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The life cycle and behavior of the social bee Lasioglossum (Dialictus) umbripenne (Hymenoptera: Halictidae)

by

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This paper consists of an account of the life cycle and behavior of a primitively social halictine bee *Lasiolossum umbripenne* (Ellis). The species was determined by Dr. George C. Eickwort who independently studied a population of the same bee in Turrialba, Costa Rica (manuscript in press). He points out significant biological differences between the Turrialba population and that of Damitas, on the Pacific, where the present study was carried out. Although there seems to be no morphological differences between the bees of the two populations, there still exists the possibility that the two groups of bees (Damitas and Turrialba) actually represent sibling species. The present study is part of an overall investigation of comparative halictine behavior started by Dr. C. D. Michener and his students in Kansas and is intended to shed light on the origin and evolution of social behavior and castes of these bees. *L. umbripenne* was first described by ELLIS (5) in 1913 on the basis of a single queen from Quirigua, Guatemala. EICKWORT (4) recently published a paper on the identity of *L. (Dialictus) umbripenne,* including the description of workers and males which Ellis omitted.

L. umbripenne is a small bee belonging to the world-wide subfamily Halictinae, a group of about 2,000 species, most of which are known as sweat bees because of their habit of lapping the skin perspiration in warm climates. This subfamily is of interest for two reasons. First, they are the most abundant wild bees in the world and secondly, they present various levels of social organization ranging from solitary to very complicated social patterns. This bee belongs to the subgenus *Dialictus,* of which *Chloralictus* is a synonym. As in other Halictinae, in the subgenus *Dialictus,* there are species with solitary life cycles, others with poorly defined castes and weak social organization and still others with distinct castes and strong social organization.

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Although presently we lack sufficient information to make definite comparative studies on the behavior of *Dialictus,* we can group the species studied thus far into various levels of social organization. In this manner, the social similarities and differences of *L. umbripenne* to other species of *Dialictus* can be easily visualized. With relation to social behavior, caste differentiation and ovarian development, the species of *Dialictus* can be divided into the following groups:

Group A (Solitary *Dialictus*)

Social behavior not yet established. Every female is fertilized and has enlarged ovaries. *Lasioglossum herbstiellum* (CLAUDE-JOSEPH, 3) and *L. opacum* (MICHENER and LANGE, 8) belong to this group.

Group B (Very primitive social *Dialictus*)

Social behavior poorly established and with castes not well defined. Fertilized and unfertilized females with fully enlarged ovaries are common. These females, regardless of size, are potentially eligible to become queens (they do so when alone); however, the smaller ones, when in a colony, tend to become workers. All intergradations between queen and workers exist. Queens are frequently replaced. The resting stage usually occurs in the old nest. This category includes *L. rhytidophorus* (8), *L. zephyrum* (BATRA, 1, 2), probably *L. seabrai* and *L. guaruvae* (MICHENER and SEABRA, 9), and even possibly *L. coeruleum* (STOCKHAMMER, 13) which nests in decaying logs.

Group C (Primitive social *Dialictus*)

Established social behavior, with more or less distinct castes differentiated from one another only by small external differences. Fertilized workers, as well as workers with fairly enlarged ovaries, are common and therefore a clear line does not exist between queens and workers. Colony multiplication is perhaps by fission: new colonies are established by opening new entrances to the surface from the over-wintering nests where the queens spend their resting stage. *L. versatum* belongs to this group (MICHENER, 6).

Group D (Social *Dialictus*)

Well established social behavior and fairly distinct caste structure. Although the queens are usually slightly larger than the workers, the size differences between castes can only be appreciated statistically. As in group C, the smallest workers are smaller than the smallest queens and the largest queens are larger than the largest workers. Workers with fairly enlarged ovaries are found in smaller proportion than in group C and very few fertilized workers can be found. Consequently there is a more conspicuous ovarian differentiation between the castes than in the previously mentioned group. The queen passes her resting stage in the old nest. This group includes *L. imitatum** (MICHENER and WILLE, 10) and possibly *L. obscurum* (6).

Group E (Specialized social *Dialictus*)

Well established social behavior with very distinct castes. In this group there is a definite difference in size between the queens and the workers. The queens' cell dimensions and food mass (size and shape) differ from those provided for the workers and males. Workers with enlarged ovaries are common, and occasionally fertilized workers are also found. The queen passes her resting stage outside of the old nest. *L. umbripenne* is the only known representative of this group, occupying the most specialized level of social organization among *Dialictus*. It is the only species known in this subgenus which shows such distinct queen-worker differentiation and in which queens are reared with a food mass shaped quite differently from that of the worker and the male.

MATERIAL AND METHODS

Observations were started in 1966 and although some research was done in 1967, the main part of the work was carried out during the dry season of 1968. Most of the field techniques described by MICHENER *et al.* (7) were used.

A new method of marking and recording the exact time when a series of queens started digging into the ground was developed. With this simple technique it was relatively easy to follow the queens' progress and to obtain specific information as to their behavior inside the nests by digging them up at different times of the day and night. The technique is based on the belief that the general behavior, life cycle, and progress of the nest is constant in every case, as is the sequence and duration of the events in a given nest. This can be illustrated by the following example: it was observed that the queen makes five pollen collecting trips in the morning and then closes the nest entrance for the remainder of the day, usually not appearing again until the next morning. In order to find out the exact sequence of events taking place inside a nest after the entrance is closed, it is only necessary to excavate several nests at a known stage of development at different times during the day or night. By digging up the nest right after the queen sealed the entrance, it was possible to learn that the queen started working immediately on the mass of dried pollen placed in the cell. Later, by excavating other nests at different time intervals, it was possible to observe further progress. When possible, observations like those above were repeated on several other occasions to confirm the facts.

The bees collected were preserved in Kahle's or Dietrich's solution and

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* Referred to as *L. inconspicuum* by MICHENER and WILLE (10).

later dissected. It was found that by dissecting bees in the field it was possible to determine whether the techniques used were suitable or if alterations were neccesary.

Each individual bee was marked on the abdomen with a quick-drying acetone base paint applied with a fine brush. The paint was allowed to dry before the bee was released or, more often, placed directly into its nest with the aid of a short glass tube.

Nests to be excavated were filled with plaster of Paris poured into the entrance until all the tunnels and pathways were full. When a nest was so close to another that its tunnels might become confused upon excavation, a different coloring agent was added to each batch of plaster of Paris to detect any unexpected nest intermingling. Data which enabled us to determine the age of the different castes, as well as the flight range of these bees, were also recorded.

HABITAT

The colonies of *L. umbripenne* were found in Damitas 14.5 to 15 km north of Quepos on the southern Pacific coast of Costa Rica, at an altitude of 200 meters, and very close to San Antonio de Damas. The nests were concentrated in four main sites and a few isolated populations were scattered along a trail (Fig. 3) approximately 1 km in length, usually in clearings, or pasture areas (Figs. 2, 4), or dispersed among thin bushy undergrowth. This whole area is surrounded by tropical rain forest (Figs. 1, 2), with an average of 2,000-4,000 mm of rainfall per year and a maximum dry season of two to three months. The region is bounded by the mean annual isotherm of 24 C.

GENERAL LIFE HISTORY

In the study area the bees are active only during the dry season, which is from January to April. The colonies present well established worker and reproductive castes, the queen being easily differentiated from the others by her larger size. The nests are burrows in the ground, with normally only one queen, although sometimes two queen were found.

At the beginning of the dry season the fertilized queens start founding their colonies. The first day the queen makes a vertical burrow about 8 to 15 cm in depth; then three to five cells (Fig. 5) are commonly constructed, usually only one every 24 hours. Each cell is made at night and is provided with pollen the next morning. An egg is then laid upon the mass, that has now been formed into a small ball, and the cell then closed. The queen keeps the entrance of the nest well sealed with soil at all times, except in the mornings when she is working or feeding. After preparing and provisioning all the cells, the queen ceases her activities and waits until the progeny reach maturity. Eggs take two days to hatch and the fast growing larvae are full-grown after four to five days. The prepupal stage lasts four days and the pupal stage eleven. The period from egg-laying to maturity is therefore about 22 days and the progeny emerge mostly as workers. From this time on the colony is continually active and the workers deepen the nest and provision other cells while the queen provides each with an egg. Workers are also known to contribute to the welfare and productivity of the colony by laying eggs. From January through April the nest becomes progressively deeper and more complicated, with additional branching and looping. The bee population and the number of cells likewise increase from month to month. In January, for instance, the nests are about 17 cm in average depth and have from one to seven branches. The population, which represents the first set of workers plus the queen, is frequently composed of four or five individuals with the number of cells usually varying between 8 and 15. By February the nests are much deeper, usually about 30 cm, and in only a few rare instances do they reach depths of 75 cm. The number of branches usually varies from 4 to 8 with a population of 7 to 20 individuals and the number of cells ranges between 16 and 35. By March the depth of the nest usually varies between 40 and 70 cm with 3 to 14 branches. The population has now increased to 25 or 30 individuals and the number of cells from 90 to 130. Later in April the nests reach their highest stage of development in both structure and population. The nests are usually more than a meter deep, some reaching 165 cm with the branches numbering from 13 to 41. The bee population ranges between 60 and 84 individuals and the number of cells from 80 to 160.

During the months of activity of the colony the queen is never replaced. She lays an egg a day, although occasionally she may lay two. Since a great proportion of the workers are able to lay eggs, males are produced throughout the existence of the colony, but an appreciable number was never observed, except in the month of April. At the end of this month or by the beginning of May there is a definite peak in the male population which is correlated with the production of new queens. This production of new queens marks the end of the colony's existence. The new queens soon mate with the males and then search for a suitable place outside the nest in which to spend the rainy season. Meanwhile, all the workers and males die and the nests are abandoned. During the next eight months there is no indication of any activity and one may assume that the new queens are in a dormant stage. Not until the beginning of the dry season, in December or January, will the fertilized new queens reappear to begin another cycle.

Founding of the colony: Most of the known species of *Dialictus* spend the long resting stage (over-wintering in the temperate zone) in the nests built the previous season. The only known exceptions to this rule are *L. rohweri* (6) and *L. coeruleum* (13) and now *L. umbripenne*.. The wintering quarters of the first two species, from Kansas, U.S.A., are still unknown. In the area in which this study was carried out, the queens begin founding their colonies at the outset of the dry season. Although the dry season in this area normally starts in December it is somewhat variable, occurring at the beginning or end of that month. However, a few queens start nests as early as 26 days before or as late as 30 days after most of the other queens have started.

In some instances a queen bee will spend considerable time crawling and flying over the ground, and will occasionally abandon her first attempts at nest construction, resuming her search-like activities. After a queen has found a suitable location, she starts digging and disappears from view in about 20 to 25 minutes. On the other hand, if the surface is composed of loose dirt the queen may disappear in as little as four minutes. Excavation is done with the mandibles, bit by bit, and the debris is passed from her front legs to the middle and hind legs and then flicked outside the burrow. As she begins digging she moves her body around the hole in a drill-like fashion. When her thorax has disappeared below the surface she seems to change her digging technique. Instead of moving her body around the hole in a circular pattern she stays in one position for about 15 seconds and then pushes the dirt out from under her abdomen and spreads it around the entrance with the aid of her hind legs, she then rotates her body and repeats the same procedure. As she digs, her body vibrates, possibly due to her efforts in loosening the bits of soil. As the hole becomes deeper, the earth is pushed out with the dorsal posterior surface of her abdomen, forming a tumulus which is spread irregularly around the entrance. At this early stage, the still slender ovaries begin to develop, reaching their full maturity in the following 40 hours.

