Rev. Biol. Trop., 14(2): 251-277, 1966

Notes on two Species of Ground Nesting Stingless Bees (Trigona mirandula and T. buchwaldi) from the Pacific Rain Forest of Costa Rica

by

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(Received por publication August 19, 1966)

This work is in part a continuation of a previous study on *Trigona (Nogueirapis) mirandula* Cockerell (WILLE, 11). It deals mainly with *Trigona (Tetragona) buchwaldi* Friese, whose nesting habits were unknown to this date. The following aspects are discussed: a description of the queen of *T. buchwaldi,* the study of the nesting habits of the same species, additional notes on *T. mirandula,* a description of the melanic queen of this species, which was not described in the previous paper.

Although species that build their nests underground are relatively few among the stingless bees, it is even less common to find these bees nesting in the soil of the tropical rain forest. This ecological habitat is characterized by a prevailing high relative humidity and lack of light penetration to the lower strata of the forest, with the ground covered by a thick layer of organic debris. To date, the only bees known to the author to nest in these conditions are those dealt with in this paper.

SYSTEMATIC POSITION AND RELATIONSHIPS OF *TRIGONA BUCHWALDI* AND *T. MIRANDULA*

There are several indications suggesting that *T. mirandula,* which belongs to the subgenus *Nogueirapis,* is a rather primitive species. For a general discussion of the systematic position and relationships of *T. mirandula* see WILLE (10). *Trigona buchwaldi,* on the other hand, belongs to the rather specialized subgenus, *Tetragona;* however, MOURE (4, 5) divides the *Tetragona* into several taxonomic groups *(Frieseomelitta, Geotrigona, Duckeola, Ptilotrigona,* and *Te-*

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tragonisca), placing *T. buchwaldi* in the subgenus he calls *Tetragonisca.* In this group he includes those American *Tetragona* which have a bristleless sericeous area on the inner surface of the hind basitarsus. Beside *T. buchwaldi,* he includes in *Tetragonisca, T. weyrauchi* Schwarz, *T. pfeifferi* Friese, and *T. jaty* Smith. Of these three species, *T. weyrauchi* is the closest relative of *T. buchwaldi,* having been originally described by SCHWARZ (7) as a variety of *T. buchwaldi.* MOURE (4), using as a base the presence of the sericeous areas, states that these four species are more closely related to *Trigona s. str.* than they are to *Tetragona.* For a detailed discussion of *Tetragonisca* versus *Tetragona* see WILLE (9).

The species named here *T. buchwaldi* was described in 1962 by the author (9) as *T. costaricensis.* The confusion arose because in that instance the specimen used for the description, collected in Ecuador by Friese in 1909, had a slightly inflated hind tibia, and consequently a short and shallow corbicula, giving it an appearance that differed from *T. buchwaldi.* Moure (personal communication) who examined the specimen later, concluded that *T. costaricensis* was actually *T. buchwaldi,* explaning the difference by assuming that the specimen was preserved in alcohol and allowed to dry, affecting in this manner its appearance.

DESCRIPTIVE ACCOUNTS

In the following description, suggestions made by Moure (personal communication), and used in a previous paper (WILLE, 11), have been followed For a complete explanation of measurements see HURD and MOURE (1).

1) Melanic queen form of *T. mirandula* (Gravid and preserved in Dietrich's fixative)

SIZE: Length 9.7 mm; length of forewing 4 mm.

COLORS General pattern similar to that of ferruginous queen (for description see WILLE, 8, 10), but much darker. Color of head, similar in both queen forms, but with whole area below large bilobed spot on upper part of head darker (Figs. 1 and 2). This area covers most frons around antennal sockets except supraclypeal area, and includes whole clypeus and a narrow area along epistomal suture on paraocular region. Thorax and legs very dark brown, except for the folowing parts which are light brown: most of prothorax, a narrow strip along lateral margin of mesoscutum, axilla, metepisternum, area of propodeum bordering metepisternum, coxae, tarsi. In some instances the difference between the two shades of brown is difficult to recognize. Color of abdomen as in ferruginous form.

PUBESCENCE, PUNCTATION, AND STRUCTURE: as in ferruginous queen

2) Queen of *T. buchwaldi* (Gravid and preserved in Dietrich's fixative)

SIZE: Length 10.8 mm; length of forewing 5.5 mm.

COLOR: General color brown with yellowish areas. Head brown with the following parts yellowish: antennae except pedicel, clypeus, supraclypeal area, lower part of paraocular area, labrum, mandibles. Thorax and legs yellowish with the following parts brown: mesoscutum (dark brown), tegula, axilla, metanotum (almost black), with a spot on the anterior and lower part of each mesepisternum, second coxae. Prontum usually appears with a few brownish spots. Articulation of legs, sutures and borders of thorax marked off with dark pigmentation. Abdomen yellowish.

PUBESCENCE: Pale brown, very short, longer on vertex, scutellum and legs.

PUNCTATION: Tegument polished, with punctation sparse and minute, punctures becoming denser on mesoscutum.

STRUCTURE: Length of eye 3 times breadth (76 × 24); inner orbits subparallel ventrally, with slight convergence above; interorbital distance larger than eye length (76: 78: 87: 82 = length of eye and upper, median and lower interorbital distance respectively(1); malar area long, its length equal to width of flagellum (11 × 11); length of clypeus about half its width and half clypeocellar distance (33 × 65: 66 = length and width of clypeus and clypeocellar distance respectively), clypeus gently convex; interalveolar distance shorter than transverse diameter of antennal sockets, and shorter than half alveolorbital distance (10 : 25 : ∅ 14 = interalveolar and alveolorbital distance, and transverse diameter of antennal socket respectively); interalveolar area gently convex; vertex slightly convex, without postocellar carina; interocellar distance about equal to ocellorbital distance, the latter almost twice the transverse diameter of median ocellus (19 : 20 : ∅ 11 = interalveolar and ocellorbital distance, and transverse diameter of median ocellus respectively); posterior margin of head strongly concave; ocelloccipital distance about equal to diameter of ocelli (12 : ∅ 11); ocellorbital distance equal to orbitoccipital distance (20 : 20); without preoccipital carina; scape longer than alveolocellar distance (55: 49) and about half length of pedicel and flagellum (118); proportional length of first four flagellar segments as follows: 10 : 9 : 9 : 9; diameter of fourth flagellar segment 11; anterior border of pronotum concave; scutellum paraboloid in contour (34 × 60); distance between lower metapleural suture and second coxa one third width of flagellum; length of propodeal spiracle 2.6 times its width (16 × 6); length of hind tibia four times its width (150 × 35); inner surface of hind tibia with a narrow glabrous depression along posterior margin; hind basitarsus 3.6 times longer than broad (65 × 18); vein (Rs) separating first and second submarginal cells relatively well indicated, the one separating second and third (1 r-m) very faintly present to virtually absent; length of marginal cell four times its width (110 × 27); submarginal angle (basal angle

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

of first R_1 cell) a right angle; base of first median cell non-petiolated (with vein separating first cubital and median cells transversally placed) hind wing with 6 hamuli.

THE NEST OF *T. MIRANDULA*

For a detailed description of the nest of *T. mirandura* see WILLE (11). The cavity that forms the nest of this species is found from 20 to 35 cm below the ground surface, with the entrance burrow usually vertical or in some cases slightly inclined. The nest proper, which is almost black in color, is spherical and protected by a hard lining of batumen with a diameter ranging from 15 to 20 cm. Vertical projections ranging from 2 to 55 cm in length and 1 to 2.5 cm in diameter (Fig. 3) may be found at the bottom of the nest. Internally these projections are burrows which may serve as drain ducts for the excess moisture. Similar burrows were also found by PORTUGAL-ARAUJO (6) in two African *Plebeia* nests *(T. tanganyikae medionigra* and *T. lendliana);* this author indicates that the drainage burrows may not always be present.

