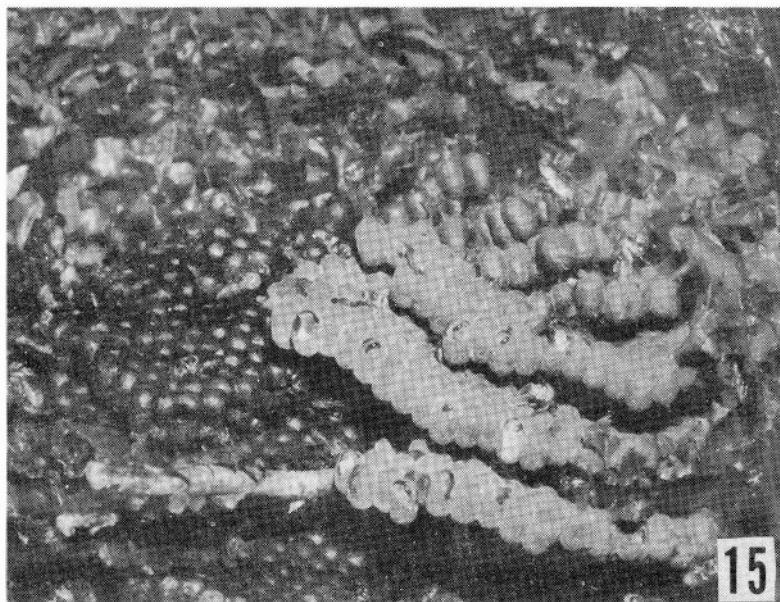
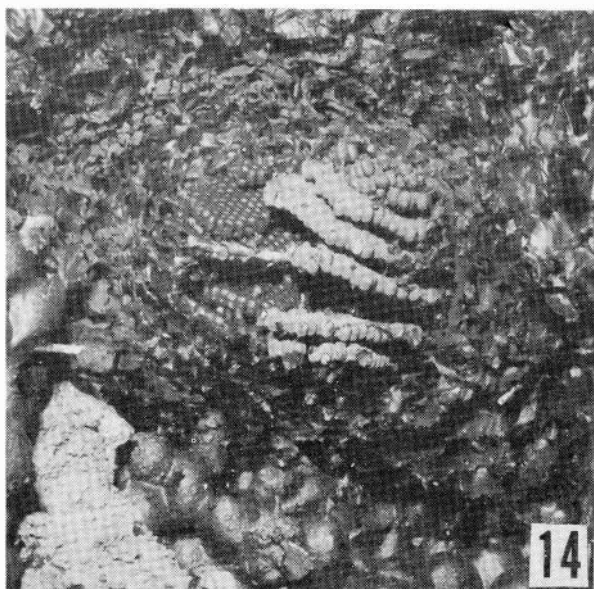