The number of queens digging in a particular area varies considerably. For instance, in an area of five square meters, 53 queens were found digging. There were other areas, however, in which the density was about one queen per square meter. At first the queen usually makes a vertical burrow in the ground, sometimes slightly curved or diagonal. The bee digs at an average of one centimeter per hour, including rest intervals. The first stage of the burrow is usually completed in about 24 hours, the queen having partially developed ovaries by this time.

The depth varied from 6 to 28 cm, with an average of 10 cm, in the 76 nests studied. Usually when the excavation reached more than 20 cm during the first 24 hours, it was found that the bees had encountered old and partially filled burrows. When the vertical burrow is completed, the queen makes her first cell. This cell is usually made between 7 and 11 PM, either along the upper or the lower part of the burrow, but more frequently in the upper area. It is interesting to note that in *L. zephyrum* the cells are made between 11 PM and 7 AM (2). Next morning, 40 to 46 hours after the first digging of the nest, the queen makes the first of the five collecting trips to provision her cell. In most areas the queens start their outside activities at about 8 AM, but in the exposed and hilly areas they start earlier, 7:00 to 7:30 AM. The queen leaves the nest cautiously, first exposing her head and looking around the entrance and upon sighting a potential enemy, immediately withdraws and waits a few seconds before making another attempt. When the queen finally leaves, she makes an orientation flight: first she walks outside, takes a turn and faces the nest entrance, then while facing the entrance she slowly flies upwards in a semicircular pattern and then flies away. This is the only orientation flight she makes during that day. On the second and succeding trips she flies directly from the hole at an angle of less than 90°, but sometimes she is seen to come out and walk around the entrance before flying away.

The queen needs only five trips to collect the necessary pollen to provision a cell. In one particular area of study several bees spent an average of 15 minutes on each trip, and about 4 minutes inside the nest (unloading the pollen and placing it in the cell). Others, however, were very irregular in their collecting activities, while still others were completely sporadic and unpredictable. After the queen has completed her fifth trip and has unloaded her last pollen mass, she closes the nest entrance. In the area of study most nests were closed at about 11:00 AM and no activity was observed during the rest of the day. It is quite interesting to note this remarkable contrast of activities. From 8:00 to 11:00 AM hundreds of queens can be observed carrying loads of pollen, and then suddenly all outside activity ceases, even the nest entrances have vanished, all being plugged with dirt. After 11:00 AM a casual observer would conclude that the queens had not started founding their colonies yet. Immediately after the queen has closed the entrance, she proceeds to work on the mass of dry pollen. First she manipulates the mass of loose pollen, moistening it slightly, and molding it like dough into a slightly flattened still quite dry ball. This operation takes about 30 minutes. She then moistens the pollen further and gradually shapes it into a rounder ball, which takes another 30 minutes. In the next 45 minutes, moistening it still further, she forms the mass of pollen into an almost spherical and smooth ball which measures, on the average, 2.79 mm in length, 2.65 mm in width and 2.11 mm in height. She then lays the egg on top of this ball, lengthwise, but since the egg is convex it usually contacts the pollen ball only at its ends (Fig. 18). The egg is laid about one hour and 55 minutes after the queen has closed the nest entrance, or two hours after her last trip outside. She immediately plugs the neck of the cell with a little soil and then remains in the nest for the rest of the day, except on two occasions: one in the afternoon when she may venture out for a few minutes for feeding; or during the night, usually between 6:00 and 11:00 PM, to discard the debris from the construction of a new cell (for this reason the tumulus is formed only during the night). The next day the queen proceeds with the provisioning of the second cell. During this founding period the queen can build from one to six cells, or in other words, she may lay from one to six eggs at the rate of one per day. This is evidently correlated with the fact that there are three ovarioles per ovary, or a total of six ovarioles, in Halictinae. Just one ovariole may develop or all six of them, but usually from three to five (Table 1). When the first cell is built in the upper part of the nest, the other cells are usually constructed one below the other. This results in a sequence in ages of the immature stages, with the oldest occupying the upper part and the youngest the lowest. On the other hand, when the first cell is found in the lower area of the burrow, the process is reversed. There are some nests, however, in which the arrangement is very irregular. Among 38 nests, for instance, 18 were of the first type, 12 belonged to the second type and 8 to the third. In the case of *L. imitatum* the first cell is usually made along the upper part (10).

Although the general behavior of the queens was very constant in most cases, there were some exceptions, as shown in the following list:

1) Nest with an empty cell, late in the afternoon. (Table 1, nest 2).
2) Nest with two empty cells, late in the afternoon (Table 1, nest 11).
3) Nest with a cell partially provisioned with pollen, late in the afternoon.
4) Nest with two cells partially provisioned with pollen, late in the afternoon.
5) Nest with a cell fully provisioned with a ball of pollen, but without an egg, late in the afternoon. (Table 1, nest 4).
6) Nest with an empty new cell and a cell containing pollen only. (Table 1, nest 9).
7) Nest kept open the whole day.

In all of these cases the queen was found to have either defective eggs or eggs delayed in their normal development. When a nest had two empty cells (or with small amounts of pollen) (Figs. 12, 13), the queen was found to have two partially developed eggs, one less developed (or more defective) than the other.

After making all the cells and laying all the eggs which the queen is capable of in this particular period, she ceases her activity and waits in the nest until the progeny reach maturity. This can be called the inactive period. The cessation of activities after the queen has laid the first few eggs has been recorded in many species, and it is probably a common phenomenon among *Dialictus* of groups B, C and D.

Inactive period and duration of the developmental stages: The inactive period begins after the queen lays her last egg and ends when all the progeny reach maturity. This rest period is usually not less than 22 days, the time it takes to complete the cycle from egg to adulthood. During this time the queen waits inside the closed nest, which is opened only when she emerges to feed. After the last egg is laid the ovaries of the queen do not produce any more large oöcytes, but remain rather slender, until commencement of a new egg-laying cycle.

Since several nests were followed from the very beginning of their foundation, it was possible to study the duration of the developmental stages in detail, and to compare the results with those of other nests. While rearing eggs and young larvae in the field was impossible, rearing full grown larvae through prepupal and pupal stages to adults was rather easy. The rate of development in artificial containers coincided with that under natural conditions. Actually the rate of development of the different immature stages was relatively consistent in every case. The duration of the egg stage (Fig. 18) was found to be from 52 to 55 hours. The larva (Figs. 20 to 29) grows relatively fast, taking only four to five days to become a prepupa; the prepupa (Fig. 30) lasts four days; the pupal stadium (Fig. 31) is the longest of all the immature stages, eleven days. A

TABLE 1

Representative sample of the contents of 20 nests during the colony founding period, before the appearance of the first brood of workers. Nests listed according to the number of cells

Nest	Cells	Empty new cell	Cells with pollen only	Eggs	Larvae	Prepupae	Pupae
1	2	—	—	—	2	—	—
2	3	1	—	—	1	1	—
3	3	—	—	—	1	2	—
4	3	2	1	—	—	—	—
5	3	1	—	—	—	—	2 (1♂)
6	4	—	—	—	—	—	4
7	4	—	—	—	—	2	2
8	4	—	—	—	2	2	—
9	4	1	1	1	1	—	—
10	4	—	—	—	4	—	—
11	4	2	—	—	—	—	2
12	5	—	—	—	—	—	5
13	5	—	—	—	5	—	—
14	5	—	—	3	2	—	—
15	5	—	—	—	2	—	3 (1♂)
16	5	—	—	—	4	—	1
17	5	—	1	2	2	—	—
18	6	—	—	—	—	—	6
19	6	1	—	—	—	1	4
20	6	—	—	1	1	1	4

white-eyed pupa takes three days to become pink-eyed and another three days to become a black-eyed white pupa (Fig. 31), this latter stage becomes entirely black four days later. The rate of development, from laying, can be summarized as follows:

1) Newly hatched larva, 2 days (Fig. 20).
2) Half-grown larva, 5 to 6 days (Fig. 27).
3) Full-grown larva, 6 to 7 days (Fig. 29).
4) Prepupa, 8 days (Fig. 30).
5) White pupa, 11 days.
6) Pink-eyed white pupa, 14 days.
7) Dark-eyed white pupa, 15 days.
8) Black-eyed white pupa, 17 days (Fig. 31).
9) Dark pupa, 20 days.
10) Black pupa, 21 days.
11) Adult bee, 22 days.

From this it can be concluded that a nest, during the colony founding period, may have the following similar stages at a given time on a specific day (Table 1):

1) 3 eggs.
2) All larvae.
3) 2 full-grown larvae.
4) 4 prepupae.
5) All white pupae.
6) 2 black pupae.

The castes: Queens, males and workers are easily differentiated. The queen is distingished from the others by her larger size, and the male by his longer antennae and slender body.

Female differences: Using the methods described by MICHENER and WILLE (10), entire populations from several nests were captured. All individuals from such nests were measured and dissected. The measurements have been restricted to the total length (T. L.), head width (H. W.) and wing length (W.L). These three measurements were highly correlated. Bees were dissected to determine ovarian development and presence or absence of sperm cells in the spermatheca. On the basis of these observations females can be divided into several groups as follows:

A. Measurements: T.L. = 5.92 to 7.40 mm; H.W. = 1.62 to 1.87 mm; W.L. = 4.07 to 4.58 mm. Fertilized, with ovaries greatly swollen, usually all ovarioles involved. Queens.
B. Measurements as in A. Fertilized, but ovaries less swollen than in group A, usually one or two ovarioles in each ovary not swollen. Queens.
C. Measurements as in A. Fertilized, with slender ovaries. Young queens with ovaries not yet enlarged, and queens during the inactive period.
D. Measurements: T.L. = 4.07 to 5.92 mm; H.W. = 1.27 to 1.53 mm; W.L. = 2,92 to 4.07 mm. Unfertilized, with slender ovaries (0.068 to 0.083 mm in width). Workers.
E. Measurements as in D. Unfertilized, with slightly developed ovaries (0.10 to 0.18 mm). Workers, possibly becoming egg-laying bees.
F. Measurements as in D. Unfertilized, with fairly well developed ovaries (0.20 to 0.28 mm), sometimes only one ovariole enlarged, sometimes one ovariole in each ovary, more rarely with more ovarioles enlarged. Egg-laying workers.

G. Measurements as in D. Unfertilized, with well developed ovaries (0.30 mm or more); sometimes one strongly enlarged oöcyte in one ovary, sometimes with more ovarioles enlarged. Egg-laying workers.

H. Measurements as in D. (one specimen was found with H.W. = 1.61 mm). Fertilized, with well developed ovaries as in group G. Egg-laying workers.

I. Measurements as in D. Fertilized, with slender ovaries. Workers.

Although bees of group I were not actually observed, one can predict their existence since workers of group H must undergo ovarian development passing through group I. Intermediates with respect to ovarian size should also exist, and in that case they have to be placed arbitrarily. Logically, all the workers emerge from the pupal stage as group D, and all the queen as group C.

Variation in size related to castes: The average size of the queens is T.L. = 6.35, H.W. = 1.72, and W.L. = 4.31 mm; while that of the workers is T.L. = 5.41, H.W = 1.43 and W.L. = 3.58 mm. Large workers, which are rarely found, reach a total length and wing length (Figs. 39, 40) similar to that of the smallest queens (T.L. = 5.92, W.L. = 4.07). On the other hand, no workers were found to reach the lowest H.W. of the queens (1.62). Among 279 workers only one was found with a head width as high as 1.61. The combination of the three measurements, however, can be used to differentiate any worker from a queen.

