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Observations on the Ethology of Neotropical Anthophorine Bees (Hymenoptera: Apoidea)[1]

BY

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ABSTRACT. This paper summarizes available data on the biology of neotropical anthophorine bees. It also presents new information, primarily on nesting behavior, for members of the following genera: *Paratetrapedia, Monoeca, Tetrapedia, Melitoma, Ptilothrix, Peponapis, Melissodes, Melissoptila, Thygater, Anthophora,* and *Centris.*

With few exceptions the biological characteristics of groups set forth by Linsley, MacSwain, and Smith (1955, 1956) are supported.

INTRODUCTION

This paper gives the results of a series of studies of bees of the subfamily Anthophorinae (sense of Michener, 1944) and their nests carried out principally in the State of Paraná, in southern Brasil. One purpose of this paper is to make available for comparative study the rather fragmentary data which we have gathered on the species mentioned below. Another purpose is to summarize the data now available on the biology of the nonparasitic Neotropical members of this large group of bees, with supplementary or comparative information on representatives from other regions, to provide a basis for constructive comparative work on the biology of Anthophorinae in the American tropics.

1. The preparation of this paper and the figures accompanying it was facilitated by a grant from the National Science Foundation. Thanks are due to Father J. S. Moure for identification of the South American bees concerned. We are also indebted to Prof. Domiciano Dias, Escola Superior de Agricultura "Luiz de Queiroz," Universidade de São Paulo, Piracicaba, São Paulo, Brasil, and to Mr. Alvaro Wille, Mr. Carl W. Rettenmeyer and Mr. Howell V. Daly of the University of Kansas for data which they gathered and which we have used in this study.

2. Department of Entomology, University of Kansas, Lawrence, Kansas, U. S. A. Field work for this author's part in the study was possible thanks to a John Simon Guggenheim Memorial Fellowship and aid kindly made available by the Campanha Nacional de Aperfeiçoamento de Pessoal de Nível Superior, Rio de Janeiro; the Conselho Nacional de Pesquisas, Rio de Janeiro; and the Rockefeller Foundation, New York. In particular, thanks are due to Father J. S. Moure for the use of facilities of the Secção de Zoologia, Faculdade de Filosofia, Universidade de Paraná, Curitiba, Paraná, Brasil, during a year of residence in Curitiba.

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TRIBE EXOMALOPSINI

Little has been published about the nesting habits of members of this tribe. So far as known, all nest in the ground. A tendency toward communal life exists in this group. In the species discussed below as well as in *Ancyloscelis* (= *Leptergatis*) (Brèthes, 1909; Jörgensen, 1912a; Michener, 1954) each female presumably makes a separate nest and indeed in *Ancyloscelis* there seems to be but one cell per burrow, but these may occur in great aggregations. Hicks (1936), however, recorded four pollen-laden females of *Exomalopsis* entering a single hole, and Dr. Paulo Nogueira-Neto of São Paulo tells us that he observed numerous females of another species of *Exomalopsis* entering a single nest. Moreover, Rozen and MacNeill (1958) surmized that various individuals of still another species were utilizing a single burrow, and they found such burrows in a large aggregation. Claude-Joseph (1926) found various individuals of *Tapinotaspis caerulea* (Friese)[1] using a single entrance hole but making separate lateral branches for cells. Linsley, MacSwain, and Smith (1954) describe how individuals of *Exomalopsis* were observed entering probably abandoned nests of other bees. Perhaps this explains how they find nests of their own species to form these common nests. A few tribal characters of the cells, based only on *Tapinotaspis*, *Paratetrapedia*, *Ancyloscelis*, and *Exomalopsis* are as follows:

Cells in series (*Tapinotaspsis* and often in *Exomalopsis*) or not (*Paratetrapedia*, *Ancyloscelis*), not separable from surrounding matrix, lined with waxlike material. Provisions in the form of a firm ball or mass of various shapes [about spherical in *Paratetrapedia* and probably in *Tapinotaspis*, elongate with a depression on one side in *Ancyloscelis* (Michener, 1954) and elongate and angulate in *Exomalopsis* (Rozen and MacNeill, 1958)], not merely packed into the bottom of the cell. Egg laid on top of provisions or, in *Ancyloscelis*, in a broad concavity along one side of an elongated mass of provisions (Michener, 1954).

Paratetrapedia oligotricha (Moure)

This is a species of the subgenus *Trigonopedia*. An enormous nest aggregation of this species was found in a vertical bank of sandy soil in Floresta de Tijuca, Rio de Janeiro, D. F., Brasil, at an altitude of 500 meters above sea level, on November 28, 1955.

1. This species is placed in a new subgenus of *Tapinotaspis*, rather than in *Exomalopsis*, by Michener and Moure (1957).

FIG. 1. Portion of a vertical bank in the Floresta de Tijuca, Rio de Janeiro, containing an aggregation of nests of *Paratetrapedia oligotricha* (Moure). The white mark at the lower right is a ruler about 11 cm. long.

There were about ten square meters densely occupied by nests (fig. 1); in one square, 10 cm. on each side, there were 41 nests. There was no evidence of old cells or nests of previous generations in this bank and Dr. Carlos Alberto Campos Seabra who took one of us to this locality had not previously seen this aggregation although he is intimately acquainted with the Floresta de Tijuca. Another bank a quarter of a mile away had been similarly densely occupied, almost certainly by this same species, three years previously according to Dr. Seabra's observations but in July, 1955,

and again in November, not a bee could be found there, only old nests with cells which contained feces and had apparently produced a crop of bees. It is clear that new aggregations can form in a brief period. Possibly additional individuals are attracted by the odor of those that have already started nesting.

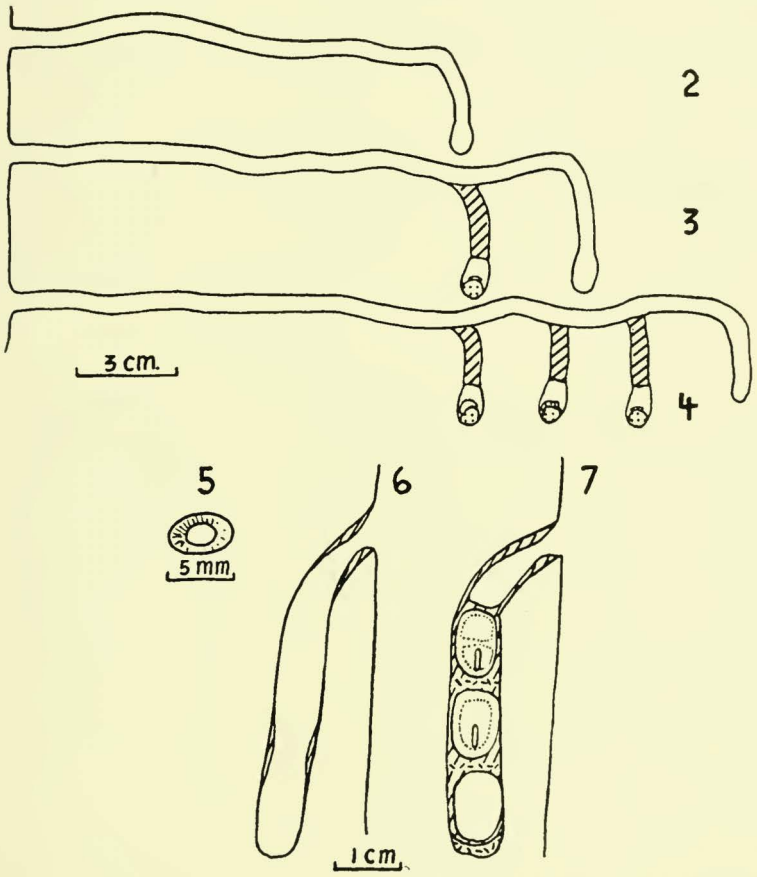
On November 28, although the bank was thick with bees in flight, some of which were starting their burrows, and the oldest larvae had not finished the last of their supplies, no males were seen. By January 9, 1956, a new generation had probably been produced, for Dr. Seabra, who visited the bank on that day, observed both sexes in flight and many pairs mating. Often pairs would roll down the bank and complete copulation at the foot of the bank. Dr. Seabra killed four pairs, taken mating, in Kahle's fixative and sent them to us. Three of the females, on later dissection showed no sperm cells in the spermatheca and therefore must have been mating for the first time when captured but the fourth already had a ball of sperms in the spermatheca. There were also sperm cells in the common oviduct. Presumably this individual must have mated previously, as the minute spermathecal entrance as well as our knowledge of the situation in *Apis* indicate that hours must be required for the entrance of a large number of sperm cells into the spermatheca. That multiple matings are not only common but the rule in *Apis* is well known (for references to pertinent literature, see Peer, 1956); it is interesting to find evidence, however fragmentary, of such behavior in other bees.