Fig. 16. Nest kept in a wood box

Fig. 17. Artificial hive showing numerous brownish-black, paper-thin sheets

Fig. 18. Masses of firm sticky material

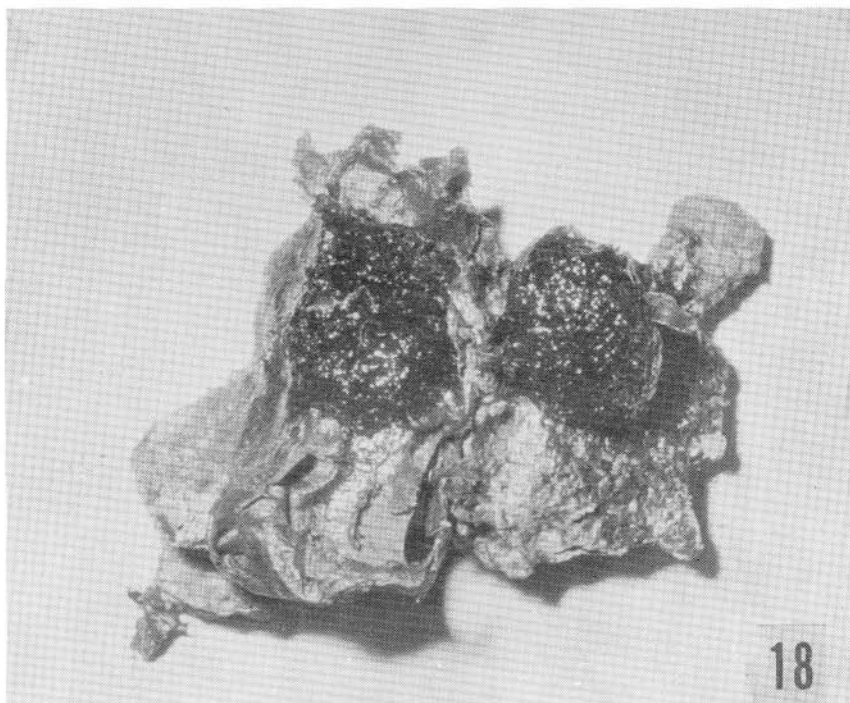


Fig. 19 and 20. Bees attracted to honey baits



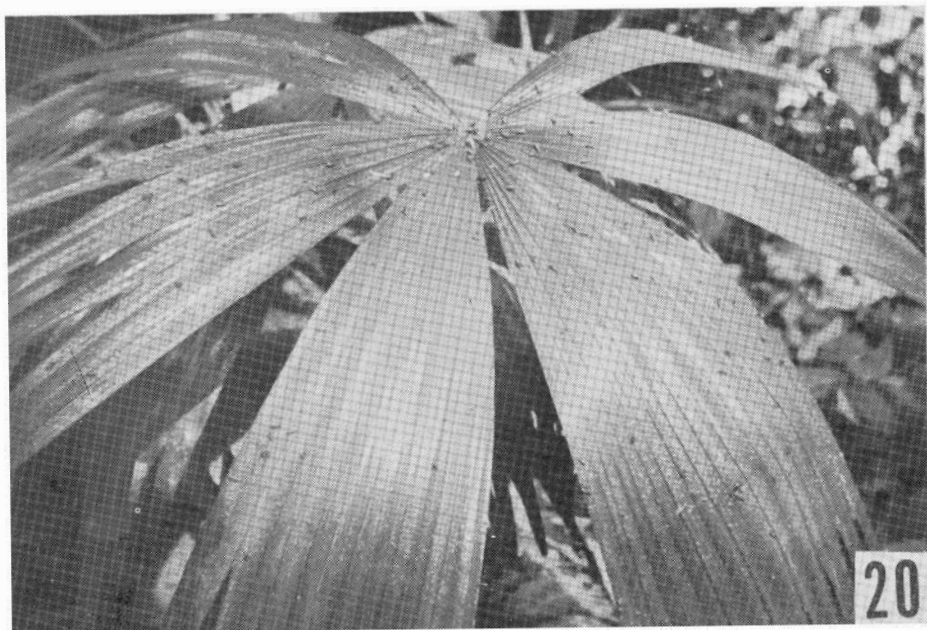
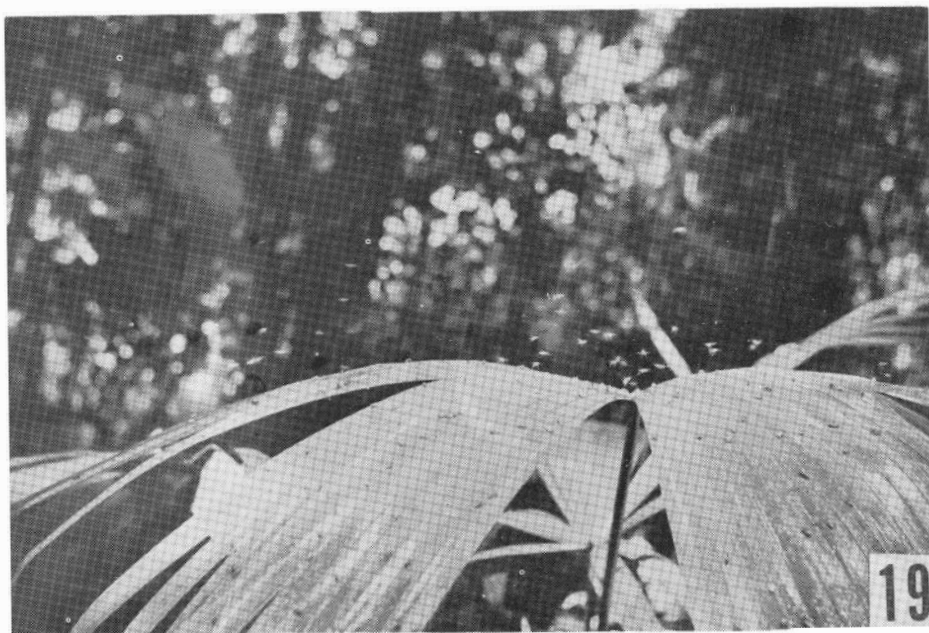


Fig. 21. View of forest where *T. mirandula* lives