The brood chamber, including several enveloping sheets, is suspended by means of pillars to the hard batumen layer which surrounds the nest cavity, providing in this way an empty space between the outermost enveloping sheet and the nest cavity. This space becomes larger below where the food pots are found (Fig. 3). Although the honey and pollen pots are partially separated in different groups, they are found together in the same chamber.

It is interesting to note that the brood chamber contains cocoons and cells in curious arrangements. Usually the cells and coccons are distributed in separate sets of combs (Fig. 3). The sets are separated from each other by gaps that vary from large (4 cm) to small, with some of the combs almost touching each other. In other cases the cells and cocoons are only partially separated in what appears to be a bicombed arrangement. These two sets of combs are actually connected at a point close to the periphery.

The population inhabiting a nest was seen to vary from 2281 to 4076 individuals.

Dr. William Dullman collected (25 May 1966) specimens of this species in Bocas del Toro: río Claro near junction with río Changena (910 m) in the Atlantic side of Panamá. This is the first record for that country.

THE NEST OF *T. BUCHWALDI*

THE NESTING SITE: *Trigona buchwaldi* is found in the tropical rain forest of the Pacific slope of Costa Rica; efforts to find it in the Atlantic slope have failed. Nevertheless a more thorough search of the area is necessary in order to determine its distribution in Costa Rica.

Like *T. mirandula, T. buchwaldi* is typically a tropical jungle species and as for the former, (WILLE 11), that *T. buchwaldi* is essentially a forest bee is indicated by the fact that it was collected only in that type of environment. Also it is of particular interest that when a nest is exposed, by eliminating the forest

cover, the nest's typical entrance turret, which is made of wax, melts easily when exposed to direct sunlight, forcing the bees to restore it in the late afternoon, when the heat of the day is over. In those areas where the forest has been eliminated the pattern of events described is repeated every day, suggesting that the bees are not well adapted to an exposed environment.

The nests are usually found in level ground. Sometimes, however, nests occur in hill sides or banks with an inclination up to about 45° (Fig. 8). In one instance a nest was found in a small ravine, two meters above the stream. The ravine was about ten meters deep, and covered with thick vegetation of seedlings and other small forest plants.

These bees usually choose soft ground to build their nests; however, occasionally nests may be found in sandstone (Figs. 9, 10). In the latter case *T. buchwaldi* takes advantage of natural cracks found in the rock (Fig. 10).

GENERAL ARRANGEMENT OF THE NEST (Fig. 4): The cavity which forms the nest is usually found from 15 to 30 cm from the surface of the ground. The nest proper is dark red to almost black in color, and is irregular in shape (Figs. 13, 16). It is protected by a hard lining of batumen and measures about 20 by 23 cm. The nest in made up of three chambers: the brood, the honey and the pollen chamber. All these chambers are well separated from each other by brittle cerumen walls. The brood chamber contains the horizontal combs and the enveloping sheets, all of them suspended by small pillars. Since the entrance burrow ends in the enveloping sheets this chamber can be regarded as the anterior part of the nest. The pollen chamber is found below the brood chamber. It is a small compartment, being widest posteriorly, sometimes including some of the space just behind the posterior side of the brood chamber (Fig. 4). The honey chamber is usually the largest compartment, in what may be called the posterior part of the nest, just behind the brood and pollen chambers.

THE ENTRANCE BURROW: In most of the nests the entrance burrow is irregular and slanting (Fig. 4), with a length of about 20 to 35 cm. In one of the nests however, the entrance burrow was vertical and very long (160 cm). This was probably due to the fact that the nest had been built in a hillside of sandstone (Fig. 8). The turret protrudes above the soil surface forming a small and fragile structure ranging from 1 to 5 cm in height depending on the amount of organic debris found on the ground (Figs. 5, 7). This turret is made of light brown to pale yellowish waxy material, and is thin and with numerous small perforations. Its diameter is usually 8 mm and it is more or less round (Fig. 6), but it can also have an irregular shape (Fig. 7). Below the ground the diameter of the burrow varies at irregular intervals from 7 to 15 mm, and it is lined with a very thin layer of waxy material. The entrance burrow penetrates the nest cavity at one side, entering the brood chamber and ending among the enveloping sheets (Fig. 4).

THE NEST CAVITY: The nest cavity, in spite of the length of the entrance burrow, is usually found from 15 to 30 cm from the surface (Fig. 17), although exceptionally it could be found at a greater depth. The cavity is completely lined by a thin batumen layer of 1 to 2 mm in thickness, being thicker in some areas.

Even though this layer is thin, it is hard and brittle providing good protection to the nest against water infiltration and ground pressure. In certain places the batumen layer looks as if it were made of three thinner layers rather than a single one. The middle layer in some instances is made up of the sticky material, commonly found among stingless bee nests (WILLE, 11). It seems obvious that the sticky material of the middle layer is used to waterproof the batumen. This lining batumen is almost black in color, with some tinge of brown; nevertheless, sometimes it may be dark red. When located in an area free of obstructions the whole cavity is more or less oval and irregular, about 20 by 25 cm in diameter, and usually slightly flat at the top (Fig. 15). Exceptionally the nest cavity can be rather flat, when the nest is located between two stones or in natural cavities inside of rocks. In one of the nests studied the bottom of the nest cavity was perforated with small holes (1 mm in diameter) which are probably used for draining the excess moisture, since the nest was located in an exposed hill side, where rain water could run down easily over the entrance. Since the nest was located in an exposed area, the entrance lacked the turret most of the time.

It seemed evident then, after studying four nests of this species, that *T. buchwaldi* always makes use of holes or cavities made by mammals as a site for its nest.

THE BROOD CHAMBER AND ENVELOPING SHEETS: The brood chamber and its protective sheets of cerumen are located in the anterior part of the nest, where the entrance burrow ends. The brood chamber is surrounded and protected by several brownish-black paper-thin sheets, most of them somewhat brittle (Figs. 20, 23). These enveloping sheets are suspended and supported by small pillars to the hard batumen layer which surrounds the nest cavity (Fig. 4). The space which is left between the enveloping sheets and the batumen cover varies from 4 mm to 1 cm. There are also 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 which make up the enveloping layer. Usually the brood chamber is partially lined by a soft, light brown sheet although in one nest five of these soft sheets were found around the combs. In nests where there is a wide gap between the combs, a soft and light sheet of the same material is usually found in the gap.

The brood chamber proper (Fig. 24), measures about 9 cm in height by 7 cm in diameter. The cells and cocoons are arranged in horizontal layers or combs. These combs are supported and suspended by pillars to the enveloping sheets. There are also small pillars between the cells and cocoon layers. These pillars vary from 16 to 40 in combs of 6 to 7 cm in diameter. The space which is left between the combs is about 2.5 mm. The cells are vertically elongated, about 5 mm high by 2.5 wide. Two fifths of the cells are filled with pollen and honey, and the eggs stand up on the surface of the food.

THE POLLEN CHAMBER: This chamber is located below the brood chamber, but does not occupy all the space available under this compartment (Fig. 20).

It usually includes also some of the space just behind the posterior side of the brood chamber (Fig. 4). It is a small compartment, of about 9 cm in length, 2 or 3 cm in width and 5 cm in height. It contains about 45 pots in the large nests, or 27 or less in the smaller ones. The pollen pots are cylindrical in shape but variable in size (Fig. 20). For example, the pots found under the brood chamber are small, usually from 3 to 4 cm in height, while those found behind the posterior side of the brood chamber measure 5 cm in height. The pollen pots have a diameter of about 1 cm.