On February 22 activity of *Paratetrapedia* was continuing in the bank according to Dr. Seabra. Although there was no certain evidence that a second generation was being reared there, it is very probable. Unfortunately road construction resulted in destruction of the bank so that subsequent observations were impossible.

The same species was also observed nesting in the Bariguí roadside banks near Curitiba, Paraná, Brasil. The number, distribution and orientation of the nests, as well as climatic and soil data, are given by Michener, Lange, Bigarella, and Salamuni (1958). The nests were very few and scattered. Doubtless because of the cool climate of the south Brazilian plateau, the season of activity is somewhat different from that of the population at Rio de Janeiro. On October 17, 1955, bees were still prepupae in their cells and on March 11 and 18 nests were being constructed.

So far as known each nest is constructed by a single female bee. The nests are more or less winding, unlined, roughly horizontal

burrows 12 to 30 cm. deep, 5-6 mm. in diameter. Descending at intervals from this main burrow are vertical branches 3 to 20 mm. long, each ending in a single cell. The nest is constructed as a short horizontal burrow which turns down near the inner end and



FIGS. 2 to 4. Nests of *Trigonopedia oligotricha* (Moure) in various stages of construction. Dotted areas represent pollen balls; lined burrows are filled with earth. In left cell of fig. 3 and right of fig. 4, egg is shown on top of pollen ball.

FIG. 5. Entrance of burrow of *Tetrapedia maura* Cresson.

FIGS. 6 and 7. Nests of *Tetrapedia maura* Cresson. Fig. 6 shows burrow without cells but with gray material (lined) narrowing entrance and starting to narrow the burrow in formation of cells. Fig. 7 shows a completed nest. Short lines in various directions represent wood particles; lined area represents hard gray material brought to nests by bees. Pollen (omitted in lower cell) has dotted lines to show margins of cavities. Eggs are shown in two upper cells. (Figures 5 to 7 modified from sketches made by Alvaro Wille and Howell V. Daly.)

ends at the first cell. When this cell is complete and provisioned, the bee continues the horizontal burrow from the point where it turned downward, at the same time filling the vertical burrow, probably with newly excavated material, and soon turns down to make a second vertical burrow and cell. The process continues so that the oldest cell is consistently nearest the entrance, the youngest deepest in the bank (figs. 2 to 4). The number of cells per nest is unknown but reaches at least four. The main burrow is apparently never closed.

The vertical cells are 6 to 6.5 mm. in diameter, 11 to 12 mm. long, lined with shining waxlike material. The provisions are in the form of a rather firm ball occupying the bottom of the cell and with the gently curved egg lying on top. Some cells were found with cocoons but these were probably made by a parasite; we believe that the *Paratetrapedia* makes no cocoon.

Monoeca sp.

A single female of an unidentified and apparently new species of *Monoeca (= Fiorentinia)* was found in a nest in a tiny bare spot among grasses near São José dos Pinhais, Paraná, Brasil, February 21, 1956. The somewhat irregular burrow, with a tumulus of loose soil at the entrance, was 20 cm. deep, 6 mm. in diameter, and ended in a single vertical cell lined with waxlike material and lacking provisions. As the wing margins of the bee were entirely worn off, and her mandibles worn until they did not meet, it was obvious that this was not the first nest of this individual. Apparently *Monoeca* makes more than one nest.

Schrottky (1901) recorded that *M. schrottkyi* (Friese) made burrows over a meter deep in a bank.

Tribe Tetrapediini

This tribe was recently separated from the Exomalopsini by Michener and Moure (1957). The biological characters of the tribe, here described, strongly support this separation.

The nests are excavated in wood, the vertical cells placed in series in the burrow in the wood. The bees apparently bring in some dark substance to form the cells and to narrow the entrance to the nest. The pollen mass is firm and rather dry, vertically elongate, against one side of the cell, with a concavity which is sometimes divided by a transverse ridge. The egg is placed in a vertical position in the lower part of the concavity. This is suggestive of *Ancyloscelis* (Michener, 1954).

Tetrapedia maura Cresson

The observations recorded below were made five miles north of Guacimo, near Limón, Costa Rica, by Alvaro Wille and Howell V. Daly, both of the University of Kansas, during the period February 17 to 20, 1954. About eleven nests were found in two of the vertical supports (old, long dead trunks of small trees) of an old jungle hut. They were protected from rain by the thatch of the hut.

In dark rainy periods there was no activity of the bees. In the morning, sun struck the poles of the hut at 7:27 a.m.; the first *Tetrapedia* left their nests at 7:30. Before they left, they stood at the entrances of their nests for a few minutes, then flew off with little or no orientation flight. These bees returned in 10 to 25 minutes without pollen, but by 8:30 bees were returning with pollen. Many of the pollen-collecting trips were very short, only a few minutes long; the bees returned carrying large yellow balls of *Cucurbita* pollen on the outside of each hind tibia. In rapid flight the long legs with the pollen are folded near the under side of the body but as the bee approaches a landing they are extended conspicuously downward. Sometimes a dark material, apparently used in nest construction (see below), was carried in the scopa instead of pollen. One bee which must have been involved in excavation was seen several times backing out of its hole with large loads of wood powder. On leaving the nest it hovered and dropped dust by rubbing the legs together in flight. Sometimes a bee was seen to enter a nest backwards. Considerable confusion was noted about recognition of holes; sometimes bees attempted to enter holes much too small; one bee was seen to attempt to enter its hole, then it dragged another bee out by the leg before entering. There was no evidence, however, that more than one bee worked jointly in a single nest, although evidence obtained on opening nests seemed to indicate that a hole may be reused. After about 10:30 a. m. activity became less intense, and in the afternoon was very slight; the last bee was seen entering its nest at 5:30 p. m. Throughout the day *Coelioxys* were flying about the poles, sometimes entering holes; they may be parasites of *Tetrapedia*.

The nests consist of simple burrows which enter the wood obliquely for about a centimeter and then turn down, vertically, parallel to the surface of the pole, and extend for 3.5 to about 5 cm. (figs. 6 to 7). The burrows are oval in cross-section, 3 mm. in short diameter, 5 to 6 mm. in the long diameter. The entrance is funnel-shaped due to the placement there of a hard gray material (figs.

5 to 7) which narrows the opening. One nest opened had this material at the entrance and only a little along the walls of the burrow (fig. 6). In others the entire burrow or much of it was narrowed by similar material from which the cells were also formed (fig. 7). The cells are about 10 mm. long, 8 mm. wide, end to end in a vertical series. Their inner walls are not smooth and shining, but are made of the gray material mentioned above. All the nests that contained cells had some wood particles occupying a small space at the bottom of the nest and some had thin transverse layers of wood particles between cells. The number of cells per nest, in those that seemed to be completed, was 3 or 4. One nest already abandoned by the mother had the oblique upper part largely filled with gray solid material.

The pollen mass is unique among known bees. It is vertically elongate, about 9 mm. long and 5 mm. wide, against one wall of the cell. There is a hollow, sometimes divided by a transverse ridge, in the exposed face of the pollen mass. The egg, which is about 3.5 mm. long, is in a vertical position in the lower part of the hollow (fig. 7). The larvae apparently feed from the surface of the pollen mass, for cells with rather large larvae still have a layer of pollen adhering to the wall of the cell.

TRIBE EMPHORINI

Some of the biological characteristics of this tribe and of the genera contained in it were recently summarized by Linsley, MacSwain and Smith (1956). As always when generalizations are based on few data, as is necessary in such biological studies at the present stage of our knowledge, certain conclusions, useful at the time, prove to be premature. The following comments, then, concern additions to the valuable summaries of biological characters listed in the above mentioned work.