Comparison of measurements of workers and queens, grouped by months, indicated that there is no seasonal variation in size in these bees as observed in other species. Likewise, no size differences were found between groups A, B, and C or between groups D, E, F, G, and H.

We assume that, as in most Hymenoptera, males are always haploid and females diploid, and that the eggs laid by unfertilized workers give rise to males only.

The queen and worker castes are apparently trophically determined. The larva of the worker caste feeds on a typical mass of pollen and honey. This mass has the form of a smooth and slightly flattened sphere; the pollen ball (Figs. 11, 17, 18) measures from 2.62 to 2.92 mm in length (average 2.79, n = 18), 2.47 to 2.81 mm in width (average 2.65, n = 18) and 1.80 to 2.47 mm in height (average 2.11, n = 18). Occasionally a rather small pollen ball can be observed, as that shown in figure 17, with a length of 2 mm. The larva of the queen feeds on a peculiar mass of pollen and honey, larger and of a different shape (Figs. 14 to 16) than that of the worker and male, having a more or less cylindrical form with truncated ends, a slight depression around the median portion, and slightly depressed on the truncated end surfaces (Fig. 16). The actual shape can be best appreciated from Figs. 14 to 16 and 24, 25. The queen pollen mass measures 3.37 to 3.67 mm in length (average 3.44, n = 25); 2.62 to 3.52 mm in width (average 3.11, n = 22); 2.25 to 3.07 mm in height (average 2.75, n = 16) and 2.47 to 2.77 mm in height (average 2.62 mm, n = 12) at the median depression (Figs. 12 and 13), where the egg is found. There are no external differences between an egg of a queen and that of a worker or male. The egg measures from 1.46 to 1.56 mm in legnth (average 1.51, n = 13) by 0.36 to 0.39 mm in width (average 0.37, n = 13) at the middle.

First brood of workers, general behavior: The first brood of workers appears 24 to 29 days after the founding of the nest. The general behavior of the worker is best studied at this time, when the nests are not complicated and deep, and the number of workers is still small. During the first three to five days the workers are active only inside the nest. One of them (frequently the youngest) stays at the entrance of the nest as a guard, and the others destroy the old cells, occasionally leaving one or two intact. The old cells are frequently used as the starting points for the first nest branches, which are often arched, ring-like (Fig. 6) or loop-like (Fig. 9). Before any outside activity is started, one or two cells are made. All the digging of new cells and branches is done during the night. As soon as a cell is ready, the worker or workers start collecting pollen to provision it. Commonly more than one worker provisions each cell. There are usually more pollen collectors per nest than cells being provisioned at the time, indicating cooperative activity. Cooperative provisioning has been shown in *L. versatum, L. imitatum,* and *L. zephyrum*. The workers, as does the queen, make only five collecting trips to produce a full-sized pollen ball. Unlike the queens, the workers always make orientation flights each time they leave the nest. As in most halictine bees, the workers are more active outside their nest during the morning hours. By noon, during this early nesting period, most cells have been provisioned and nest entrances plugged, generally between 3:00 and 4:00 PM. In older nests the workers do not plug the entrance; they are active during the whole day. Unlike *Lasioglossum imitatum,* the dirt excavated in extending the burrows is never put in abandoned cells, but carried to the surface. The workers start their outside activity from 7 to 8 AM, depending on weather conditions and the topography of the area. After a rainfall, the activity is very low, unless rainfall occurs in the morning and is then sunny afterward.

The potentiality for ovarian development is retained by the worker. In all primitive social bees there are always some workers which have the ability of laying eggs, even when the queen is present in the colony. This tendency occurs in *L. umbripenne* more frequently than first expected, with almost 50 per cent of the worker population showing ovarian development (Table 2).

This development was observed in the young as well as the older workers, in which age can be calculated by the extent of mandible wear (10). In most queens also, a progressive wearing of the mandibles can be noticed as the nest becomes older. However, in the very old workers presenting very much worn mandibles, the ovaries tend to be slender. This can be due either to a regression in the ovarian development or to its complete absence. The fact that workers with slightly, well, and much worn mandibles were found to have

TABLE 2

Ovarian development in a sample of 279 workers (measurements are of ovarian widths, in mm)

Undevelopd ovaries (0.068 to 0.083)	Slightly developed ovaries (0.10 to 0.18)	Fairly well developed ovaries (0.20 to 0.28)	Well developed ovaries (0.30 or more)	Fertilized, well developed ovaries
145	46	47	41	7

slender ovaries suggests that many workers never develop the ability to lay eggs.

The frequency of fertilized workers tends to be relatively high. For instance in a sample of 279 workers, 2.5 per cent were found to be fertilized and with well developed ovaries (Table 2), which is not surprising, since males are produced throughout the season. It would be very interesting to find out what type of offspring, if any, are produced by these fertilized workers.

As is common among social bees, the removal of the queen from the colony leads to an increase in the laying of eggs by the workers. This is illustrated by two nests found without queens (Table 3, nests 18 and 19). However, since these two nests have the most cells, the queens in these two cases may have finished their job and died, which is perhaps part of the normal nest development. In nest number 18, 18 workers with well development ovaries were found; in three they were slightly developed, and in one young worker they were slender. The nest was also found to contain 20 eggs, 12 male pupae and 3 male adults. It is possible that in the halictine bees an odor or volatile pheromone plays an important role in inhibiting ovarian development in the workers. This pheromone is logically produced by the queen, since in her absence this inhibitory factor is not present. Assuming this to be true, then the pheromone in the case of *L. umbripenne* in the queen's presence is very weak.

As in most social halictine bees, the guarding of the nest entrance is one of the most important activities of the younger workers. In older nests, there are one or more bees just behind the guard bee; these replace the guard at different intervals of time. In guarding the nest, the entrance is plugged most of the time by the head of a worker bee. If this guard is disturbed, for instance with a blade of grass, the bee fights back by biting, and if the disturbance continues, the guard turns its body and plugs the entrance very firmly with the dorsum of the abdomen. In general, the guarding operation and other activities at the nest entrance are very similar to those of *L. imitatum* (10).

General behavior of the queen: The life history of the queen can be divided into three periods: the resting stage, founding of the nest, and the nesting period. During the resting stage the queens are probably dormant. This period lasts eight months and is spent outside of the nest. Although no queens have

TABLE 3

Representative sample of 20 nests showing the composition of the brood and adults after appearance of workers, January though April

Nest N° and month	cells	empty new cells	cells with pollen only	eggs	larvae	prepupae	pupae	queens	workers with undeveloped ovaries (0.068 to 0.083 mm)	workers with slightly developed ovaries (0.10 to 0.18)	workers with fairly well developed ovaries (0.20 to 0.28)	workers with well developed ovaries (0.30 or more)
1 - Jan.	11	1	2	3	4	1	-	1	4	-	-	-
2 - Jan.	9	1	3	2	3	-	-	1	3	-	1	-
3 - Jan.	6	2	-	3	-	-	-	1	-	6	-	-
4 - Jan.	8	1	2	1	4	-	-	1	1	2	-	1
5 - Jan.	12	2	-	7	2	-	1	2	-	1	-	1
6 - Jan.	8	2	1	-	5	-	-	1	3	-	-	-
7 - Jan.	15	-	-	-	5	1	9	1	2	1	-	-
8 - Jan.	7	2	2	2	3	-	-	1	2	1	-	1
9 - Jan.	5	-	-	3	2	-		2	4	-	-	-
10 - Feb.	66	10	-	8	24	7	17	1	6	4	5	2
11 - Feb.	16	-	-	-	7	1	7	1	3	-	1	1
12 - Feb.	58	4	-	2	23	8	21	1	3	2	1	-
13 - Feb.	28	-	1	3	8	7	9	1	2	1	1	-
14 - Feb.	24	-	-	5	12	-	7	1	13	4	-	1
15 - Feb.	29	1	-	10	15	1	2	1	14	3	1	-
16 - Feb.	24	1	-	2	11	3	7	1	4	2	2	2
17 - March	95	4	5	4	34	23	25	1	8	4	8	1
18 - March	129	3	5	20	60	18	23	-	1	3	6	12
19 - April	152	1	2	8	45	16	80	-	10	3	1	8
20 - April	80	-	-	-	17	8	37	1	41	3	11	5

been observed during this stage, one can assume that they spend this period in some protected place, as under a fallen log, in a tree hole, under a big leaf, etc. Since dormant bees are often found in groups, like sleeping male bees, one could also suspect that the queens may be found in small groups.

The behavior of the queen during the nest founding period was discussed previously and we need only add here that during this period mortality is higher than during the nesting period. In one area of study, for instance, the rate of mortality of queens was 60 per cent. Most of the queens died during provisioning or feeding trips.

During the nesting period the queen always remains within the nest and is never replaced by another queen. The rate of mortality among queens during this period is low, until near its end when it is presumably 100 per cent. Since there is no direct exchange of food among halictine bees, the queens may feed in cells that are being provisioned, as has been observed in *L. zephyrum* (1).

There are not more than two large oöcytes present at one time (one per ovary), of which one is always more developed than the other. Therefore, the queen can only lay one egg at a time. Assuming that no workers lay eggs and that the queen lays just one egg per day, then a nest should reach an equilibrium within a short time. This equilibrium can be calculated if one knows the duration of the developmental stages and the life span of the workers. After a month, if no other factors intervene, a nest of *L. umbripenne* should theoretically reach and maintain at constant equilibrium, a colonial population presenting the following ratio: number of cells in use, 23; number of eggs, 3; number of larvae, 6; number of prepupae, 4; number of pupae, 11; number of workers, 30. However, this theoretical nest would probably never be found in nature (Table 3) due to the following possibilities: a) workers laying eggs, b) queens occasionally laying two eggs a day, and c) two queens in a nest. This last possibility, proved not to be a very rare phenomenon. In 40 nests observed, for instance, four were found in this condition. How the two queens became associated is not known. It is possible that association may occur when the queens are beginning to establish their nests.

During the month of April a series of slightly larger cells are made; the pollen balls found in them, as already indicated, are larger and of a different shape. These cells are the queen cells and the new virgin queens emerge from them. In April about 50 per cent of the cells found in a nest are queen cells, and since the majority of males are also born during this month, the other 50 per cent of the cells, which are identical to those of the workers, are probably male cells. Actually, all of the pupae found in nests during the middle of April were either males or queens.

It should be pointed out that no increase in cell size was found as the season progressed. The queen cells are usually found in April but may appear sporadically before this month; however, if the dry season starts earlier or later, the queens may appear either before or after April. Notes from 1966, for instance, in which the queen cells were made in May, show that the colony was started almost in the middle of January.

General behavior of males: Males are produced throughout the activity of the colony and sometimes can be encountered even among the first brood produced by the queen (Table 1, nests 5 and 15). Among 19 nests dug up containing pupae, and representing the first brood of workers, we were able to count 66 pupae of which 61 were females and 5 males. The males, however, never reach a significant proportion until the end of the season. Unfortunately we cannot give the percentage of males in the first brood or at monthly intervals.

We know that males are produced during the whole season because a few of them appeared among the pupae of the nests dug up. However, we cannot base any percentage of males on just the few pupae from the nests studied. We never were able to collect males flying around the nesting areas, except in one year, during April.