THE HONEY CHAMBER: This chamber is usually the largest compartment of the nest (Figs. 12, 19). It is located behind the brood and pollen chambers. but sometimes it also extends to one side of the other chambers. It measures from 10 to 15 cm in length by 5 cm in width and 18 cm in height. The honey chamber is separated from the other compartments by a brittle and resistant dark wall, perforated by several holes, which permit the passage of the bees. It may contain up to 75 pots with honey. The pots are cylindrical in shape (Fig. 21), commonly 5 cm in height, but ranging from 3.5 to 6 cm, with a diameter of about 12 mm which also varies from 9 to 15 mm. The honey pots are attached by pillars to the batumen layer and to the separating wall; in particular cases they may even be held on to roots that cross the nest (Figs. 17, 19). The pots are distributed in the chamber by groups. The honey is yellowish in color, somewhat watery and sour to the taste.

ADDITIONAL REMARKS: When the nest is found in an unusual location, as between stones or rocks, the arrangement of the food chambers may vary, c. g., in the nest found in sandstone, the pollen chamber was located above the honey chamber, the later was found at the bottom of the nest.

Masses of sticky material were found abundantly in some of the nests, among the enveloping sheets. These masses were light brown to even whitish in color. It is possible that this material is waterproofing stored for use in lining batumen.

In one nest, a deposit of feces or dry pollen material was found, below the brood chamber, and among the enveloping sheets. Previous to the digging of this nest, bees were observed carrying this apparent waste material to the outside of the nest.

The population of three nests was recorded as follows: 1326, 2028, and 2979.

ECOLOGICAL FACTORS IN RELATION TO THE NESTING HABITS OF *TRIGONA MIRANDULA* AND *T. BUCHWALDI*

The heavy rainfall of over 400 mm (= 157.5") that characterizes the tropical rain forest, as well as the type of soil found in the working area, may determine some of the traits previously described for the nest of *T. mirandula* and *T. buchwaldi.* Among the most important environmental adaptations, the following could be mentioned: a) depth of the nest cavity in relation to the surface of the ground, b) impermeability of the nest outer walls, c) type of

entrance turrets, d) presence of drainage ducts or openings at the bottom of the nest.

a) DEPTH OF THE NEST CAVITY IN RELATION THE SURFACE OF THE GROUND: The nests of *T. buchwaldi* are found closer to the surface than most ground nesting stingless bees. In the area of study nests were commonly found at depths that vary between 15 and 35 cm. This seems to be an adaptation to the soil condition found in the tropical rain forest. Characteristics of the soil in this area are: an upper layer of about 50 cm of partially decayed organic matter which gradually becomes mixed with the upper part of the heavier B horizon. This fine textured upper layer is very porous and very permeable to water. Furthermore, at the depth of 15 to 40 cm the profiles of these soils are often marked by abandoned soil-filled passages and nests of rodents, the so-called crotovines (krotovines), that can be used by the bees as nesting sites. Beyond the transitional zone between the organic layer and the B horizon, the latter becomes more compact and coarse with a higher content of clay, which makes for a greater water-holding capacity and poor porosity. Taking into consideration the above mentioned factors the upper layer seems the most suitable nesting site.

b) IMPERMEABILITY OF THE OUTER WALLS OF THE NESTS: The protective covering of the nests is identical in both species. It consists of a thin batumen layer, almost black in color, which is hard and brittle and impermeable to water, providing good protection to the nest against water infiltration and ground pressure.

c) TYPE OF ENTRANCE TURRET: In both nests the entrance turret is made of wax, protruding above the soil surface. This structure is capable of keeping the running water from entering the nest. Furthermore, it constitutes an easy way for closing the entrance of the nest when in danger or at night.

d) PRESENCE OF DRAINAGE DUCTS OR OPENINGS AT THE BOTTOM OF THE NESTS: Where water may run inside the nest cavity, the bees build a drainage system which varies in the two species. *Trigona mirandula* constructs vertical burrows at the bottom of the nest which may serve as drain ducts for the excess moisture. The nest shown in figure 3 presents a duct 55 cm in length by 1 to 2.5 cm in diameter. This particular nest was located in a ground depression where the rain water could accumulate during a heavy storm. Conversely *T. buchwaldi* builds a series of small holes at the bottom of the nest which may be drain passages for excess moisture. The nest with perforations at the bottom was located in an exposed hillside, therefore lacked the turret most the time, allowing rain water to penetrate the nest.

PRIMITIVE AND SPECIALIZED CHARACTERS IN THE NEST OF *TRIGONA MIRANDULA* AND *T. BUCHWALDI*

Ground nesting is a primitive habit among bees. Indications to this effect can be derived from comparative study of Sphecoidea and solitary bees. However, in specialized groups such as Meliponini, in most cases ground nesting habits can be regarded as secondary evolutionary adaptations: It is significant

that a large number of species of stingless bees known to be subterranean belong to the most primitive groups (11). The rather primitive position of *T. mirandula* and the more advanced characters of *T. buchwaldi* have been pointed out; with regard to the nests most of the differences found between the two species are due to specialized characters found in the latter. Two such features in the nests of *T. buchwaldi,* unusual among the stingless bees, are the cylindrical shape of the food pots and the separation of the honey and pollen pots, as a consequence of which the nest has an irregular shape (Fig. 13), rather than a spherical one as in *T. mirandula.* From these considerations, it would apear that the subterranean nest of *T. mirandula* is primitive, while that of *T. buchwaldi* is a secondary adaptation.

One of the characteristics of the nest which seems to be of great evolutionary interest is the arrangement of the brood cells. Nests with spherical cells clustered together in a mass which is surrounded by an involucrum, are regarded as primitive by MICHENER (2, 3). On the other hand, nests with the cells arranged in concentric layers with space between them, as has been found in one Australian species, could serve, according to the author, as the basis from which the bees with horizontal combs of cells may have arisen. This being the case, the nests of *T. mirandula* and *T. buchwaldi,* like most species of stingless bees, do not show a primitive cell arrangement.

GENERAL BEHAVIOR OF *TRIGONA BUCHWALDI*

The bees are very timid and never fly at a person when their nest is opened. Unlike *Trigona mirandula, T. buchwaldi* is not easily attracted to honey baits, and when it is, it never gathers in great numbers.

The nest where the following observations were made had a population of 2028 individuals. Records kept for three days show that over 200 bees were foraging. Records kept for three days show that over 200 bees were foraging, most of them making trips that lasted a little over 30 minutes. If one could generalize from this nest, then about ten per cent of the bee population is active outside. Of these, only about twenty per cent or less collect pollen, while the other bees either collect nectar, explore the area, or carry out waste materials. When raining, they continue outside activities in an apparently normal way. The bees start their activity about 5:45 A.M., sometimes earlier or later according to the light penetration of the forest. First they open the nest, which is closed for the night. To accomplish this a bee makes a small slit in the roof of the turret which is progressively enlarged into a round hole.

When the aperture is still rather small, some of the bees usually leave the nest. After about 15 minutes the round hole is enlarged to its maximum, eliminating in this way the turret's roof. The activity increases gradually from 6:00 A. M. on. Foraging becomes rather active at 9:00 A. M., very active at 10:00 A. M., and extremely active at noon (see table 1). Then slowly and gradually activity decreases. At 5:00 P. M. it diminishes considerably and at 5:30 P. M. or later the bees start to close the entrance of the nest by adding

waxy material around the inner border of the turret, thus forming a small rim. The rim is then progressively enlarged until occlusion is completed. The nest is usually closed by 6:15 P. M.