At least some of the South American *Ptilothrix* nest in vertical banks or in adobe walls, in contrast to North American species (see Strand, 1909; von Ihering, 1904; Ducke, 1901; and species discussed below). *P. fructifera* places its cells in series, unlike other species of the genus whose biology is known. *Diadasia chilensis* (Spinola), according to Claude-Joseph (1926), starts its turrets with the first soil excavated from the nest. This species and possibly *D. analis* (Vachal) (Bertoni, 1925), and also some *Ptilothrix* seem fully as gregarious as *Melitoma* (Strand, 1909; von Ihering, 1904; Ducke, 1901).

Among the most important characters are the form of the pollen mass, which in North American species, as shown by Linsley, MacSwain and Smith (1956) occupies the bottom of the cell and is not formed into a ball, and the position of the egg, which in these species is beneath the pollen mass. In *Diadasia baeri* (Vachal) (see Janvier, 1955) and *D. chilensis* (Spinola) (see Claude-Joseph, 1926), the egg is placed on top of a more or less spherical pollen mass, and Ruiz (1940, 1942) supports this statement in at least a general way for *D. chilensis*. In *Diadasia analis* (Vachal) also, the pollen mass is a ball, but the egg is placed at the side and beneath it, as in North American members of the genus (Janvier, 1955).

The observations reported below indicate that the egg of *Ptilothrix plumata* is on the surface of the ball-like pollen mass. As this was based on observation of a single nest it might seem to be an error. Strand (1909), however, also refers to the pollen mass of this species as a ball. Moreover, von Ihering (1904) describes the pollen mass as an oval, and states that the egg is laid after the provisioning is completed. From this we believe he meant that the egg is on top of the provisions.[1]

Tribal characters, modified from those listed by Linsley, MacSwain, and Smith (1956), are as follows: Nests usually with turrets at entrances; cells arranged serially or singly, urn-shaped, the walls constructed by the bee so that in some genera (*Melitoma*) the cells are easily separable from the matrix; waxlike linings of cells exceedingly thin or perhaps absent; cell cap not lined with waxlike material. Provisions a firm mass usually filling lower part of cell, sometimes ball-like. Egg usually below mass of provisions, sometimes on top of it. Feces (or unused pollen) spread as a layer over entire inner surface of cell, no separate pellets visible in this layer but may be visible at top of cell. Cocoon very thin.

Melitoma euglossoides Lepeletier and Serville

This species has been seen by one of us (C. D. M.) nesting in large aggregations in banks near Yautepec, Morelos, Mexico and in adobe walls near Lima, Perú, and has been recorded nesting in sim-

1. On reading the manuscript of this paper, Dr. E. G. Linsley of the University of California made some comments that seem important in this connection. He notes that he and his associates have repeatedly observed partial pollen masses of *Diadasia* and *Ptilothrix* in cells which were being provisioned. An egg was never present until the pollen mass was completed. This indicates that the egg is laid in its position beneath or at the side of the pollen mass after the mass is completed. Thus von Ihering's statement that the egg is laid after provisioning is complete may not mean that the egg is on top of the pollen. Moreover, Dr. Linsley suggests that a point of this type is very subject to observational error since pollen balls readily shake loose during excavation by an observer. It would be desirable to restudy the position of the egg in the South American species that are reported to place their eggs on top of the pollen masses.

ilar aggregations by Bertoni (1918, 1929). Moreover, the closely related *Melitoma taurea* (Say) of the United States nests in aggregations (Rau, 1929). It is therefore of interest that we found no dense aggregations of *M. euglossoides* in Brasil, but only a few nests, sometimes entirely isolated. Rau also noticed similar scattered nests for *M. taurea* in the United States and assumed that they were in unsatisfactory locations where high mortality due to lack of shelter of the bank prevented establishment of aggregations. Doello-Jurado (1912) in Argentina recorded not only an isolated nest of *M. euglossoides* but a cluster of about 25 nests in an area of four square feet in a large bank. Most of our observations were made in the Bariguí roadside banks where, as noted by Michener, Lange, Bigarella, and Salamuni (1958), this bee nests in two small, especially hard areas of the generally hard dry-looking soil of layer B, which is scarcely used by other bees of the region. In these two areas a total of 16 nests were found; sometimes two or three were close together but most were half a meter from their nearest neighbors. As *Ipomoea* flowers, on which these bees are largely dependent, are not common in the vicinity, lack of food may be the factor that limits population growth. In this connection, it is interesting to note that this bee visits flowers of cotton in large numbers near Lima, Perú.

During the season of adult activity the nests usually have a distinct turret, although frequent rains often destroy it. Only one nest in a protected situation had a long downcurved turret. During the rest of the year, when the adult bees are not active, the nests stand open. One such nest was excavated on September 16, 1955. The only two cells not moldy contained prepupae. Adults were seen in flight and constructing nests in late February and March, 1956. The nests are 5 or 6 cm. deep with several branches, each of which becomes completely filled with series of cells (figs. 8 and 9). Three nests excavated after the season of adult activity had 4, 8, and 12 cells each. By contrast, three nests excavated from shaded unbaked bricks in a porch foundation at Fazenda Salta, São Carlos, São Paulo, Brasil on April 1, 1956, after the season of adult activity, had only three or four cells each. At this locality Dr. Domiciano Dias observed bees actively making and provisioning cells, and other cells containing large larvae, as early as January 12, 1946. There is no evidence that more than one bee works in a single nest.

The cells are urn-shaped (fig. 10), horizontal to vertical, usually somewhat inclined, constructed of soil (as mud) in the cavity ex-

cavated by the bee so that they are readily separated from the matrix. The walls are about 1 mm. thick. The following measurements shown as means and their standard errors (with the number of cells measured indicated in parentheses) show the rather variable sizes of the cells: outside length, 15.48±.16 (18); inside length, 10.80±.17 (13); greatest outside diameter, 9.63±.13 (18); outside diameter at neck, 7.98±.15 (18); greatest inside diameter, 7.48±.11 (16); inside diameter at neck, 5.30±.10 (15). The outside of the cell is rather rough, the inside very smooth and very thinly covered with waxlike material which is not readily separable from the earth of the cell wall and does not quite reach the cell cap. The provisions, which have a yeastlike smell, are a stiff paste which occupies the lower part of the cell and covers the egg. The cell cap shows a conspicuous spiral pattern on the inner surface but the outer surface is beautifully smooth and concave, forming the base for the next cell in the series.

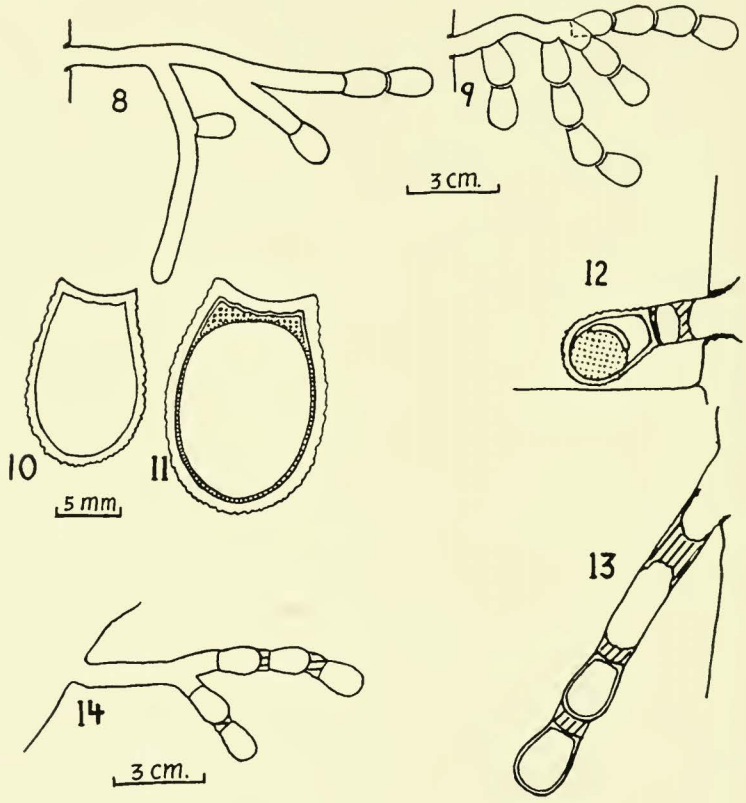
Dark feces are placed against the cell cap; the pellets are evidently soft when produced for they merge together and round out the roughness of the inner surface of the cap. A layer of white pollen .3 to .4 mm. in thickness, perhaps fecal, perhaps merely uneaten, lines the entire cavity quite uniformly, covering the dark feces. A pale brown cocoon, so thin as to be very inconspicuous, and apparently incomplete in the bottom of the cell and thickest near the cell cap, is appressed against the pollen layer. The cocoon is composed of fibers and the usual amorphous material.