The males leave the nest relatively soon after emerging from their cells and never come back. In the latter part of April, the males become most abundant and can be seen flying about the nesting areas. The males usually zig zag over the area, flying a few centimeters above the ground. Commonly they dance in loose groups, and once in a while a few can be observed resting on blades of grass. Although new queens are produced at this time the actual mating was not observed.

Life span of the queen, worker and male: In general, the queen lives one year, the worker about a month, and the male less than two weeks. The queen goes through a long dormant period of eight months, and during the four months of activity she never leaves the nest except at the beginning when founding the colony. On the other hand, the worker is more active, guarding, digging and foraging with a great deal of activity outside the nest. Finally, the male never has the protection of a nest. The life span of the worker and the male was, for the most part, inferred.

The nest shown in Fig. 8 gave us the necessary clue which allowed us to determine the age of at least one of the workers. It was possible to infer that a bee was about 30 days old, since: a) the four workers of the first brood survived the hatching of two workers of the second brood, giving a lapse of time of 22 days for the complete life cycle of the second brood; b) to this we may add three more days, since the first bee to be hatched from the first brood was three days older than the last bee; c) likewise, one of the bees of the second brood was one day older than the other one, adding another day; d) finally we should add three to five days as a lapse of time between the hatching of the first brood and the beginning of foraging by the workers, giving a total of about 30 days (Fig. 8).

Workers do not live much over a month as suggested by the relationship between the average of the population of bees and the number of cells as they increase each month (Table 4 and Figs. 32, 35 and 38). The life span of males was also inferred indirectly. For one thing, the peak of the male population occurred about April 20 in one season, with hundreds of males present. Before that date the male population was quite low and on May 1 most of the males had disappeared.

Flight range: In order to find the flight range of these bees, marked pollen collecting bees were released at different distances from their nests. It was assumed that if most of the marked bees found their way back in less than an hour, they probably had been liberated inside their normal flight range. Bees released at 30, 50, 60, 80 and 100 meters from their nests returned without much difficulty. All the bees returned in less than an hour, and from the 46 bees used in the experiment 44 returned to their nests (these bees belonged to three different nests). Two of these bees were poorly marked; this fact may account for the two missing. On the other hand, most bees released at distances beyond 100 meters failed to return: thus, of 16 bees released at 105 meters, eleven returned to the nest. From 30 bees released at 115 meters only five were able to return. Finally, 30 more bees were released 160 meters away, and only three of them found their way back. From this we may conclude that the actual flight range of these bees is a circle of about 100 meters around their nests.

Natural Enemies: Outside the nests the adults are subject to common predators, which may account for the relatively high rate of mortality of the queens during the founding period. Except for a small mutillid, *Pseudomethoca willei,* (MICKEL, 11), natural enemies which attack the nests of these bees are not known as yet. *Pseudomethoca* are more evident during the founding period, and may occasionally penetrate the nest. Later, during the resting period of the queen, they are kept from entering because the dirt plug is fairly hard and thick. One hundred and five normal nests were studied during the founding period and none of them were parasitized by the mutillids. However, if a nest lost its queen, it was easily preyed upon. In one of the sites studied, 31 queenless nests were parasitized by mutillids and their larvae found feeding on the pollen provisions in the cells. In two instances, two larvae were observed in the same cell. It is possible that these nests had been parasitized by two different mutillids. It is interesting that the mutillid larvae may live up to a half hour in pure Kahles' solution, while a bee larva dies in a few seconds.

Nest structure: The nest architecture of most of the species of the subgenus *Dialictus* can be placed according to the system of SAKAGAMI and MICHENER (12) in group OCh^nB, subtype IIIb or IIIc. *L. herbstiellum,* however, makes a primitive type of nest with lateral burrows, each ending in a cell, subtype IIIa, $O(LCh)^nB$.

The nests of *L. umbripenne* are vertical burrows in the soil, usually considerably branched and often meandering, of the subtype IIIb, OCh^nB (Figs. 9, 10). Sometimes, however, the nest may present a ring burrow around a group of cells (Fig. 6), similar to type IVb. The structure of the nests changes during the months January-April as the population of bees increases. The burrows range from 3 to 3.75 mm in diameter, rarely reaching 4 mm in certain parts. At the entrance the burrow narrows to 2 to 2.5 mm in diameter. There is no depressed area around the entrance as in *L. imitatum,* but sometimes a small turret 1.5 to 2 mm high, may surround each entrance. These turrets develop as the excavated earth is placed around the entrance and the rain washes the loose dirt away. They are temporary structures and may often be absent.

The cells are similar to those found in related species (e. g., *L. imitatum*). The cells of workers and males measure 3.5 to 4 mm in diameter by 7 to 11 mm in length, the latter with a mean of 9.5 mm. The necks of the cells (Fig. 21) are usually about 2 mm wide (2 to 2.5 mm). Each cell is closed after oviposition with a plug of loose soil which extends into the neck for a distance of about 2 mm (Fig. 22). The cells of the queens, slightly larger than those of the workers and males, are 4.5 mm in diameter by 11 mm long (Fig. 21). The depth of the occupied cells increases during the dry season (Figs. 36, 38).

From January to April, as the population increases, the nests become progressively deeper and more branched, often meandering considerably (Figs. 5, 10). Nests made by single queens during the founding period are simple, unbranched, vertical burrows 8 to 15 cm in depth and with 3 to 5 cells (Fig. 5). With production of workers the nests are extended deeper into the ground and become branched. Branches are counted as the total number of blind-end burrows that are longer than cells (Figs. 9, 10). They may form curves and arches and sometimes unite to form rings (Fig. 6) and loops. At about the middle of each month, from January to April, the depth of the nest and the number of branches, loops and arches doubles, while the number of bees and cells triples (Table 4). A recently founded nest, for instance, is a simple burrow of about 8 cm in depth, with one bee (the queen) and about 3 cells. If it is assumed that this nest may double its number of branch burrows, arches and loops (except in the beginning when obviously none of these exist) and also its depth, and at the same time triple its number of bees and cells at the middle of each month, we then have an increase in nest complexity as shown in Table 5. If these theoretical results are compared with the actual results shown in Table 4, a close parallel can be observed between the two. The only major discrepancy between the calculated and the actual data is found in the number of cells during April. It seems that the number of cells doubles rather than triples from March to April.

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TABLE 4

Mean number of bees, cells, branch burrows, loops and arches, and mean nest depth, January-April. Each entry consists of the mean, the extremes in parentheses, and the number of nests examined.

	January	February	March	April
Number of bees	3.2(1-7)36	7.7(1-24)17	27.6(26- 30)3	75.6(60- 84)3
Number of cells	7.6(1-22)34	27.1(9-67)16	84 (23-131)3	146 (89-165)3
Depth of nest (cm)	16.4(10-33)33	29.2(12-78)15	62.3(45- 74)3	99.5(38-165)8
Number of branch burrows	2 (0-7)32	5.4(0-18)16	10 (3- 14)3	23.2(13- 41)4
Number of arches and loops	0.24(0-2)32	2.1(2-7)16	4 (2- 7)3	9.7(6- 15)4

TABLE 5

Hypothetical nest and its increase in complexity during the months January-April.

	Newly founded nest	January	February	March	April
Number of bees	1	3	9	27	81
Number of cells	3	9	27	81	243
Depth of nest (cm)	8	16	32	64	128
Number of branch burrows	0	2	4	8	16
Number of arches and loops	0	0	2	4	8

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SUMMARY

The present study consists of the life history and behavior of a primitively social halictine bee *Lasioglossum umbripenne*. The work was conducted 15 km north of Quepos (200 meters altitude) on the southern Pacific coast of Costa Rica. The bees are active only during the dry season, January through April. The colonies contain well established worker and reproductive castes, the queen being easily differentiated from the others by her larger size. Cells destined to produce queens differ from those that produce workers and males in the size and shape of the food mass and in cell dimensions. The nests are burrows in the ground, normally with only one queen.

In founding the nest, the queen digs a burrow 8 to 15 cm deep and constructs from one to six cells, one each night, which she provisions the following morning. Provisioning requires five pollen collecting trips. An egg is laid upon the mass, now in the form of a small sphere, and the cell is then closed. The queen keeps the entrance of the nest well sealed with soil at all times except in the morning when she is working or feeding. After preparing and provisioning all the cells, she ceases her activities and waits until the progeny reach maturity. The development from egg to adult requires 22 days and the progeny emerge mostly as workers. From this time on, the nest is continually active and the workers deepen the nest and provision other cells while the queen provides each with an egg. Many workers can also lay eggs; in fact, almost 50 per cent of the population showed ovarian development. Occasionally fertilized workers are also found. The flight range of these bees is a circle of about 100 meters around their nests.

From January through April the nests become progressively deeper and more complicated, with additional branching and looping. The bee population and the number of cells likewise increase from month to month.

The queen generally lives one year, the workers about a month, and the males less then two weeks. During the months of activity of the colony the queen is never replaced. She lays an egg a day (rarely two). Males are produced throughout the existence of the colony, but an appreciable number was never observed except at the end of April. This peak in the male population is correlated with the production of new queens and marks the end of the colony's existence. The new queens soon mate with the males and then leave the nesting area. Meanwhile all the workers and males die and the nests are abandoned. Not until the beginning of the dry season will the new fertilized queens reappear to begin another cycle.

RESUMEN

El presente trabajo consiste en un estudio sobre la etología de una abeja halíctida social primitiva, *Lasioglossum umbripenne*. La investigación se realizó 15 km al norte de Quepos (Altura: 200 m), en la vertiente del pacífico húmedo de Costa Rica. Estas abejas son activas únicamente durante la es-

tación seca, de enero a abril. Las colonias presentan castas obrera y reproductora bien definidas; la reina se diferencia fácilmente por su mayor tamaño y también en relación al tamaño y forma de la masa de polen, así como por la dimensión de la celda. Los nidos, que son pequeñas madrigueras en el suelo, contienen sólo una reina, aunque ocasionalmente se pueden encontrar dos.

Al comienzo de la estación seca las reinas comienzan a fundar sus colonias; durante el primer día la reina hace un agujero individual vertical de unos 8 a 15 cm de profundidad, seguidamente construye de 1 a 6 celdas, generalmente de 3 a 5, a razón de una diaria. Construye la celda durante la noche y la aprovisiona con polen a la mañana siguiente, para lo cual necesita hacer 5 viajes de recolecta. Una vez aprovisionada cada celda deposita un huevo sobre la masa de polen y la sella. La reina mantiene la entrada general del nido cerrada todo el tiempo, excepto durante la mañana, cuando está trabajando o sale a alimentarse. Después de preparar todas las celdas, cesa su actividad y espera en el nido hasta que la progenie llegue al estado adulto. Los huevos duran dos días para eclosionar. Las larvas crecen rápidamente, llegando a su máximo desarrollo en 4 o 5 días. El estado de prepupa dura 4 días y el de pupa 11 días. El detalle de su metamorfosis, a partir de la postura del huevo, se puede resumir en la forma siguiente:

1) Eclosión = 2 días
2) Larva a medio desarrollo = 5-6 días
3) Larva en desarrollo total = 6-7 días
4) Prepura = 8 días
5) Pupa totalmente blanca = 11 días
6) Pupa blanca con ojos rosados = 14 días
7) Pupa blanca con ojos oscuros = 15 días
8) Pupa blanca con ojos negros = 17 días
9) Pupa totalmente oscura = 20 días
10) Pupa totalmente negra = 21 días
11) Adulto = 22 días.