TABLE 1

Bee activity during the day

Time	From 6:16 to 8:00 A. M. Bees out	Bees in	
6:16	1		
6:22	1		
6:30	1		
6:35	1		
6:38	1		
6:39	1		
6:40	4		
6:42	1		
6:47	2	1	
6:49	1	1	
6:50	3		
6:51	16		
6:52	21		
6:54	8		
6:56	3		
6:57	6		
7:00	4		
7:03	4	1	
7:06	2		
7:09	4	1	
7:13	4	1	
7:17	16	3	
7:20	11	3	
7:23	12	3	
7:25	17	1	
7:26	10	2	
7:28	11	4	(1 with pollen)
7:30	19	2	
7:32	12	3	
7:34	6		
7:36	12	1	
7:38	12	3	
7:40	9	1	
7:42	15	2	
7:44	7	5	(1 " ")
7:46	10	4	
7:48	10	2	(1 " ")
7:50	10	7	
7:53	8	6	(3 " ")
7:55	6	7	
7:58	5	3	
8:00	6	2	(" ")
Total	313	75	

From 10:00 to 10:29 A. M.

Time	Bees out	Bees in
10:00	5	4
10:01	9	9 (3 with pollen)
10:02	9	6 (4 " ")
10:03	6	7 (2 " ")
10:04	12	9 (2 " ")
10:05	15	6 (2 " ")
10:06	8	5 (1 " ")
10:07	14	6
10:08	10	10 (2 " ")
10:09	10	8 (3 " ")
10:10	16	11 (1 " ")
10:11	6	6 (3 " ")
10:12	9	7 (4 " ")
10:13	12	7 (3 " ")
10:14	16	6 (2 " ")
10:15	11	11 (6 " ")
10:16	9	11 (4 " ")
10:17	11	8 (2 " ")
10:18	7	11 (5 " ")
10:19	10	10 (2 " ")
10:20	9	12 (3 " ")
10:21	20	8 (1 " ")
10:22	13	6 (1 " ")
10:23	19	8 (2 " ")
10:24	13	10 (2 " ")
10:25	8	5 (1 " ")
10:26	17	8 (1 " ")
10:27	10	11 (6 " ")
10:28	10	8 (3 " ")
10:29	6	15 (2 " ")
Total	330	249

From 12:00 to 12:19 A. M.

Time	Bees out	Bees in
12:00	21	11
12:01	9	13 (1 with pollen)
12:02	19	9 (4 " ")
12:03	18	20 (2 " ")
12:04	7	22 (2 " ")
12:05	15	17 (2 " ")
12:06	13	17
12:07	19	15
12:08	9	17 (4 " ")

Time	Bees out	Bees in
12:09	9	23 (4 " ")
12:10	10	18 (3 " ")
12:11	16	14 (4 " ")
12:12	18	22 (7 " ")
12:13	13	23 (8 " ")
12:14	19	14 (3 " ")
12:15	11	24 (2 " ")
12:16	21	25 (8 " ")
12:17	12	13 (1 " ")
12:18	20	18 (2 " ")
12:19	19	18 (2 " ")
Total	298	353

From 2:00 to 2:14 P. M.

Time	Bees out	Bees in
2:00	17	9
2:01	18	20 (2 with pollen)
2:02	14	22 (2 " ")
2:03	10	15 (3 " ")
2:04	14	14 (2 " ")
2:05	21	9 (3 " ")
2:06	17	18 (5 " ")
2:07	13	20 (1 " ")
2:08	18	14 (1 " ")
2:09	15	18 (1 " ")
2:10	11	11
2:11	12	18 (1 " ")
2:12	19	13 (2 " ")
2:13	15	11 (1 " ")
2:14	7	17 (1 " ")
Total	221	229

From 3:45 to 3:56 P. M.

Time	Bees out	Bees in
3:45	3	7 (2 with pollen)
3:46	4	9 (1 " ")
3:47	5	9 (4 " ")
3:48	9	11 (3 " ")
3:49	4	13
3:50	16	6 (3 " ")
3:51	12	8 (1 " ")
3:52	9	6 (1 " ")
3:53	11	12 (2 " ")
3:54	5	9 (2 " ")
3:55	12	5 (1 " ")
3:56	10	17 (5 " ")
Total	100	109

Time	From 4:45 to 4:58 P. M. Bees out	Bees in
4:45	2	1
4:46	2	4 (2 with pollen)
4:47	1	2 (1 " ")
4:48	3	3 (2 " ")
4:49	4	3 (1 " ")
4:50	1	2 (1 " ")
4:51	1	4 (2 " ")
4:52	3	3 (2 " ")
4:53		4
4:54	3	4 (2 " ")
4:55	2	6 (2 " ")
4:56	1	5 (1 " ")
4:57	2	6
4:58		4 (1 " ")
Total	25	51

It is interesting to note that most bees, when leaving the nest, do not make any orientation flight. They simply fly upwards in a straight line, about 45° from the horizontal, seemingly going toward the canopy of the trees. This behavior was observed also in another nest. Some of the bees, however, do make an orientation flight. For instance, from 311 times that bees were observed leaving a nest, only 31 were seen making the orientation flight. To do this, the bee coming out turns at the border of the turret until its head is toward the entrance and its abdomen outwards. Then it takes off very slowly and always facing the nest entrance, it flies in a zig-zag manner and gently gets higher and farther apart, always flying backwards, up to a distance of about 1.5 meters or less from the nest, at which point they fly normally. The first flight movement upon leaving the nest has a side flight of about 2 cm, which just covers the front of the nest entrance. Then the zig-zag movement becomes wider and wider to reach a side flight of about 10 cm. Such a zig-zag distance is then maintained by the bee until the end of the orientation flight. It is also interesting to note that, unlike *T. mirandula,* the bees do not get lost very often; even the falling down of new dry leaves on the nest entrance does not seem to affect much their finding the nest. When the bees get lost it is only for relatively short periods.

ACKNOWLEDGMENTS

This is one of a series of studies made possible to Drs. Paul D. Hurd, Jr. and Ray F. Smith by the National Science Foundation Grant G-20016, "Palaeoentomological studies of Tertiary insect-bearing amber, Chiapas, México". I wish to thank Drs. Hurd and Smith also for their encouragement and suggestions during the period of the field observations. Señor Egidio Díaz and Prof. María Bozzoli de Wille assisted in many ways in the field. Dr. Ronald Echandi read the manuscript and offered suggestions. I acknowledge their cooperation with gratitude.