Melitoma sp. ?

This species was first identified as *M. bifax* Vachal. After this paper was in press, Father J. S. Moure examined the type of that species in Paris and found it to be quite different. Our species is probably undescribed.

An aggregation of five or six nests was found in a vertical earth bank near Campo Largo, Paraná, Brasil, on January 27, 1956, by Prof. W. E. Kerr of the Universidade de São Paulo, Piracicaba. The general nest form is probably similar to that of *M. euglossoides*. There were no turrets, but the bees were not active at that time. A total of 13 cells containing living bees was excavated. Of these, two contained female pupae; five, male pupae; and six, prepupae. In the laboratory the latter did not pupate; possibly they would have remained as prepupae until the following summer. The pupae matured and all became adults by February 12.

The cells are similar to those of *M. euglossoides* in appearance but differ in some details. They differ from the description given above only as indicated below. Dimensions are as follows (based on 4 cells): outside length, 17 to 19 mm.; inside length 13.5 to 14.2 mm.; greatest outside diameter 11.7 to 13.5 mm.; outside diameter



FIGS. 8 and 9. Two nests of *Melitoma euglossoides* Lepeletier and Serville. Both were abandoned, but there is a possibility that the first was abandoned because of some mishap which befell the bee and not because she would normally have left a nest with only four cells.

FIG. 10. Longitudinal section of cell of *Melitoma euglossoides* Lepeletier and Serville.

FIG. 11. Longitudinal section of cell and cocoon of *Melitoma bifax* (Vachal). The coarsely stippled area represents feces, with a partial cocoon represented by the row of fine dots around the outside of the stippled area. The innermost line represents the cocoon proper, and the row of fine dots outside of it represents a layer of pollen.

FIGS. 12 and 13. Nests of *Ptilothrix plumata* Smith. Dotted area represents pollen mass with egg on top of it; lined areas represent earth plugs. (These diagrams were modified from drawings made by Prof. Domiciano Dias.)

FIG. 14. Nest of *Ptilothrix fructifera* (Holmberg). Shaded areas represent earth plugs between cells.

at neck, 9 to 9.8 mm.; greatest inside diameter 9.5 to 10 mm.; inside diameter at neck 6 to 7 mm. There is a thin partial cocoon, not attached to the cocoon proper, outside of the feces, obviously spun before defecation (fig. 11). The feces are whitish. The white pollen layer is thinner than in *M. euglossoides*.

Ptilothrix plumata Smith

The following observations were made by Prof. Domiciano Dias of the University of São Paulo who kindly allowed us to use material from his notebooks. The identification of the bee was made by Father J. S. Moure. The observations were made at Fazenda Salto, São Carlos, São Paulo, Brasil. The bees were nesting in a wall of incompletely baked brick. On January 12, 1946, three nests were found. One female started to dig at 1:30 p. m., worked until 5:37 making a hole 1.3 cm. deep in which she spent the night. On January 13 the bee worked all day to make the hole 2.3 cm. deep. On January 14 the single cell was completed, provisioned, and closed. The nest is diagrammed in figure 12. Some other nests contained two cells in a series (fig. 13) but obviously the bees must normally make several nests. Strand (1909) also records this species making nests containing a single cell each, although much deeper, probably because they were in a relatively soft sandy earthen bank.

During the digging process the bee makes numerous trips for water to soften the clay; after the small turret at the entrance is constructed she kicks pellets out of the hole with the legs as she digs. It was noticed that the bee enters the nest rapidly, without any wandering about or looking for the entrance.

The walls of the burrow are rather smooth but unlined. When the nest is completed, it is closed near the surface by a mud plug. The cell is roughly granular on the outside, its walls made of clay, apparently the material of the brick moistened and reworked. The inside of the cell is smooth and thinly covered with waxlike material. The cell cap shows a strong spiral pattern on the inside, is smooth and concave on the outside. The pollen is a firm mass, almost a ball, with the large curved egg (4 mm. long, .7 mm. wide) on its top surface. Von Ihering (1904) noted a coating of pollen lining old cells, showing that this species agrees with other Emphorini in this habit.

Father J. S. Moure tells us that he has seen enormous numbers of this bee nesting in a mud wall in Guarulhos, a suburb of the city of São Paulo, in February of various years, and von Ihering (1904)

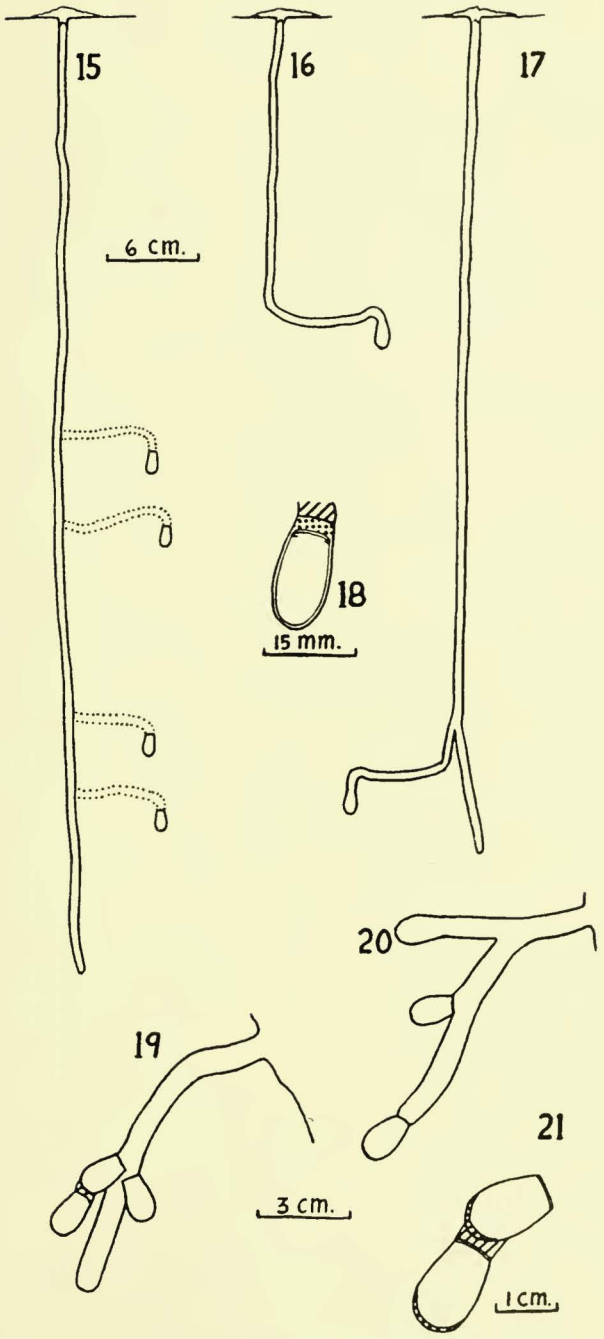
and Strand (1909) also record large aggregations of this bee in banks or termite nests.

According to Dias' description and sketch and the observations of von Ihering (1904), the nests and behavior described above agree remarkably well with those described for the North American species of the genus, *P. bombiformis* (Cresson) and *sumichrasti* (Cresson), except for (1) the shallowness of the nests, (2) the long time required to dig them in very hard material, (3) the fact that they are constructed in vertical walls, and (4) the position of the egg on top of the pollen mass. Linsley, MacSwain and Smith (1956) summarize this material for North American species and list the publications of previous authors relating to them.

Ptilothrix fructifera (Holmberg)

An abandoned nesting site was found in a subvertical bank of very hard soil along a gulley near Restinga Seca, 20 km. east of Palmeira, Paraná, Brasil, on January 27, 1956, and was excavated with the help of Dr. W. E. Kerr of Piracicaba, São Paulo. The nests were identifiable as those of this species by two living adult bees found in cells; no other living bees of any stage were present among hundreds of cells opened. The nests were so dense that their branches interdigitated, and it was with difficulty that one could be separated from its neighbors. Adjacent large areas of apparently similar banks were without nests.