La primera generación está compuesta de obreras aunque ocasionalmente pueden presentarse algunos machos. Las obreras profundizan los nidos y aprovisionan otras celdas, y la reina deposita un huevo en cada una de ellas. Una gran proporción de las obreras puede también poner huevos, tanto así que casi el 50 por ciento de la población mostró desarrollo de los ovarios y ocasionalmente se encontró obreras fertilizadas. Se comprobó que el radio de acción es de aproximadamente 100 metros alrededor de sus nidos.

De enero a abril los nidos se complican en forma progresiva; se hacen más profundos y se construyen ramas adicionales en diferentes niveles hasta formar un sistema sumamente complejo. La población de abejas y el número de celdas de cada nido también aumenta mes a mes. Durante enero, por ejemplo, los nidos son de 8 a 33 cm de profundidad, con 1 a 7 ramas colaterales; la población de abejas, que representa la primera generación más la reina, es frecuentemente de 4 a 5: el número de celdas varía de 8 a 15. Durante febrero los nidos son más profundos, de 13 a 53 cm, llegando algunos a alcanzar hasta 75 cm, y el número de ramas es de 4 a 8; la población en este tiempo es de 7 a 20 abejas y el número de celdas de 16 a 35. En marzo la profundidad de los nidos varía entre 40 y 70 cm, teniendo de 3 a 14 ramas colaterales, con una población de 25 a 30 y un número de celdas de 90 a 130. Durante abril los nidos llegan a su máximo desarrollo, con una profundidad mayor de un metro; algunos sobrepasan metro y medio, con 13 a 41 ramas; la población fluctúa entre 60 y 90; el número de celdas entre 80 y 160.

La reina generalmente vive un año, las obreras cerca de un mes, y los machos menos de dos semanas. Durante los meses de actividad, la reina nunca es reemplazada por otra, como sucede en otras especies afines. Ella pone un huevo por día, raramente dos. En vista de que hay una gran proporción de obreras que ponen huevos, los machos se producen durante toda la existencia de la colonia; sin embargo, no se observó un número apreciable de machos sino hasta fines de abril; esta alta producción de machos está correlacionada con la producción de nuevas reinas, así como con el final de la existencia de la colonia. Las reinas se aparean con los machos y luego buscan un lugar apropiado, fuera del nido, para pasar la estación lluviosa; mientras tanto todas las obreras y los machos perecen y los nidos son totalmente abandonados. Durante la estación de lluvias, por este motivo, no existe actividad alguna entre estas abejas, y no es sino hasta el comienzo de la estación seca que las nuevas reinas despiertan de su estado de letargo para comenzar un nuevo ciclo de actividad.

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Figs. 1-4. General habitat of the nest colonies.
Figs. 1-2. Nest sites surrounded by tropical rain forest.
Figs. 2-4. Nest sites in pastured areas.
Fig. 3. Nest site along a trail.

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Figs. 5-8. Diagrams of nests. Cells indicated by broken lines are old cells. Since these old cells are hard to recognize, most of them were omitted.

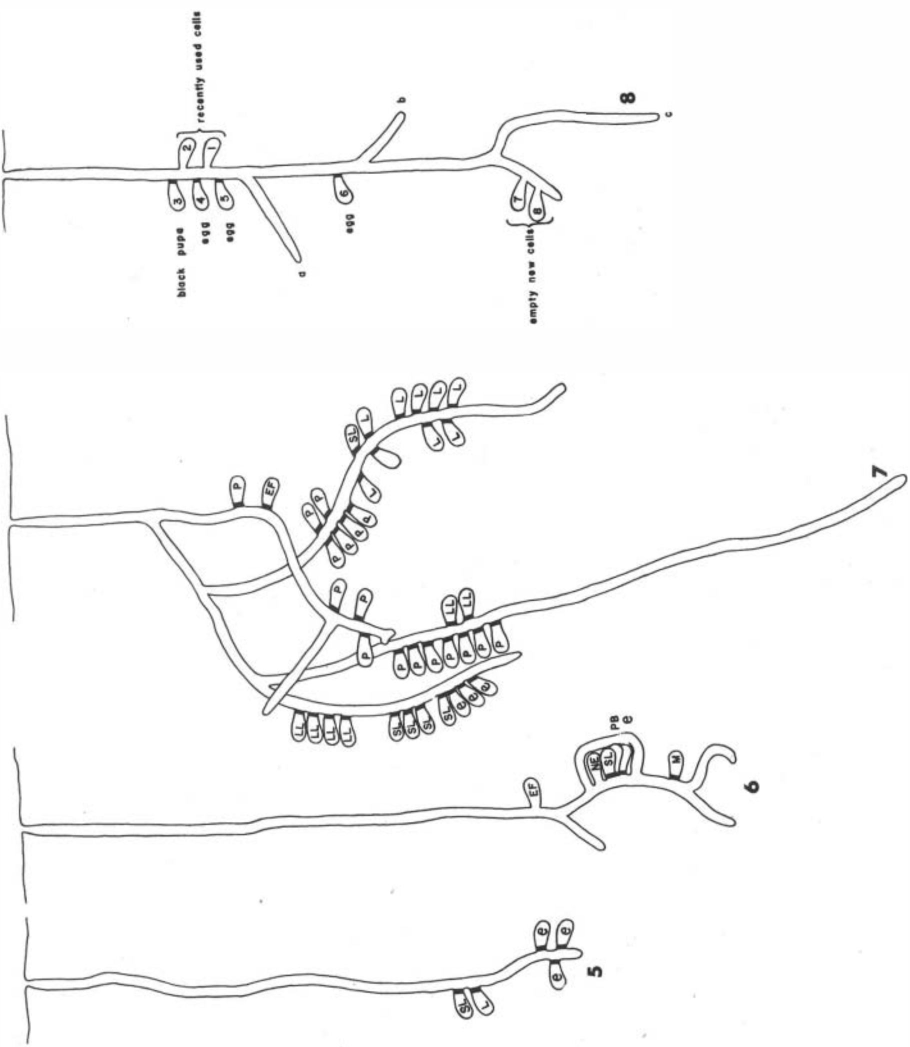
NE = newly made
EF = empty except for larval feces
PB = pollen ball (but no egg or larva)
SL = Small larva
LL = large larva and prepupa
E = empty
M = cell contents destroyed by mold
e = egg
L = larva of moderate size
P = pupa

Fig. 5. A queen nest opened on January 4; 12 cm deep; occupied by a single queen.

Fig. 6. Nest opened on January 17 showing a ring burrow around a group of cells; 22 cm deep, with the ring burrow at 19-20 cm; occupied by a queen and two workers.

Fig. 7. Nest opened on February 17; 30 cm deep; occupied by seven workers, the queen was not found; two workers had well developed ovaries.

Fig. 8. Nest opened on January 22; occupied by a queen and six workers. Upper cells 1, 2 and 3 represent the second brood. Cells 4 to 8 belong to the third brood. Branch burrows a, b, and c may well represent some of the cells of the first brood. Broods usually overlap, but in this nest they are separated; apparently the queen was not able to lay eggs for some time after laying the three of the second brood.


recently used cells
black pupa
egg
egg
empty new cells
8
7
6
5

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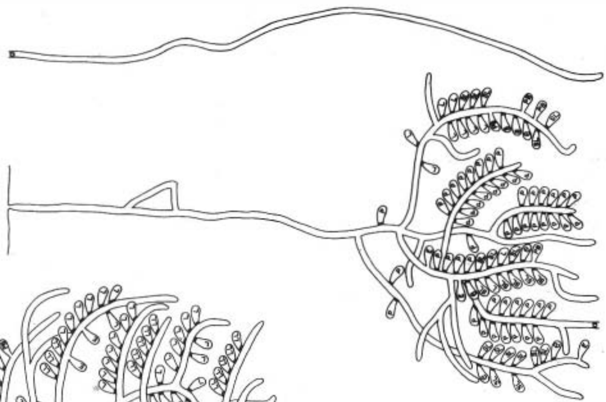
Figs. 9-10. Diagrams of nests.

Fig. 9. Nest opened on April 17; depth 127 cm with two large concentrations of cell groupings, one at 82 cm and the other one at 113 cm. For the composition of the brood and adults of this nest see Table 3.

Fig. 10. Nest opened on April 30; depth 68 cm with one large concentration of cells at 25 cm. For the composition of the brood and adults of this nest see Table 3.



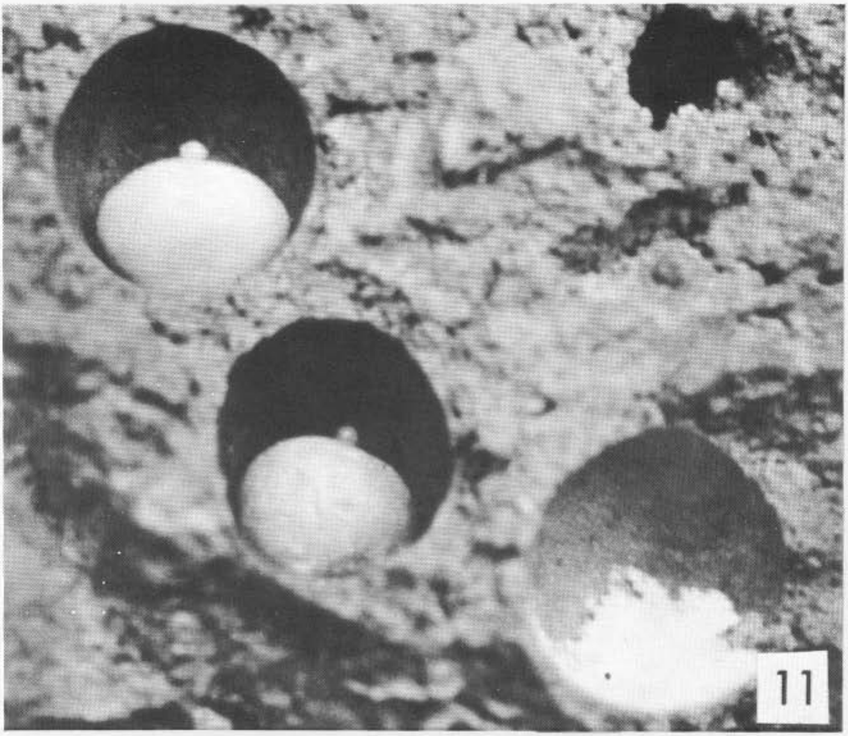
10

9

Fig. 11. Cross section of cells, the lowest cell showing some pollen.

Fig. 12. Longitudinal section of a cell showing some pollen.