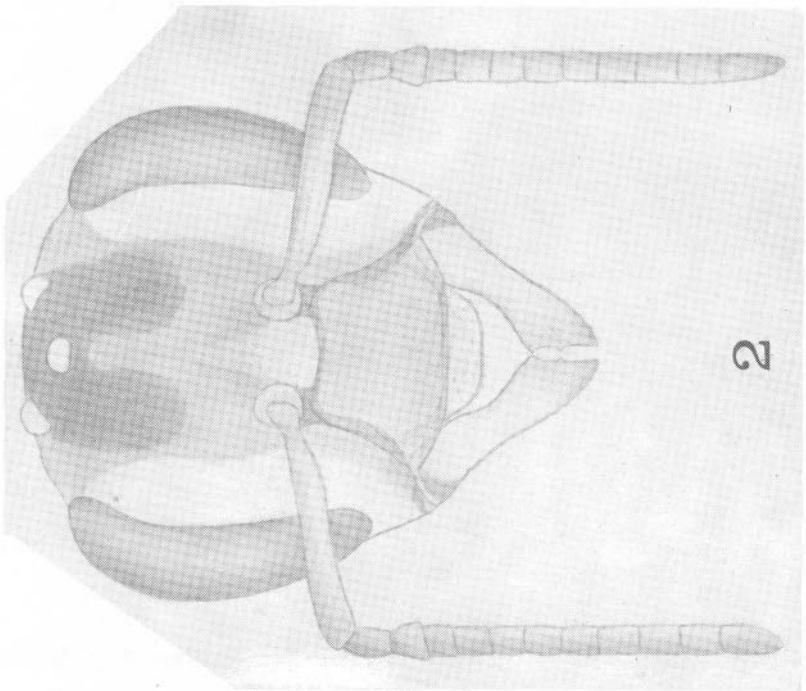
SUMMARY

The present study includes the following aspects: 1 Systematic position and relationships of *Trigona buchwaldi* and *T. mirandula.* 2) A description of the melanic queen form of *T. mirandula.* 3) A description of the queen of *T. buchwaldi.* 4) A brief account of the nest of *T. mirandula* with data previcusly unreported. 5) A detailed description or the nest of *T. buchwaldi.* 6) Ecological factors in relation to the nesting habits of the two species, which include: a) depth of the nest cavity in relation to the surface of the ground, b) impermeability of the outer walls of the nests, c) type of entrance turret, d) presence of drainage ducts or openings at the bottom of the nest. 7) Primitive and specialized characters in the nests of both species. 8) General behavior of *Trigona buchwaldi.*

RESUMEN

Este estudio trata de las relaciones y posición sistemática de *Trigona buchwaldi* y *Trigona mirandula;* contiene una descripción de las reinas de ambas especies, en el caso de *T. mirandula* de su forma melánica. Se incluye una descripción de la arquitectura del nido de *T. mirandula*: nido negro y esférico, con la cámara de cría e involucrum en la parte superior; la cámara de los alimentos, formada por los vasillos de miel y polen, en la parte inferior o debajo de la cámara de cría; se describe también un nido con un tubo de drenaje de 55 cm de largo. Se presenta una descripción detallada del nido de *T. buchwaldi*: nido negro de forma irregular, compuesto de tres cámaras separadas por medio de paredes de cerumen, a saber, la cámara de cría e involucro en la parte anterior del nido, donde desemboca el tubo de entrada; la cámara del polen, que se encuentra debajo de la de cría; la cámara de miel, que ocupa la parte posterior del nido, detrás de las cámaras de cría y polen; se describe también un nido con perforaciones en el fondo que aparentemente funcionan como aberturas de drenaje. Se tratan factores ecológicos en relación con los hábitos de anidar de ambas especies, a saber, profundidad de la oquedad del nido con respecto a la superficie, impermeabilidad de las paredes externas, tubo de entrada y presencia de conductos o aberturas de drenaje en el fondo del nido. Entre los caracteres primitivos y especializados en los nidos de ambas especies se comentan por ejemplo dos rasgos especializados del nido de *T. buchwaldi*: la separación de los vasillos de miel y polen en diferentes cámaras y la forma cilíndrica de los mismos. El trabajo termina con notas sobre el comportamiento general de *Trigona buchwaldi* incluyendo un cuadro de la actividad diaria.

Figs. 1 and 2: Queens' heads of *Trigona mirandula.*
Fig. 1 Ferruginous form.
Fig. 2. Melanic form.



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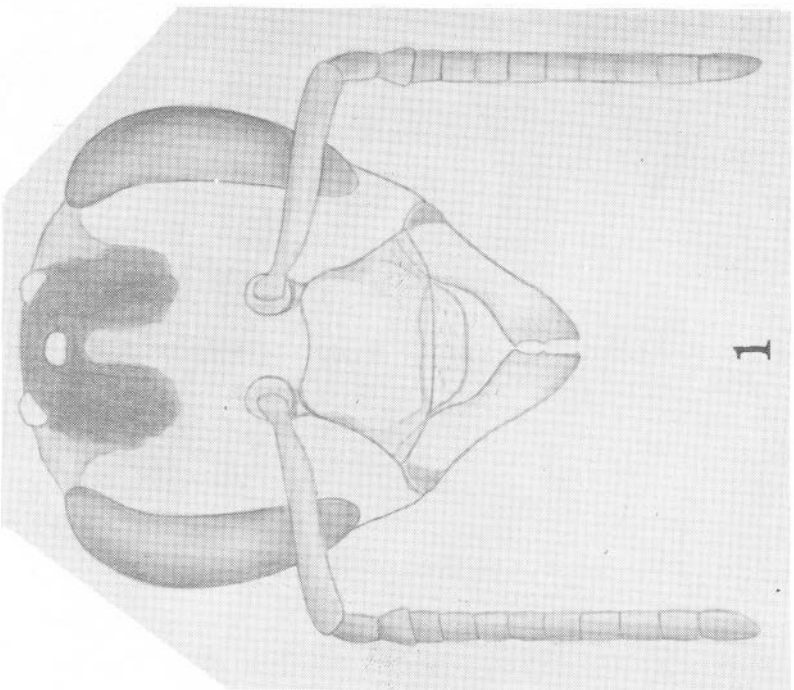

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LITERATURE CITED

1. HURD, P. A., AND J. S. MOURE
1963. A classification of the large carpenter bees (Xylocopini) (Hymenoptera: Apoidea). *Univ. Calif. Publ. Entomol.,* 29: 1-365.

2 MICHENER, C. D.
1961. Observations on the nests and behavior of *Trigona* in Australia and New Guinea (Hymenoptera, Apoidea). *Am. Mus. Novitates,* 2026: 1-46.

3. MICHENER, C. D.
1964. Evolution of the nests of bees. *Am. Zoologist,* 4: 227-239.

4. MOURE, J. S.
1951. Notas sobre Meliponinae (Hymenopt.—Apoidea). *Dusenia, Curitiba,* 2: 25-70.

5. MOURE, J. S.
1961. A preliminary supra-specific classification of the Old World Meliponine bees (Hym., Apoidea). *Studia Entomol.,* 4: 181-242.

6. PORTUGAL-ARAUJO, V. DE
1963. Subterranean nests of two African stingless bees (Hymenoptera: Apidae). *J. N. Y. Entomol. Soc.,* 71: 130-141.