The burrows, which are 9 to 10 mm. in diameter, lacked turrets, probably due to weathering, and were not plugged near the surface. They entered the bank for 4 to 9 cm., branched typically into two, although some were simple and others trifid. The cells formed series, usually of two or three, occupying nearly the entire lengths of the branch burrows (fig. 14). The general nest architecture is much more like that of *Melitoma euglossoides* than like other known *Ptilothrix*. Obviously nests were sometimes re-used, for one was found in which new cell walls had been built up in the open spaces of two previous cells. This shows clearly that the cell walls are constructed with moistened soil and are not made of soil *in situ* treated in any way. The cell walls are often more or less separable from the adjoining soil but the cells do not easily come out of the soil intact, as in *Melitoma*. The cells are vertical to nearly horizontal, the plug spirally marked on the inside, rough and not concave on the outside, thus quite unlike *Melitoma* and other *Ptilothrix*. Sometimes the cells of a series are separated by several millimeters of



Figs. 15 to 17. Nests of *Peponapis fervens* (Smith). Lateral burrows shown as dotted, leading to closed cells, were completely filled with earth and their exact positions not determined.

Fig. 18. Sectional view of cell and cocoon of *Peponapis fervens* (Smith). The dotted area represents feces; the lined area was earth filled.

Figs. 19 and 20. Nests of *Anthophora paranaensis* Holmberg.

Fig. 21. Sectional view of cell series from nest of same. Coarse dotted areas in bases of cells represent feces; lined area was earth filled.

burrow filled by loose soil; this is unlike *Melitoma* in which the cells are regularly close together. Internal cell measurements are as follows: length 12 to 15 mm.; maximum diameter 8.8 to 10 mm.; diameter of neck 6 to 7 mm. As in *Melitoma* and other *Ptilothrix*, a layer of white pollen is deposited, doubtless by the mature larva, between the thinly waxed cell surface and the very thin, brown cocoon.

TRIBE EUCERINI

Some of the biological features of this tribe were well summarized by Linsley, MacSwain, and Smith (1955[1], 1956). The study of various species unfamiliar to these authors naturally necessitates some changes in the tribal characters which they list. For example, some Eucerini, notably *Thygater analis* [also *Eucera longicornis* (Linnaeus) see Nielsen, 1941 and *Alloscirtetica gilva* (Holmberg), see Jörgensen, 1912a], nest in vertical banks as indicated below. *Thygater analis* sometimes occurs in aggregations (see Bertoni and Schrottky, 1910 and 1911, and observations recorded below), perhaps only because of limited nesting areas, but *Alloscirtetica herbsti* (Friese) nests in large aggregations (Claude-Joseph, 1926; Ruiz, 1940) as does *A. gilva* (Holmberg) (Jörgensen, 1912a), *A. tristrigata* (Spinola) (Ruiz, 1940), *Melissoptila dama* (Vachal) (Jörgensen, 1911, 1912), *Eucera notata* Lepeletier (Cros, 1939), and *E. longicornis* (Linnaeus) (Smith, 1855). Cells are single and vertical in most Eucerini, but as Claude-Joseph (1926) shows, they may be horizontal or slanting in such forms as *Alloscirtetica gayi* (Spinola) (*chilensis* Herbst) and may be end to end in modified series in this species and also in *A. tristrigata* (Spinola) and *herbsti* (Friese). These features may be characteristic of the genus *Alloscirtetica* and suggest that the "*Tetralonia* sp." found by Janvier (1955) using a nest entrance in common with *Diadasia baeri* was an *Alloscirtetica*. The three species of *Alloscirtetica* mentioned are in different subgenera. The cells are also horizontal in "*Tetralonia*" *decemcincta* Janvier (1955), a species whose correct generic position is unknown.

Much confusion has arisen from Friese's descriptions and figures of nests of *Eucera difficilis* (Dufour) (see Friese, 1919, 1923). Fortunately Höppner (1901) had given an accurate account of the nesting of this same species, indicating that the food is a paste oc-

1. In their list of genera of Eucerini, these authors were much influenced by certain errors in a previous paper of one of us (Michener, 1944). A more accurate treatment of the genera will be found in Moure and Michener (1955).

cupying the bottom of the cell, and not a ball as Friese states. The matter is further clarified, for different species of *Eucera* by Nielsen (1902), Nielson (1941) and for *Eucera* and *Tetralonia* by Iuga (1950). These authors show that in these species the food material is packed into the bottom of the cell as in other Eucerini and is not in the form of a ball. Iuga also makes clear with figures, as did Höppner verbally, the positions of the cells which were not well illustrated by Friese.

Several species of Eucerini often make nests in which two or more bees enter the same hole but probably each makes separate lateral burrows or groups of cells below the surface. This is reminiscent of the Exomalopsini and is recorded for such unrelated Eucerini as *Melissodes* sp., *Svastra (Epimelissodes) obliqua* (Say) (Custer, 1928), *Svastrides melanura* (Spinola), *Alloscirtetica tristrigata* (Spinola) (Claude-Joseph, 1926), and one nest of *Eucera longicornis* (Linnaeus) (Nielsen 1902). It probably occurs in *Melissoptila paraguayensis* (Brèthes); see below.

Tribal characters, modified from those listed by Linsley, MacSwain, and Smith (1955, 1956) are as follows: Nests (in Western Hemisphere) without turrets; cells usually arranged singly, elongate, usually vertical, with thin waxlike linings; cell cap not lined with waxlike material. Provisions a rather soft mass filling bottom of cell. Egg on top of provisions. Feces at top (cap) of cell. Cocoon thin, anterior end with multiple layers.

It is interesting that, although most Anthophorinae pass the winter as prepupae, *Eucera notala* Lepeletier metamorphoses in the fall and winters as an adult (Cros, 1939). This is contrary to the principal biological character of the subfamily brought forward by Linsley, MacSwain, and Smith (1956) to justify its elevation to family rank.

Peponapis fervens (Smith)

This is the bee that collects pollen from flowers of squash (*Cucurbita*) in the early mornings in Argentina, Uruguay, Paraguay, and southern Brasil, just as do species of *Peponapis* and *Xenoglossa* in North America. Also as in North America, *Peponapis* occurs around cultivated patches of squash (*abobora*) in regions where the plant apparently was never wild. Our observations were made at Curitiba, Paraná, Brasil, where nests were found in flat ground only a few meters from a squash patch, and at São José dos Pinhais, Paraná, Brasil, where a nest was found in flat ground 50 meters or

more from the nearest squash flowers. All excavations were made from February 16 to 21, 1956.

There was no evidence that more than one female occupied a single nest. Nests were found in the process of construction with no cells, and with larvae of all ages up to prepupae. The main burrow of each nest is vertical, very straight, 6.5 to 7.5 mm. in diameter (figs. 15 to 17). The inner walls of the burrow are very smooth but not lined with any visible material. Nests being excavated have large tumuli which completely close the entrances with loose dirt through which bees dig on entering or leaving.

Lateral burrows 4 to 7 cm. long extend at intervals from the main burrow; near their ends each turns downward and terminates in a single cell. In the only nest excavated which had several (4) such laterals and cells, the upper was the oldest. Laterals leading to closed cells are completely filled with soil and indistinguishable or nearly so. Cells were found from 20 to 60 cm. deep and one main burrow extended to a depth of 63 cm. There is evidence that a bee makes more than one nest, for a female with badly worn mandibles was found in a hole with only a single lateral and no completed cell.

Cells are vertical, 8 to 9 mm. in maximum diameter, 14 to 16 mm. long, lined with a waxlike material almost to their upper ends. They are not separable from the surrounding matrix like those of Emphorini but the soil on all sides of a cell, for a distance of 3 mm., is harder than adjacent earth as though impregnated with some material. The cell plug is rough on the inside and shows no spiral pattern.

The cocoon spun by the mature larva is thin, although thicker than in *Melitoma,* and easily pulled from the cell wall, pale brown, made of fine fibers and a brownish amorphous material. At the upper end the cap is conspicuously double and there is an inner flange or partial third layer (fig. 18). The feces, which are in the form of small fused pellets, are above the cap.