Fig. 13. Longitudinal section of a cell showing a queen's pollen ball (but no egg or larva).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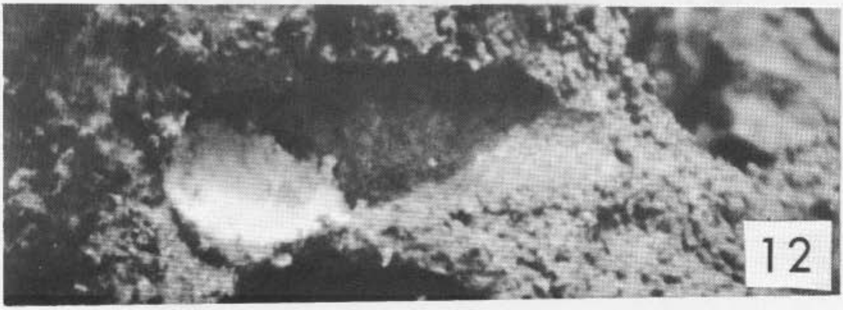
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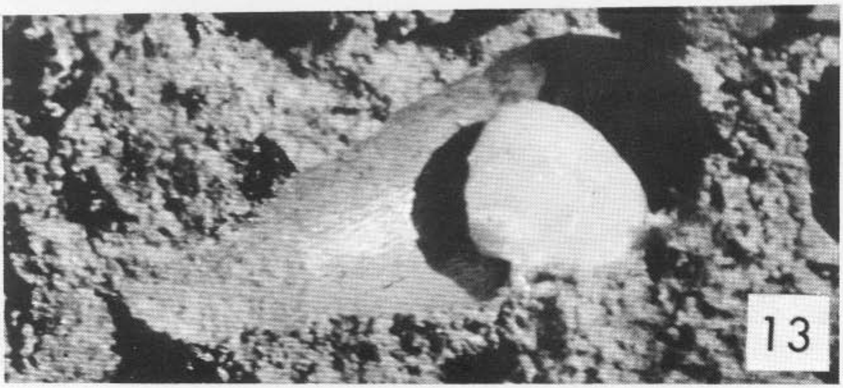
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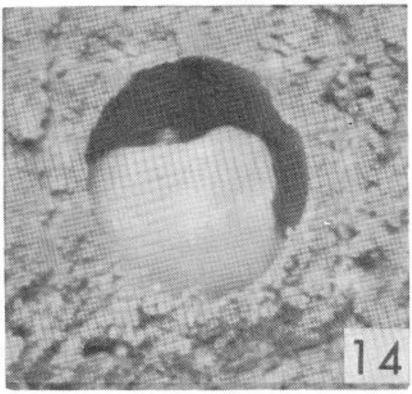
Figs. 14-17. Cells showing the difference between the queen's and worker's pollen balls.

Figs. 14-15. Front view of a queen's pollen ball.
Fig. 16. Dorsolateral view of a queen's pollen ball.
Fig. 17. Size difference between two worker pollen balls.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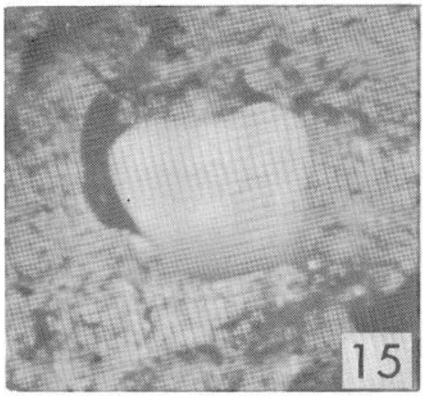
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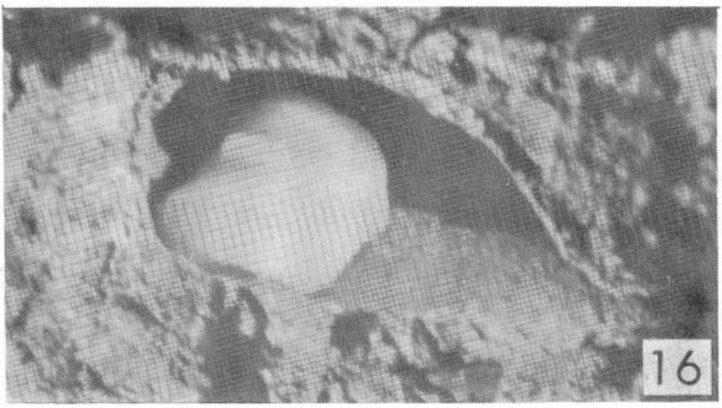
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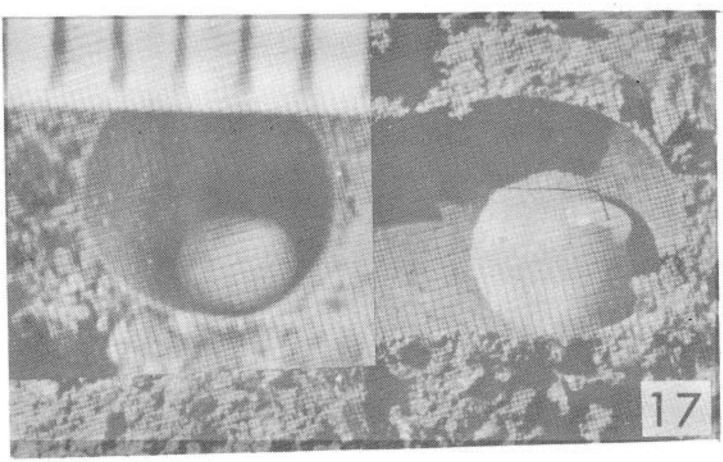
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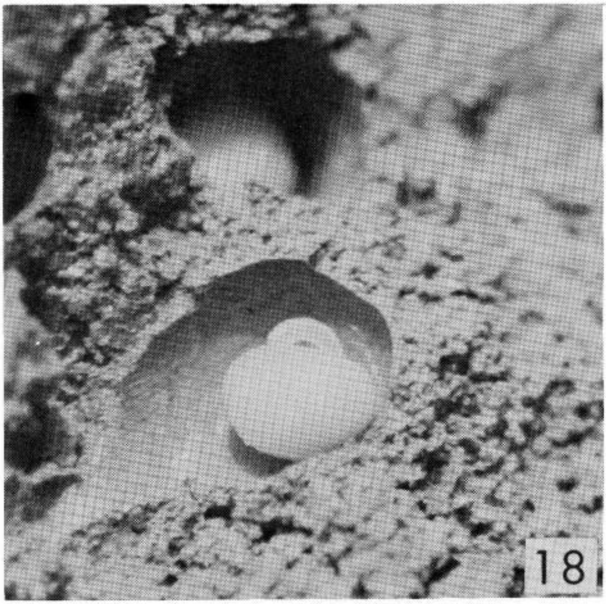
Figs. 18-19. Pollen balls showing eggs.
Fig. 18. A worker's egg.
Fig. 19. A queen's egg.



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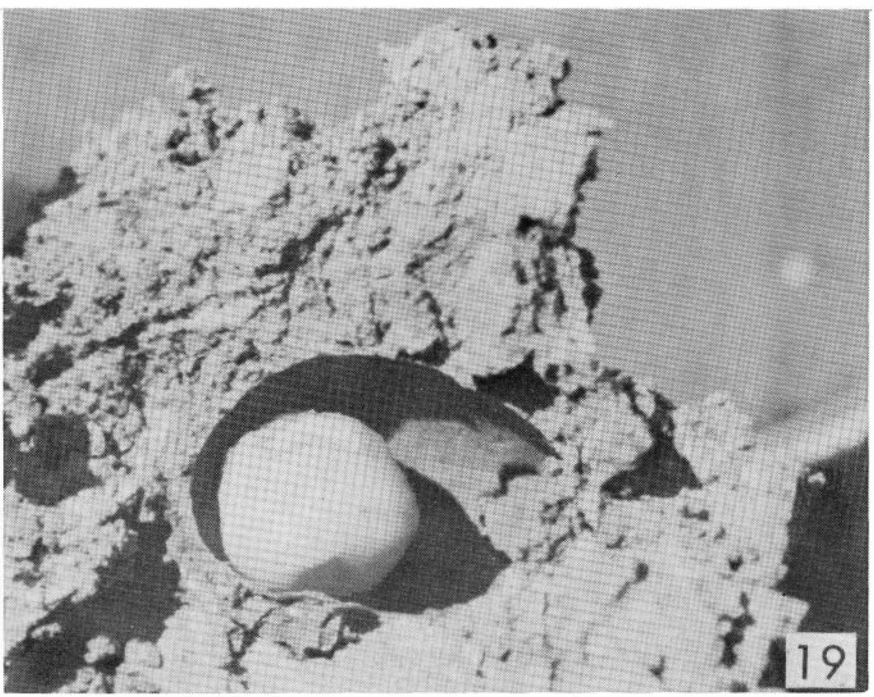


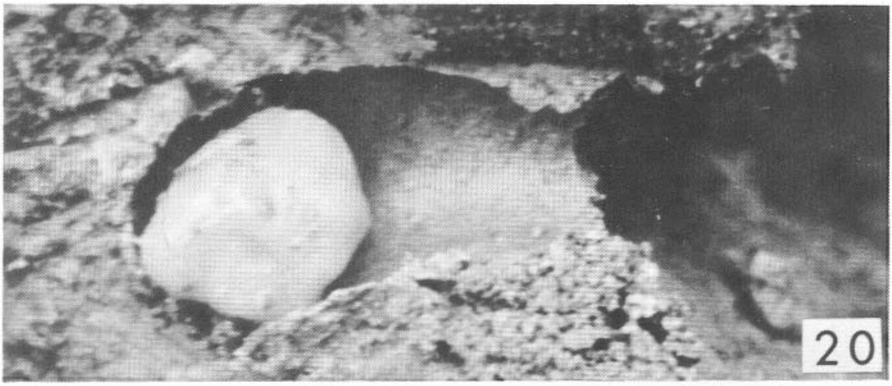
19

Figs. 20-22. Cells showing small queen larva.

Fig. 20. A newly emerged larva.

Fig. 21. Longitudinal section of a cell showing a very small larva. Scale at bottom of the figure is in millimeters.

Fig. 22. A small larva, note neck of cell plugged with dirt.



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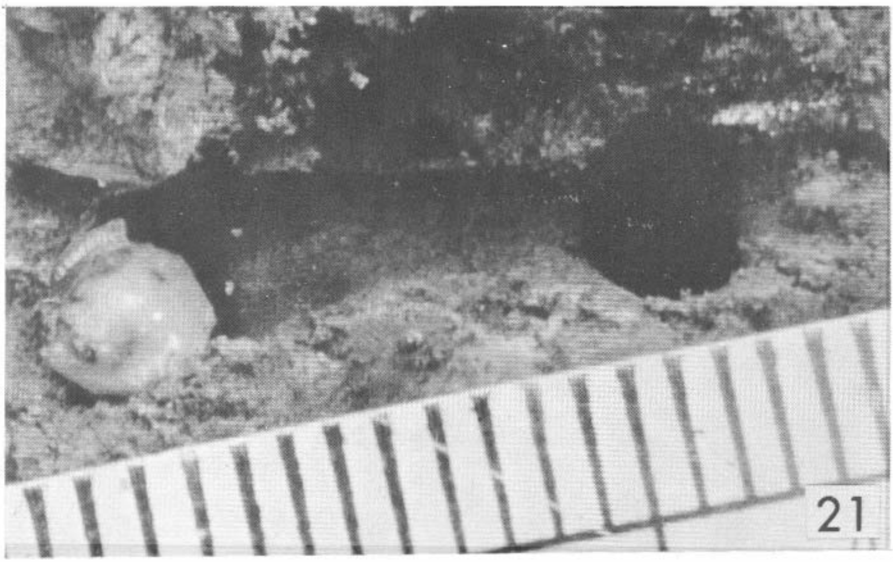