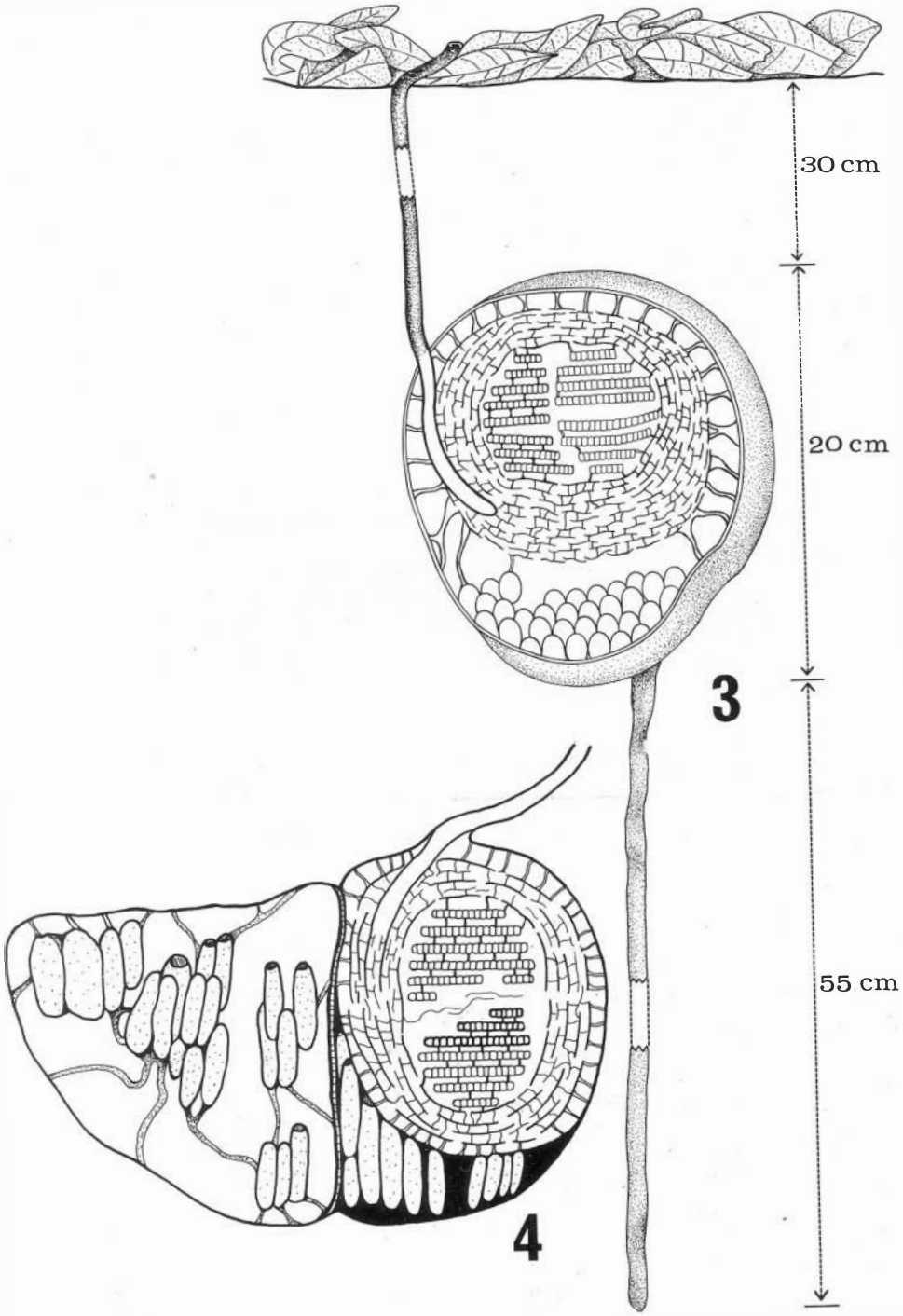
7. SCHWARZ, H. F.
1943. New *Trigona* bees from Peru. *Am. Mus. Novitates,* 1243: 1-10.

8. WILLE, A.
1962. A new species of stingless bee (Meliponini) from Costa Rica. *Rev. Biol. Trop.,* 10: 177-181.

10. WILLE, A.
1962. A revision of the subgenus *Nogueirapis,* an archaic group of stingless bees (Hymenoptera: Apidae). *J. N. Y. Entomol. Soc.,* 70: 218-234.

11. WILLE, A.
1964. Notes on a primitive stingless bee *Trigona (Nogueirapis) mirandula. Rev. Biol. Trop.,* 12: 117-151.

Figs. 3 and 4: Diagram of nests.
Fig. 3. *Trigona mirandula,* nest showing a vertical drain duct.
Fig. 4. *Trigona buchwaldi.*


30 cm
20 cm
3
55 cm
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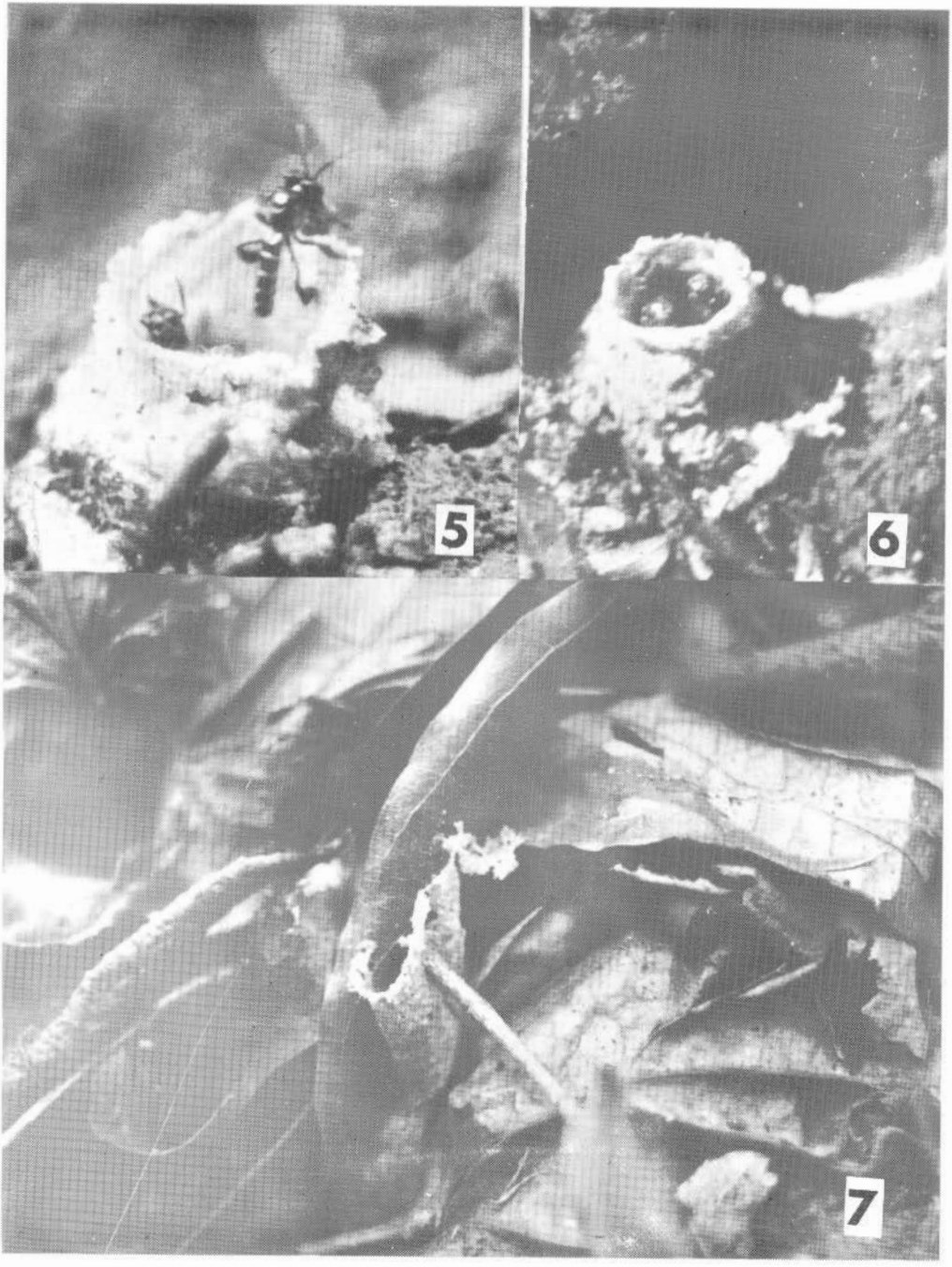
Figs. 5 - 7: Entrance turret of nest of *Trigona buchwaldi.*