Male *Peponapis* often spend the day in closed flowers of *Cucurbita,* just as among North American species of *Peponapis* and *Xenoglossa.*

Melissodes nigroaenea (Smith)

A single nest in a nearly vertical bank near São José dos Pinhais, Paraná, Brasil, was found on February 21, 1956. It was 7.5 cm. deep and contained two cells, one provisioned and closed and the other empty. The cells were end to end (*i. e.,* in series) at the bottom of

the burrow; the provisions were a paste entirely occupying the bottom of the cell. The wing margins of the bee were entirely worn off and the mandibles were very much worn; if she produced a reasonable number of cells during her life this must have been at least her second nest.

Nests of *Melissodes sexcincta* (Lepeletier), another South American species, were described by Janvier (1955).

Melissoptila paraguayensis (Brèthes)

Two nests were found in small subvertical earth banks, one near São José dos Pinhais, Paraná, on February 21, 1956, the other in a suburb (Xaxim) of Curitiba, Paraná, Brasil, on March 12, 1956. The latter was 8 cm. deep and ended in a single vertical empty cell. The former was more interesting as it was 24 cm. deep and ended in a single vertical empty cell but contained two female bees, one in a small diverticulum near the entrance. Both bees had the wing margins entirely worn away and the mandibles much worn. They must have worked elsewhere, then joined, as senile bees, in this nest.

In another species, *M. dama* (Vachal), which, however, belongs to another subgenus, Janvier (1933) reports that each nest contains 6 to 10 cells.

Thygater analis (Lepeletier)

Aggregations of nests of this bee have been recorded previously (Bertoni and Schrottky, 1910, 1911) and one of us (R. B. L.) has studied an aggregation nesting in a small bank in the city of Curitiba. At least in this latter case, however, suitable banks were very scarce while bushes and trees of *Cassia*, a favorite food source for this bee, are abundantly planted as ornamentals; we presume that the density of nests in this case may have resulted from the small nesting space available and not from any innate aggregative tendency. In the Bariguí roadside banks, as shown by Michener, Lange, Bigarella, and Salamuni (1958), nests of this *Thygater* are widely scattered. During February and March, 1956, females of *Thygater* were often seen flying about the banks as though looking for nesting places. Special attention is characteristically given in such flights to depressions or cavities in the banks and nests are usually constructed in such depressions or beneath a small overhang. There was never any evidence of more than one bee occupying a nest.

Details of the life history of this bee will be reserved for a subsequent paper by one of us (R. B. L.). It will suffice here to note

that the main burrow is roughly horizontal although usually strongly undulating and extends from 15 to 28 cm. into the bank and that the cells are located at the terminations of burrows descending at intervals from the main burrow, one cell per branch burrow, so that the nest plan roughly resembles that of *Paratetrapedia oligotricha*, described above. The descending burrows are not really vertical but alternate, one inclined to the right, the next to the left, etc., as in nests of *Eucera* and *Tetralonia* (references under Tribe Eucerini, above). The mature larvae construct light brown cocoons and pass the winter as prepupae, pupate in the spring, and emerge as adults in summer.

The nests attributed to this species by Janvier (1955) must have belonged to a different form, for he records largely vertical burrows in flat ground ending in a palmately arranged group of five or six cells.

TRIBE ANTHOPHORINI

Some of the biological characters of the tribe Anthophorini can be summarized as follows (following the excellent account of Linsley, MacSwain and Smith, 1956):

Cells usually arranged in series (sometimes very short), urn-shaped, not separable from surrounding matrix, with thick lining of waxlike material; inside of cell cap thinly lined with waxlike material except in center. Provisions with a strong fermenting odor, semi-liquid at least at surface. Egg floating on surface of provisions. Larval feces in bottom of cell, pellets not separate. No cocoon.

The species described below agrees with other Anthophorini in the characters listed above; these features are therefore not repeated in the following account. In connection with the statement that cells are arranged in series, attention should be called to the twice trifid series described by Claude-Joseph (1926) for *Anthophora incerta* (Spinola), and to the description by Fahringer and Tölg (1912) of clusters of cells in a chamber for *A. garrula* (Rossi).

Janvier (1955) reports two or more females entering a single nest in *Anthophora incerta* Janvier (not Spinola) and *A. escomeli* Brèthes.

Anthophora paranaensis Holmberg

Nests of this bee were found isolated, never in aggregations, in banks at Araucaria, Restinga Seca, São José dos Pinhais and in the Bariguí roadside banks at Curitiba, all in Paraná, Brasil. The first nests were found on January 13, 1956, at which time some bees had already completed up to three cells while others were still un-

emerged adults in their natal cells. On January 27 two cells were found still containing white pupae; kept in the laboratory at 20° C. adults did not emerge until March 12. On February 21 and again on March 3 newly started nests were found. Probably there is but one generation per year but the time of emergence is obviously protracted. One nest excavated on January 13 contained three cells, one being provisioned, another containing a live mature female *Anthophora* still sealed in the cell and the third containing only mold. This indicates either an extremely long life for the maker of this nest, or more likely, the use of an old nest by another bee.

Nests lack turrets, the soil excavated from them merely tumbling down the bank from the nest entrance. They are most often constructed in very hard soil but one was found in a soft, rapidly eroding bank. Burrows are 5 to 10 cm. deep, 7.5 to 8 mm. in diameter, and extend inward and downward. The walls of the burrow are rough, unlined. The number of cells per nest was small in all cases, varying from 1 to 3, and the four nests examined which were constructed in late February and March had only one or two cells each. This seems to indicate that a single female makes more than one nest. Not over two cells were ever found end to end in a series. The cell position varies from nearly horizontal to nearly vertical. Cells are sometimes in the end of the main burrow, sometimes in short lateral burrows (figs. 19 and 20). Cells measured (3 in number) were 14 to 14.5 mm. long, 8.8 to 9.5 mm. in maximum width, and 6.5 mm. in width at the mouth of the cell. The latter point is clearly constricted in relation to the diameter of the burrow. The cell plug is concave on the inside, without any evident spiral or other pattern, and made of a layer of very fine soil about half a millimeter thick (fig. 21). Eggs are white, strongly curved, of uniform diameter, 3.5 mm. long, .75 mm. thick.

It is interesting that Holmberg (1903) mentioned *Coelioxys colobopteryche* Holmberg as a parasite, presumably taken from the nest, of *Anthophora paranaensis*, but did not describe the nest.

TRIBE CENTRIDINI

Little is known about the biology of members of this tribe. The nest locations are varied; some species of *Centris* make burrows in flat ground. Dr. W. E. Kerr of Piracicaba, São Paulo, Brasil, has reported to us the nesting of enormous numbers of *Centris aenea* Lepeletier in the flat ground about the airport at Porto Atlantida, Mato Grosso, Brasil, in July, 1954. Mr. Carl W. Rettenmeyer has ob-

served a female of *C. poecila* Lepeletier going in and out of a burrow in flat ground at San Carlos, Panamá, and Schrottky (1904) records similar nesting sites for *Centris*. Other species nest in banks or mud walls (Claude-Joseph, 1926; Bertoni, 1929; Ruiz, 1940; Vesey-FitzGerald, 1939; Jensen-Haarup, 1908; Jörgensen, 1912a; Janvier, 1955). Some do not make their own burrows but take advantage of available holes, such as those in an old *Sceliphron* nest (Vesey-FitzGerald, 1939) or old holes made in wood (Jörgensen, 1912, 1912a, and *lanipes* discussed below). Such holes are partially filled with earth, or in the case of *C. labrosa* Friese and *minuta* Moesary, with leaf fragments, in which the cells are placed.

We have not observed the carrying of materials to fill holes, but Mr. Carl W. Rettenmeyer of the University of Kansas has kindly allowed us to extract data pertaining to this matter from notes which he made on Barro Colorado Island, Panama Canal Zone. In April and May, 1952, March, 1955, and February to July, 1956 he noticed *Centris dichrootricha* Moure and *C. vittata* Lepeletier collecting mud in a bare area near the laboratory. A minimum of seventy-five females of *C. vittata* were collecting mud at this place during the six months of 1956 when he made these observations. The soil was a rather loose, sandy dirt. The bees appeared rather gregarious in their collecting. Up to four bees might be seen working in an area 20 cm. x 20 cm., although similar soil, often otherwise without bees, occupied an area of over five square meters. As many as ten bees might be in sight at the same time, arriving, leaving, and gathering dirt. The bees fly low over the area and may land several times before they start gathering soil. They visit various sections of the large area and after one bee settles, others often alight near it. The soil is carried on the scopa of the hind legs, like pollen, and Mr. Rettenmeyer has specimens in which the scopa is thickly covered with dirt. He has seen one *Centris* (possibly *dichrootricha* but not collected for identification) carry soil on the scopa into a hole in the side of one of the laboratory buildings.