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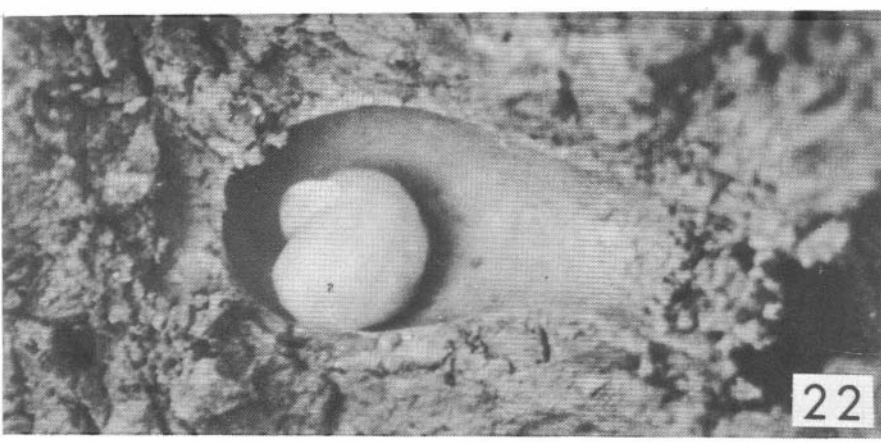
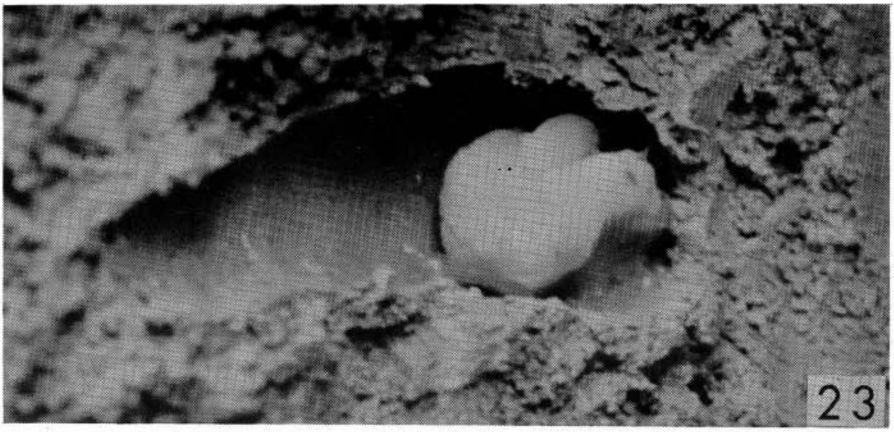


22

Figs. 23-25. Cells showing the progressive growth of a relatively small queen larva.

Fig. 23. Anterolateral view.
Fig. 24. Dorsal view.
Fig. 25. Lateral view.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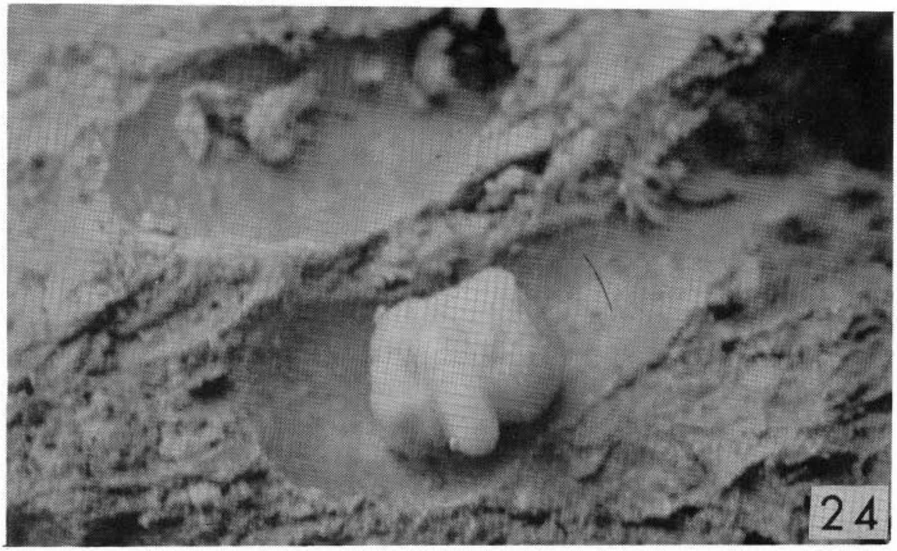
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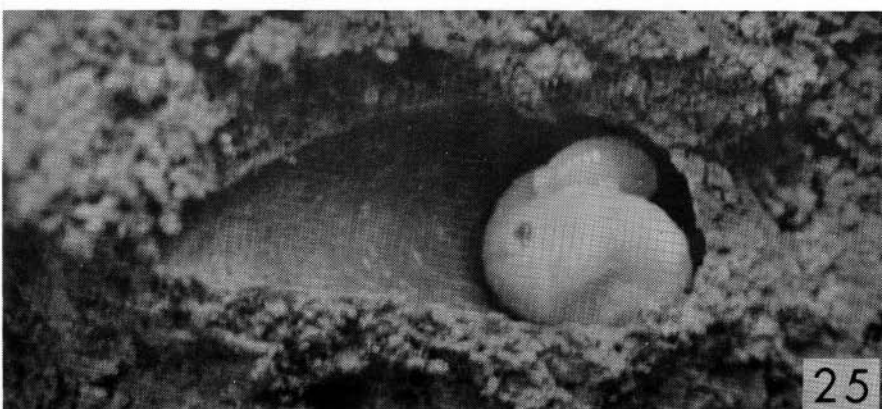
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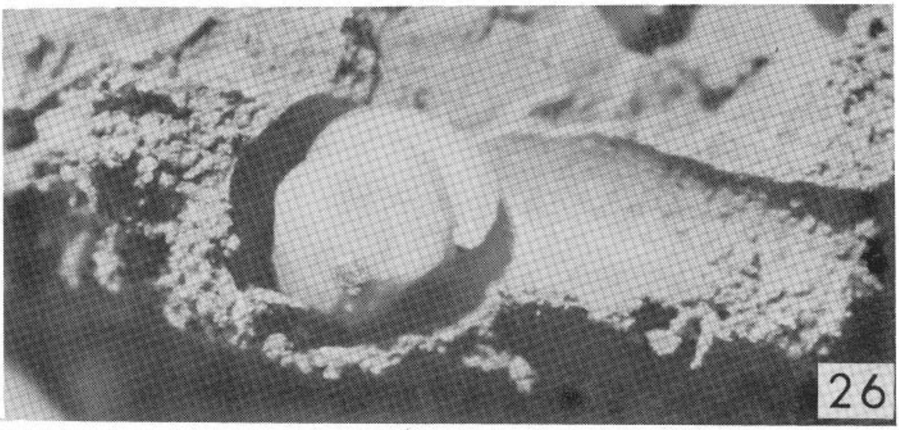
Figs. 26-28. Cells showing the progressive growth of a moderate sized queen larva. Lateral view.



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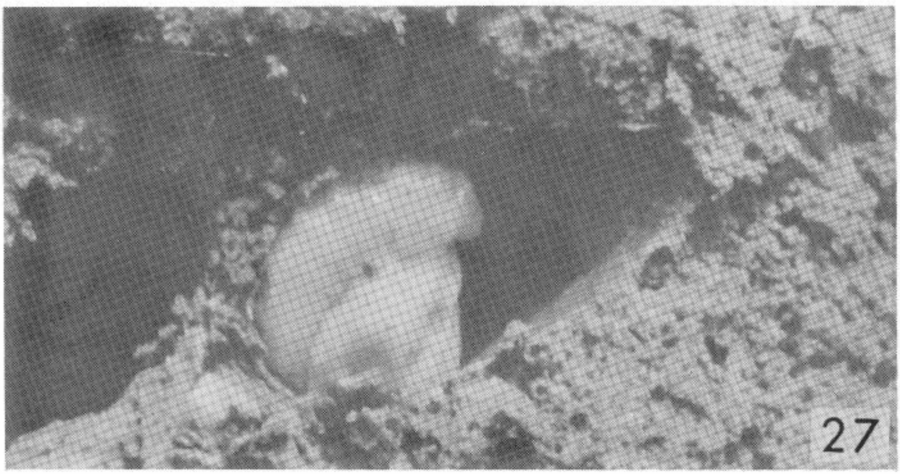

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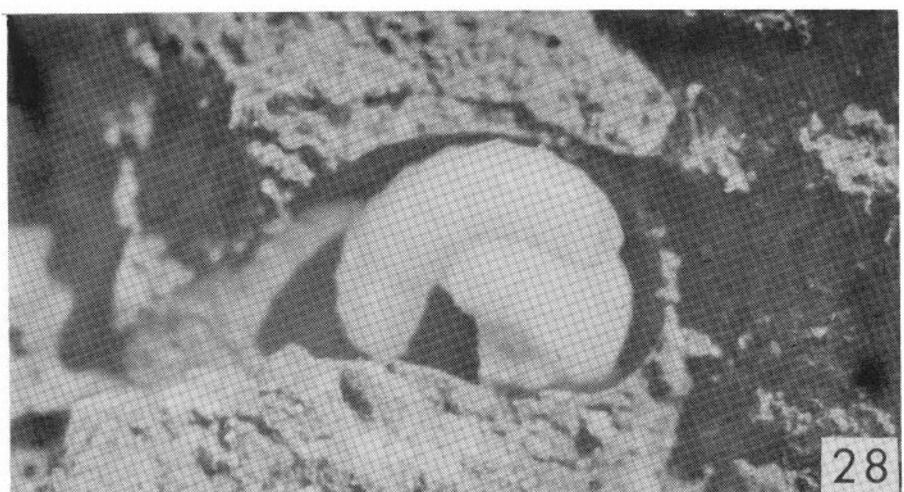
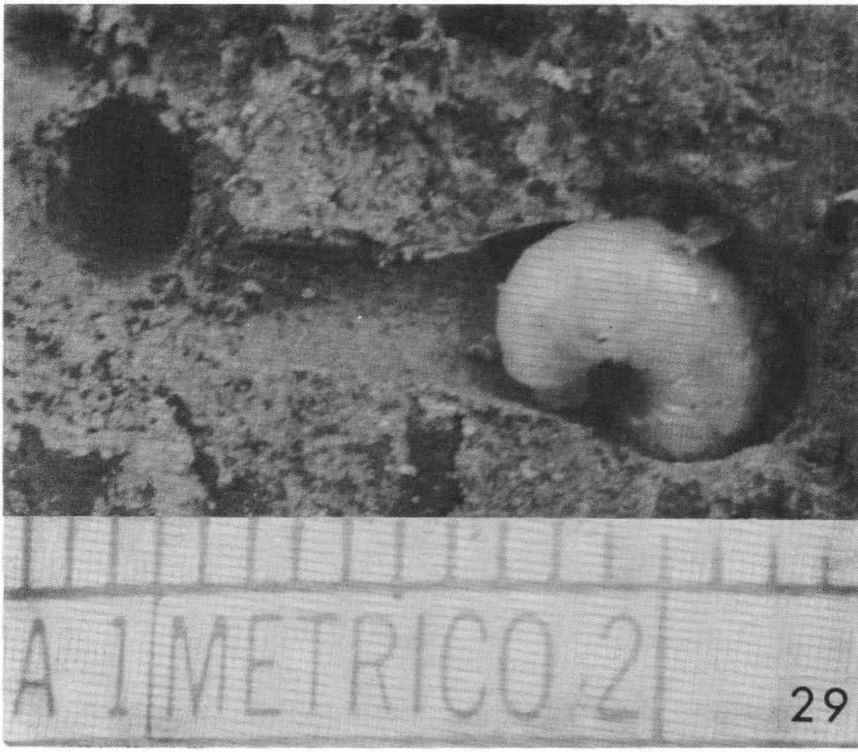


28

Fig. 29. Full grown larva.
Fig. 30. Prepupa.