Fig. 5. Nest entrance showing a bee ready to fly.
Fig. 6. Nest entrance showing two guard bees.
Fig. 7. Nest entrance projecting through a thick layer of organic debris.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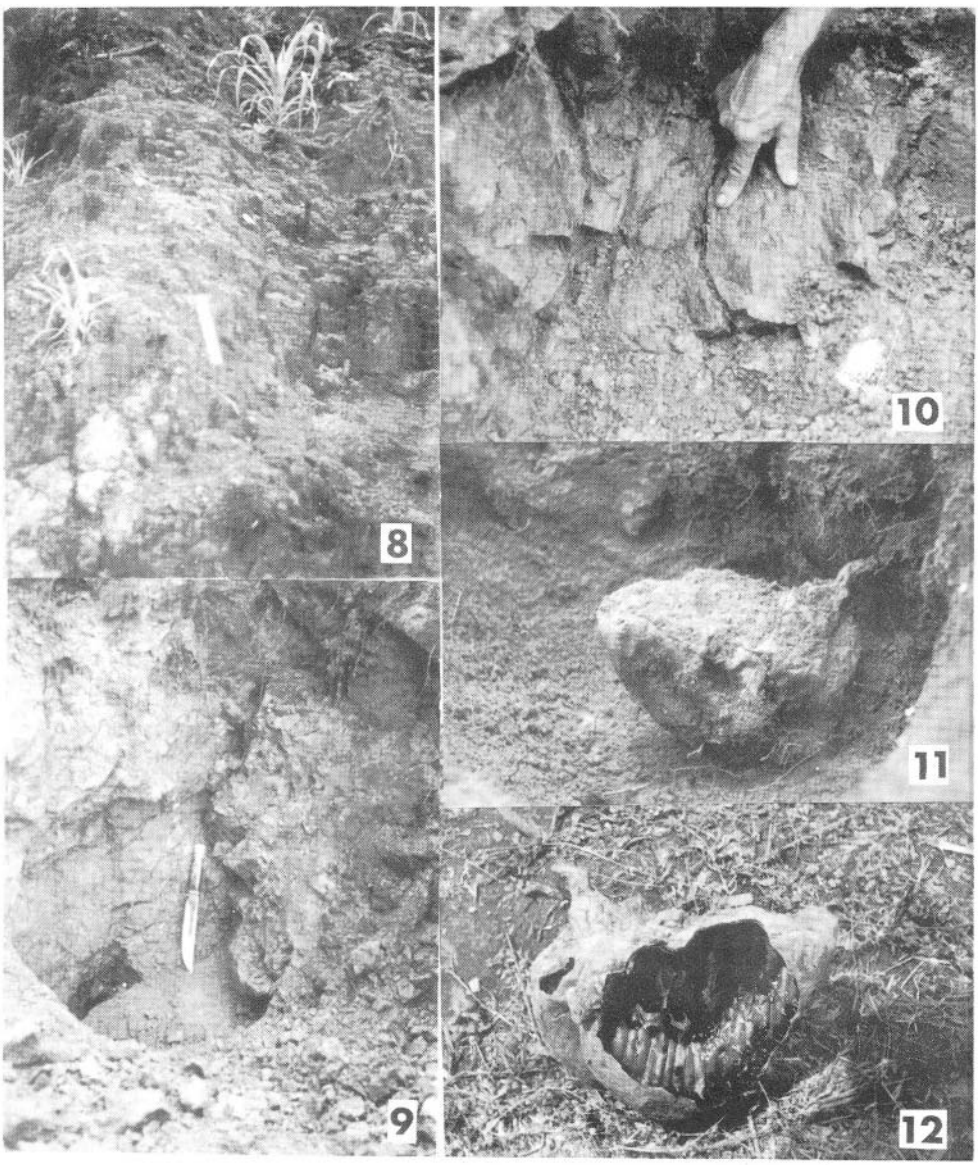
Figs. 8 - 12: Nesting sites of *Trigona buchwaldi.*
Fig. 8. Nest located in an exposed hill side.
Figs. 9 and 10: Nest located in sandstone.
Fig. 11. Nest located in soft ground.
Fig. 12. Nest with the honey chamber exposed.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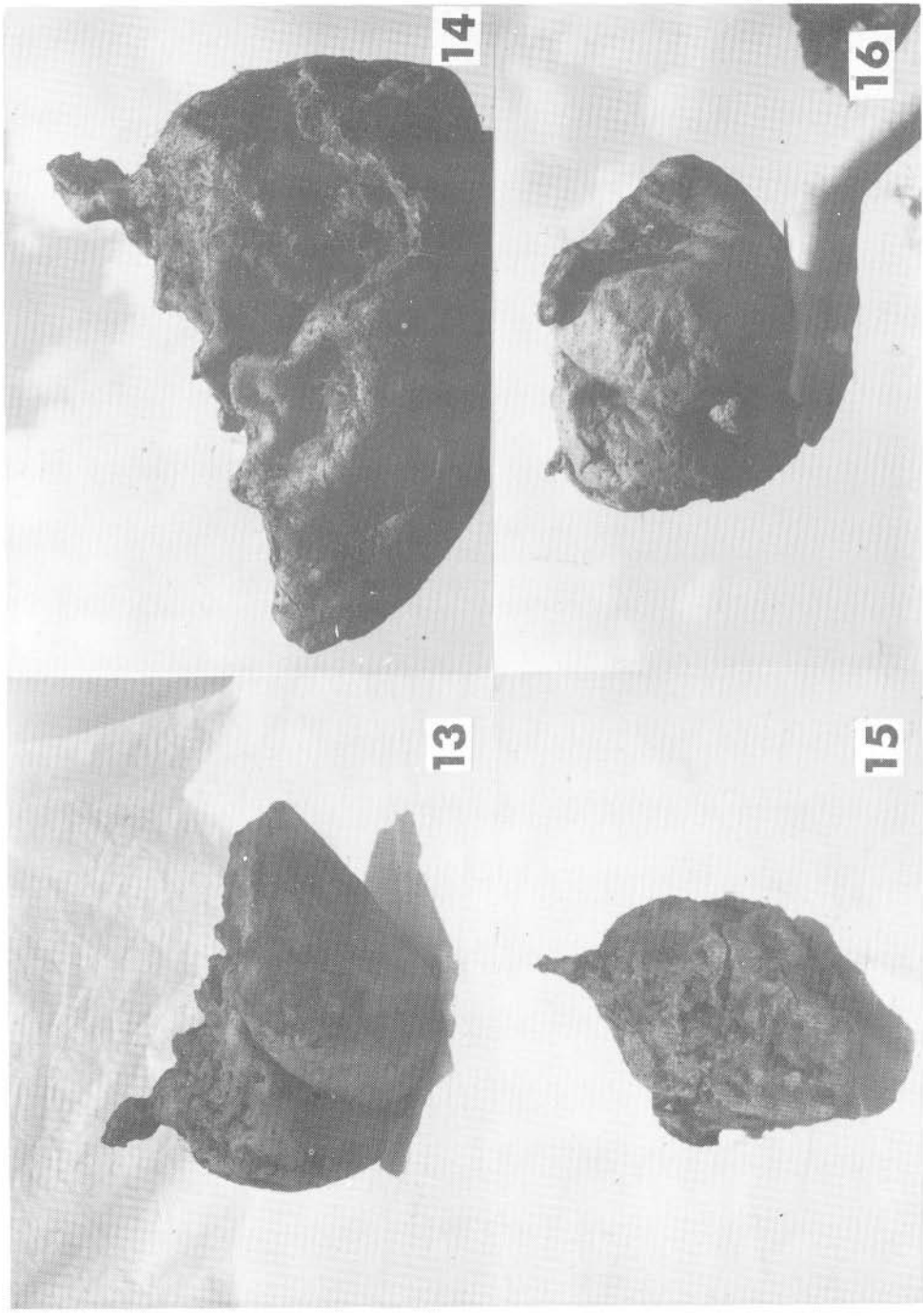
Figs. 13 - 16: External views of a nest of *Trigona buchwaldi*.