Centris thoracica Lepeletier, *C. sponsa* Smith, and *C. derasa* Lepeletier have been recorded as nesting in termite nests (Silvestri, 1903; Pickel, 1928; Vesey-FitzGerald, 1939) and this seems to be the usual and perhaps only site for *C. sponsa*, according to Pickel, who remarks that the cocoons of this species are so well constructed that the termites are unable to perforate them. Various species are known to nest in large aggregations, usually in banks.

Some species of *Epicharis* also nest in banks (Vesey-FitzGerald, 1939). *E. rustica* (Olivier) was seen by that author, as was *E. ele-*

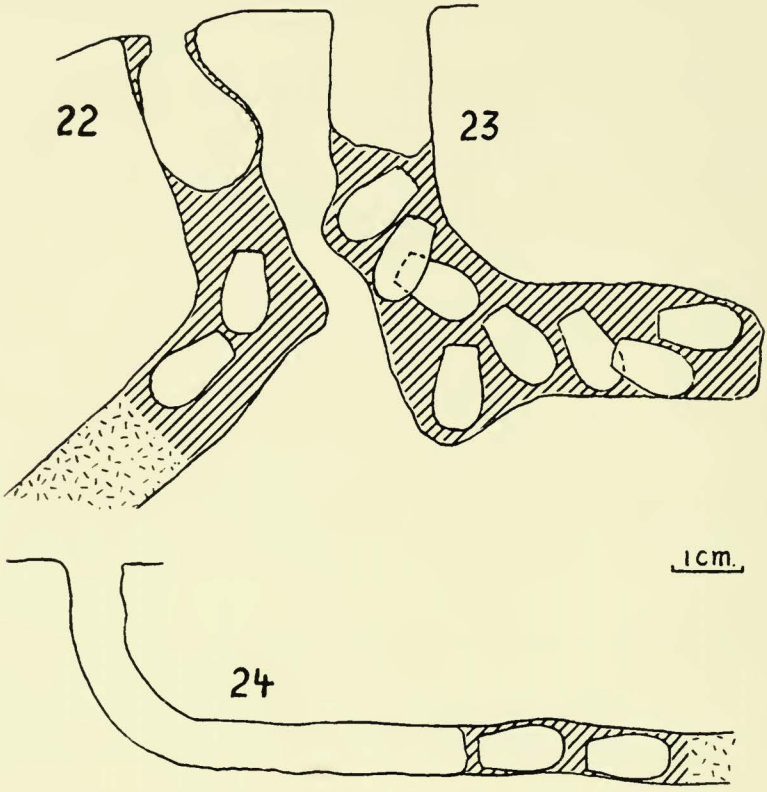
gans Smith at El Salto, San Luis Potosí, Mexico, by C. D. M., nesting in banks which were so overhung in cave and mine mouths as to be in permanent twilight.

Cells are usually arranged singly, not in series, except when (as in fig. 24), limited space forces cells into series. In *C. autrani* Vachal (Janvier, 1955), however, the cells are arranged in rather long series in burrows in earthen walls. In *C. sponsa* the cells are arranged in series of two to four; adults emerge to the side and make separate exit burrows, a behavior pattern which is not surprising since termites quickly close the original nest burrow with their nesting material (Pickel, 1928). Nests of some species have cells, one each, at the ends of very short laterals (Claude-Joseph, 1926). In *C. furcata* Fabricius the cells descend directly, without individual burrows, from the subhorizontal burrow (Janvier, 1955). The cells are elongate urn-shaped, the inner walls heavily waxed. In the two species of *Centris* discussed by Claude-Joseph the cell plugs have a hollow conical projection in the middle but this was not observed by Vesey-FitzGerald who mentions that the cell of *Centris rufosuffusa* Cockerell is closed by a disk of waxy material, and does not occur in *C. sponsa, C. autrani,* or *C. furcata.* Provisions are in the form of a paste occupying the lower half of the cell and sometimes covered with a layer of liquid. The egg is on the surface of the provisions. The cocoon is strong and in the species discussed by Claude-Joseph has a protuberance extending into the hollow projection of the cell cap.

Centris lanipes Fabricius

Bertoni (1918) mentions finding hundreds of nests of this species in the mud walls of a house, and a single nest among those of an aggregation of *Melitoma.* He says that the burrows, one for each female, penetrate horizontally or obliquely for a few centimeters. In 1929 the same author mentions large mixed colonies of these two species of bees, and mud walls completely mined over a period of years by the *Centris* burrows so that the holes intercommunicate and the cells touch one another. He also describes turrets at the nest entrances but to us it seems likely that these belonged to intermixed *Melitoma* nests since turrets are not elsewhere described for *Centris.* As there has been taxonomic confusion among relatives of *lanipes,* he may not have referred to the same species as that discussed below.

Nests of this species were found by Father J. S. Moure in old pieces of logs and in wooden buildings near the beach at Caiobá,



FIGS. 22 to 24. Nests of *Centris lanipes* (Fabricius) in holes in old wood. Frass and wood fragments in the holes are represented by short lines variously oriented; the lined areas represent sandy clay perhaps placed in the holes by the bees.

Paraná, Brasil. He kindly brought one large piece of a long dead tree containing six *Centris* nests to the laboratory in Curitiba. The journey over rough roads apparently destroyed the eggs, so that their position in the pollen mass could not be determined when the nests were opened on December 5, 1955.

The nests were all in old holes made by wood boring Coleoptera. These holes were often partially filled by frass and wood fragments evidently left there by the borer. However, the outer several centimeters were filled by sandy clay, no doubt placed there by the bees, and the cells were constructed in this earth (figs. 22 to 24). In one case (fig. 22) earth formed a plug, perforated by a hole 5.5 mm. in diameter at the entrance. In this case the large space behind the

plug gave the impression of being a cell under construction; the other cells in the nest were of recent construction as they contained no larvae; probably the bee was still bringing clay to the nest when its work was interrupted.

From two to eight cells were formed in each nest, depending partly on the size of the space available for cell construction. The cells occupy all possible positions from horizontal to vertical. They are lined with waxlike material; dimensions of the cells are as follows: length 11 to 13 mm.; maximum diameter, 6 to 7 mm.; diameter at mouth of cell, 4 to 5 mm. The provisions were semiliquid. Larvae of all sizes, but no prepupae or pupae, were found in the cells.

Jörgensen (1912) records very similar nests of *Centris nigriventris* (Burmeister) in an earth filled bamboo stem and (1912a) in abandoned insect burrows in posts.

LITERATURE CITED

BERTONI, A. DE WINKELRIED

1918. Notas entomológicas (Biológicas y Sistemáticas), Anal. Cient. Paraguayos, ser. 2, no. 3, pp. 219-231.

1925. Himenópteros nuevos o poco conocidos, Rev. Soc. Cient. Paraguay, vol. 2, no. 1, pp. 74-79.

1929. Nidificación en colonias de abejas Antofóridas, Rev. Soc. Cient. Paraguay, vol. 2, no. 5, pp. 223-224.

BERTONI, A. DE W. and C. SCHROTTKY

1910. Beitrag zur Kenntnis der mit *Tetralonia* verwandten Bienen aus Südamerika, Zool. Jahrb., abt. f. Syst., vol. 29, pp. 563-596.

1911. Geschlechtsdimorphismus in der Bienengattung *Thygater* Holmbg. (Hym.), Deutsche Ent. Zeitschr., pp. 402.

BRÈTHES, J.

1909. Una *Anthophorina* parásita?, An. Mus. Nac. Buenos Aires, ser. 3, vol. 12, pp. 81-83.

CLAUDE-JOSEPH, F.

1926. Recherches biologique sur les Hyménoptères du Chili, Ann. Sci. Nat., Zool., ser. 10, vol. 9, pp. 113-268.

CROS, AUGUSTE

1939. *Eucera notata* Lep. (Syn. Eucera obesa Dours), Verhandlungen VII Internat. Kongr. Entom. [Berlin], vol. 2, pp. 1079-1088.

CUSTER, CLARENCE P.

1928. On the nesting habits of *Melissodes* Latr. (Hymenop.), Canadian Ent., vol. 50, pp. 28-31.

DOELLO-JURADO, M.

1912. Apuntes entomologicos. Nidificación y habitos de una abeja silvestre, la *Entechnia*, Bol. Soc. Physis [Buenos Aires], vol. I, pp. 52-56.

DUCKE, ADOLF

1901. Beobachtungen über Blümenbesuch, Erscheinungszeit etc. der bei Pará vorkommenden Bienen, Zeitschr. Syst. Hymenopterologie Dipterologie, vol. 1, pp. 25-32, 49-67.

FAHRINGER, JOSEF and FRANZ TÖLG

1912. Beiträge zur Kenntnis der Lebensweise und Entwicklungsgeschichte einiger Hautflügler, Verhandlungen Naturforschenden Vereines in Brünn, vol. 50 (for 1911), pp. 242-269.

FRIESE, H.

1919. Die Langhornbiene *Eucera difficilis* Duf. Perez und ihr Nestbau bei Arten, Deutsche Ent. Zeitschr., pp. 61-62.

1923. Die europäischen Bienen (Apidae), Walter de Gruyter and Co., Berlin and Leipzig, viii + 456 pp., 33 pls.

HERBST, PAUL

1923. Beiträge zur Biologie der Chilenischen Arten der Gattung *Centris* F. (Apidae), Zeitschr. Wissenschaftliche Insektenbiol., vol. 18, pp. 345-350.

HICKS, C. H.

1936. Nesting habits of certain western bees, Canadian Ent., vol. 68, pp. 47-52.

HOLMBERG, EDUARDO LADISLAO

1903. Dilectus Hymenopterologicus Argentinus, Anal. Mus. Nac. Buenos Aires, ser. 3, vol. 2, pp. 377-512.

HÖPPNER, HANS

1901. Weitere Beiträge zur Biologie nordwestdeutscher Hymenopteren, I. *Eucera difficilis* (Duf.) Perez, Allgemeinen Zeitschr. Entom., vol. 6, no. 3, pp. 33-35 (a figure for this paper appears on page 132).

IHERING, R. VON

1904. Biologia das abelhas solitarias do Brazil, Rev. Mus. Paulista, vol. 6, pp. 461-481.

IUGA, VICTORIA G.

1950. Observatii biologice asupra albinelor solitare miniere: *Tetralonia ruficornis* F. si *Eucera clypeata* Er., Buletin Stüntific, Acad. Republicii Populare Române, ser. Geol., Georg., Biol., Stünte Tehnice si Agr., vol. 2, pp. 251-268.

JANVIER, HIPPOLYTE

1933. Étude biologique de quelques Hyménoptères du Chili, Ann. Sci. Nat., Zool., ser. 10, vol. 16, pp. 209-356.

1955. Le Nid et la nidification chez quelques abeilles des Andes tropicales, Ann. Sci. Nat., Zool., ser. 11, vol. 17, pp. 311-349.

JENSEN-HAARUP, A. C.

1908. Biological researches amongst the Argentine bees with special reference to flowers they visit, Flora og Fauna, pp. 95-108.

JÖRGENSEN, LAVRIDS

1920. Smaa lagttagelser af nogle danske Biers, Ent. Meddelelser, vol. 13, pp. 153-159.

JÖRGENSEN, P.

1911. Los crisididos y los himenópteros aculeatos de la provincia de Mendoza, Anal. Mus. Nac. Buenos Aires, ser. 3, vol. 15, pp. 267-338.

1912. Beitrag zur Biologie einiger südamerikanischer Bienen, Zeitschr. Wissenshaftliche Insektenbiol., vol. 8, pp. 268-272.

1912a. Revision der Apiden der Provinz Mendoza, Republica Argentina (Hym.), Zool. Jahrb., Abt. f. Syst., Geogr., u. Biol. der Tiere, vol. 32, pp. 89-162.

LINSLEY, E. G., J. W. MACSWAIN and RAY F. SMITH

1954. A note on the nesting habits of *Enomalopsis solani* Cockerell (Hymenoptera, Anthophoridae), Pan-Pac. Ent., vol. 30, pp. 263-264.

1955. Biological observations on *Xenoglossa fulva* Smith with some generalizations on biological characters of other eucerine bees (Hymenoptera, Anthophoridae), Bull. So. California Acad. Sci., vol. 54, pp. 128-141.

1956. Biological observations on *Ptilothrix sumichrasti* (Cresson) and some related groups of emphorine bees (Hymenoptera, Anthophoridae), Bull. So. California Acad. Sci., vol. 55, pp. 83-101.

MICHENER, CHARLES D.

1944. Comparative external morphology, phylogeny, and a classification of the bees (Hymenoptera), Bull. Amer. Mus. Nat. Hist., vol. 82, pp. 151-326.

1954. Bees of Panamá, Bull. Amer. Mus. Nat. Hist., vol. 104, pp. 1-155.

MICHENER, CHARLES D., RUDOLF B. LANGE, JOAO JOSÈ BIGARELLA and RIAD SALAMUNI

1958. Factors influencing the distribution of bees' nests in earth banks, Ecology, in press.

MICHENER, CHARLES D. and JESUS S. MOURE

1957. A study of the classification of the more primitive nonparasitic anthophorine bees, Bull. Amer. Mus. Nat. Hist., vol. 112, pp. 395-452.

MOURE, J. S. and C. D. MICHENER

1955. A contribution toward the classification of neotropical Eucerini (Hymenoptera, Apoidea), Dusenia, vol. 6, pp. 239-331.

NIELSEN, ERIK TETENS

1941. Nestbau von *Eucera longicornis* L., Ent. Meddeleiser, vol. 22, pp. 142-149.

NIELSEN, J. C.

1902. Biologiske Studier over danske enlige Bier og deres Snyltere, Videnskabelige Meddelelser fra den Naturhistoriske Forening i. Kjöbenhavn, pp. 75-106.

PEER, D. F.

1956. Multiple matings in queen honeybees, Jour. Econ. Ent. vol. 49, pp. 741-743.

PICKEL, BENTO

1928. Contribuição para a biologia de *Centris sponsa* e *Acanthopus excellens* (Hymen.), Boletim Biologico [São Paulo], vol. 14, pp. 135-143.

RAU, PHIL

1929. The biology and behavior of mining bees, *Anthophora abrupta* and *Entechnia taurea*, Psyche, vol. 36, pp. 157-181.

ROZEN, JEROME G. and C. DON MACNEILL

1958. Biological observations on *Exomalopsis* (*Anthophorula*) *chionura* Cockerell, including a comparison of the biology of *Exomalopsis* with that of other anthophorid groups, Ann. Ent. Soc. Amer., vol. 50, pp. 522-529.

RUIZ P., FLAMINIO

1940. Apidologia chilena, Rev. Chilena Hist. Nat., vol. 44, pp. 281-377.

1942. Notas biologicas de algunos generos de abejas solitarias de Chile, Bol. Sanidad Vegetal [Ministerio de Agricultura, Santiago], vol. 2, no. 1, pp. 8-16.

SCHROTTKY, C.

1901. Biologische Notizen Solitärer Bienen von S. Paulo, Allg. Zeitschr. Ent., vol. 6, pp. 209-216.

1904. Beitrag zur Kenntnis einiger südamerikanischer Hymenopteren, Allg. Zeitschr. Ent., vol. 9, pp. 344-349.

SILVESTRI, F.

1903. Contribuzione alla conoscenza dei Termitidi e Termitofili dell' America meridionale, Redia, vol. 1, pp. 1-234.

SMITH, FREDERICK

1855. Catalogue of British Hymenoptera in the Collection of the British Museum, Part 1, pp. 1-252.

STRAND, EMBRICK

1909. Beitrag zur Bienenfauna von Paraguay auf Grund der im Berliner Museum vorhanden Sammlung von Karl Fiebrig, und der Bestimmungen von Dr. H. Friese zusammengestellt, Deutsche Ent. Zeitschr., pp. 227-237.

VESEY-FITZGERALD, D.

1939. Observations on bees (Hym.: Apoidea) in Trinidad, B. W. I., Proc. Royal Ent. Soc. London, ser. A, vol. 14, pp. 107-110.