Fig. 13. Left side view.
Fig. 14. Right side view.
Fig. 15. Dorsal view.
Fig. 16. Anterior view.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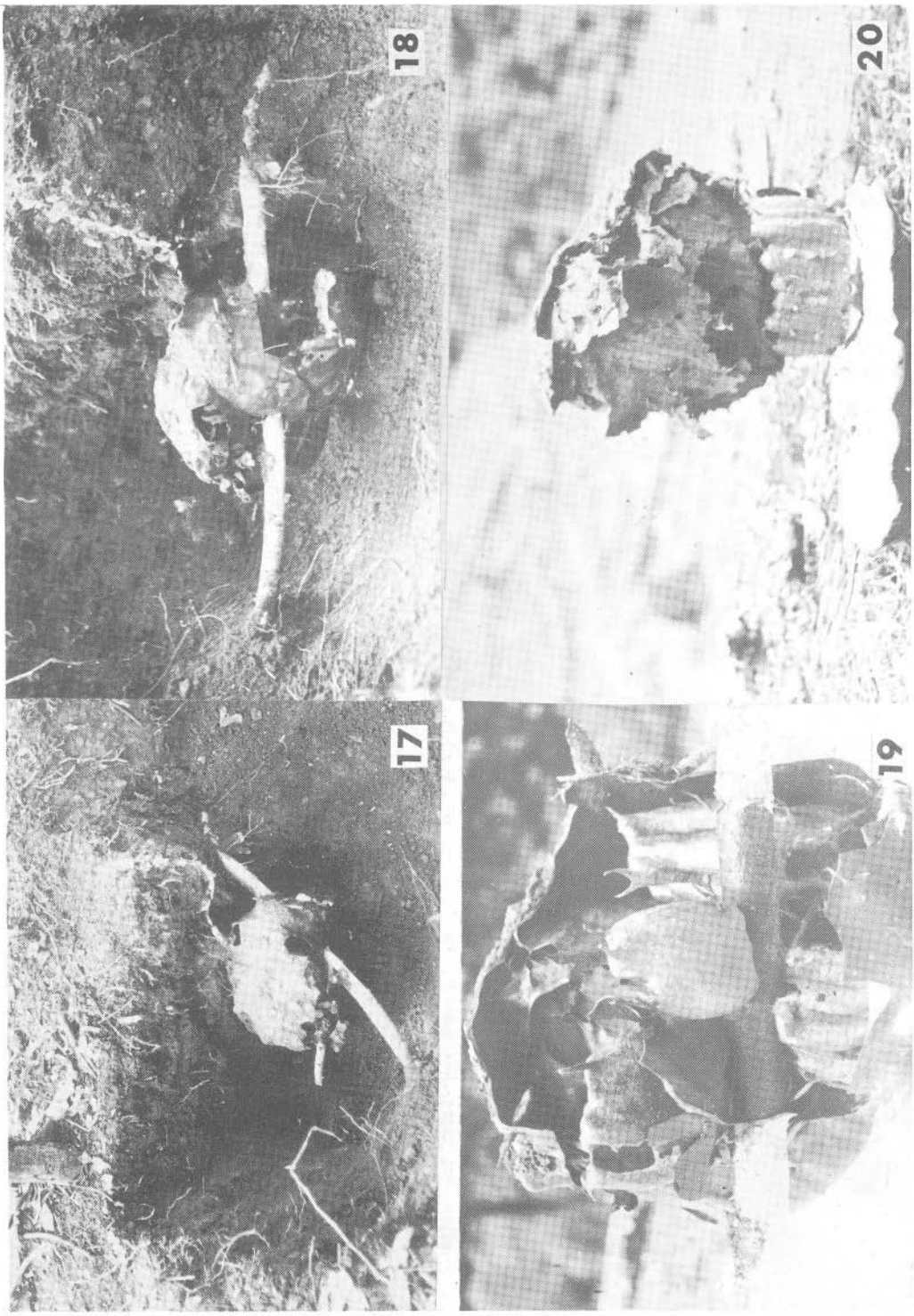
Figs. 17 - 20: Nest of *Trigona buchwaldi.*
Figs. 17 and 18: Nest *in situ.*
Fig. 19. Nest with the honey chamber exposed.
Fig. 20. Nest showing the enveloping 'sheets' and the pollen pots below.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Figs. 21 - 24: Nest of *Trigona buchwaldi.*

Fig. 21. Honey pots.
Fig. 22. Pollen pots.
Fig. 23. Brood chamber with enveloping sheets.
Fig. 24. Brood chamber showing advancing front.


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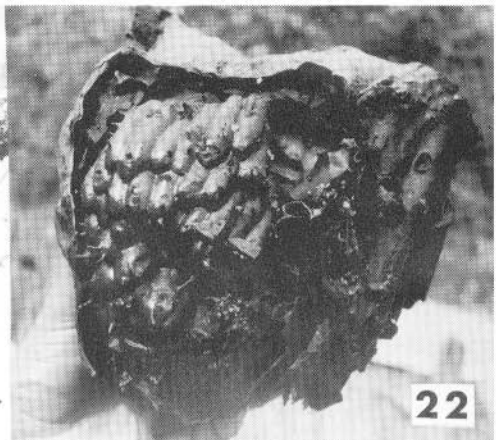
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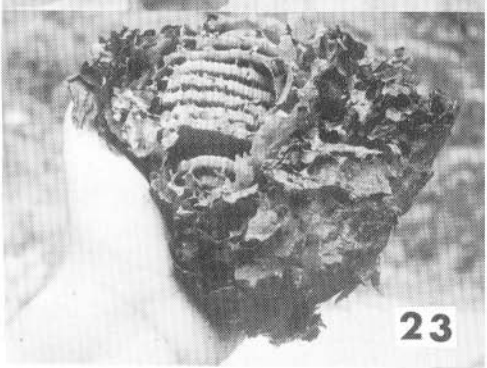
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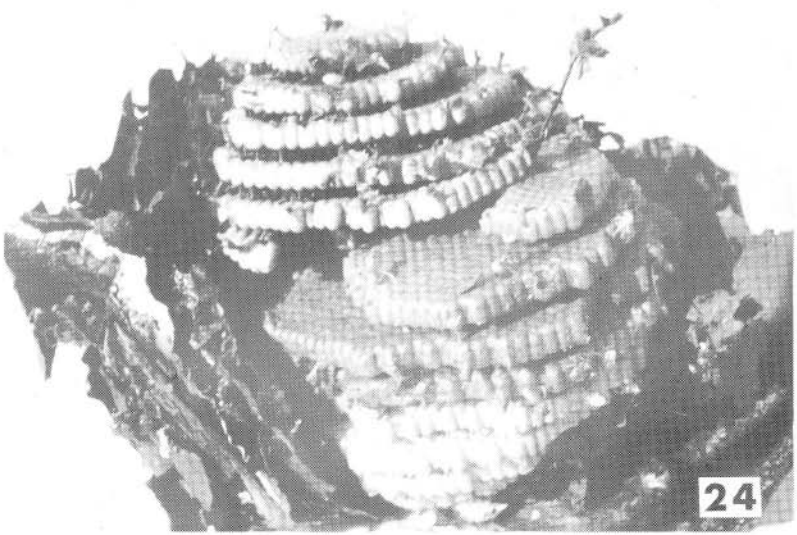
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