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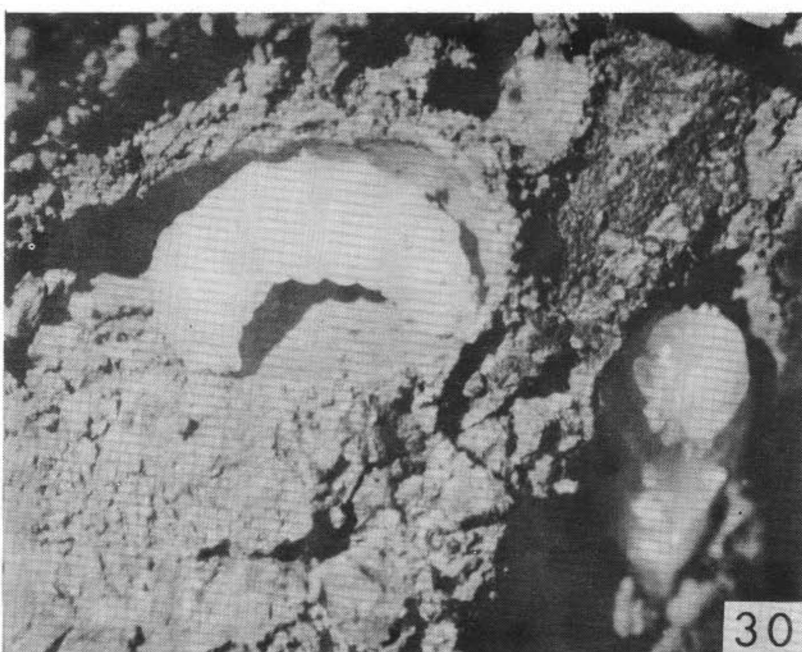

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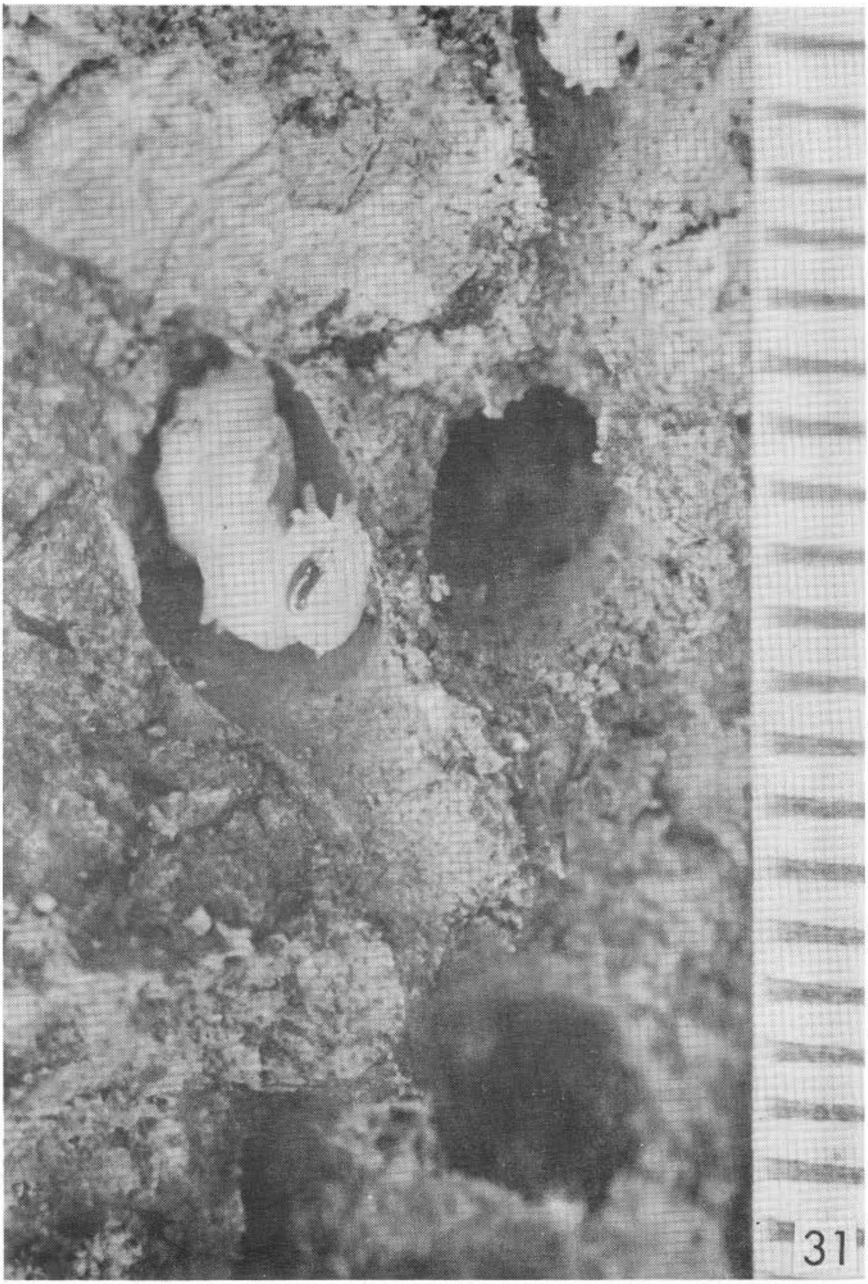
Fig. 31. Pupa in the cell.


31

Figs. 32-37. Histograms showing the means of different details of the nest throughout the months of activity.

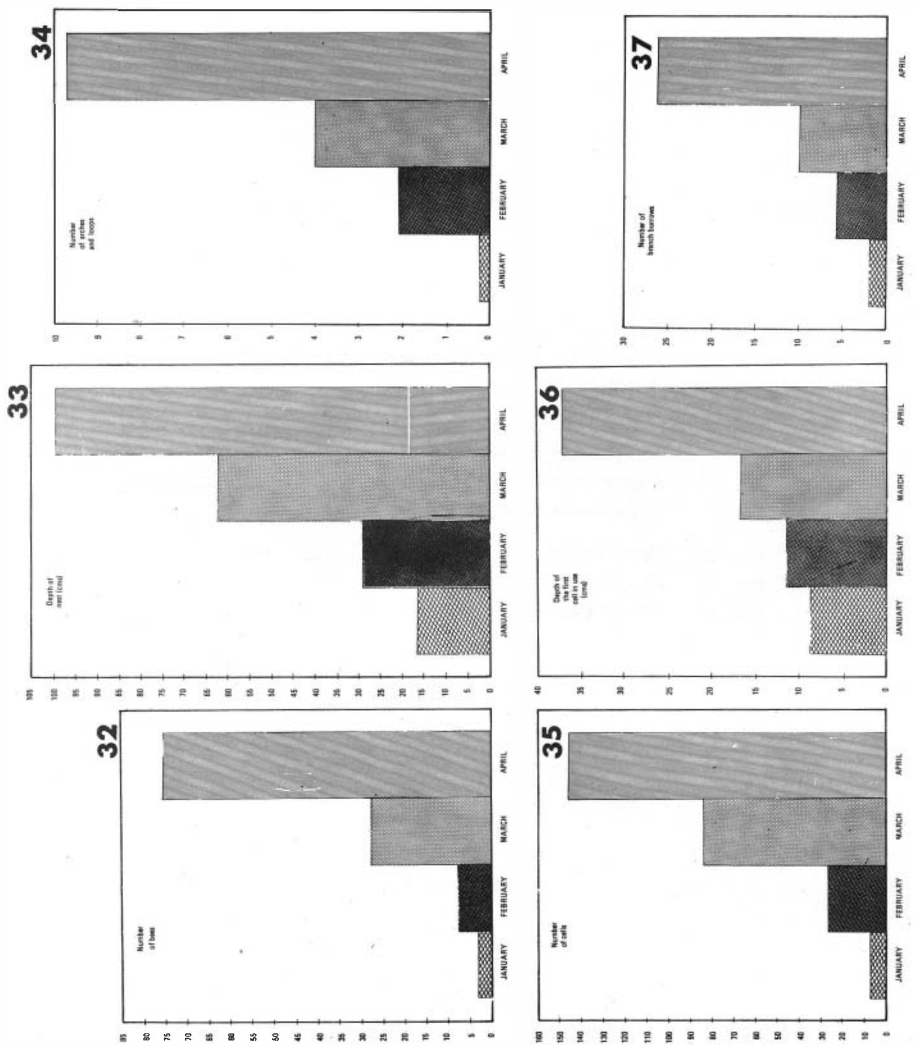

32
Number of bees
JANUARY
FEBRUARY
MARCH
APRIL
33
Depth of nest (cms)
JANUARY
FEBRUARY
MARCH
APRIL
34
Number of arches and loops
JANUARY
FEBRUARY
MARCH
APRIL
35
Number of cells
JANUARY
FEBRUARY
MARCH
APRIL
36
Depth of the first cell in use (cms)
JANUARY
FEBRUARY
MARCH
APRIL
37
Number of branch burrows
JANUARY
FEBRUARY
MARCH
APRIL

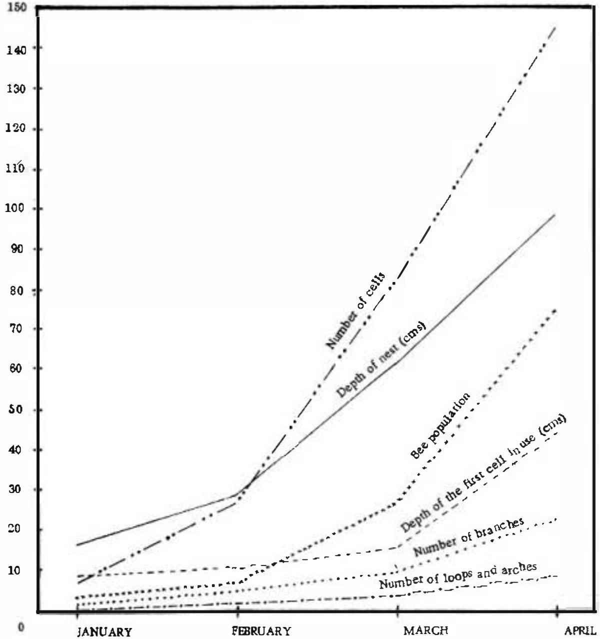
Fig. 38. Mean number of cells, branch burrows, loops and arches, bee population, depth of nest and depth of the first cell in use.

Figs. 39-41. Graphic comparison of the range of variation and mean value of the total length, head width and wing length of the workers and queens. Standard deviation is indicated by double lines.

Fig. 39. Total length.

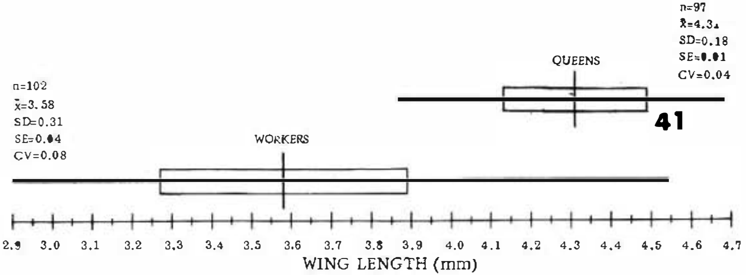
Fig. 40. Head width.

Fig. 41. Wing length.



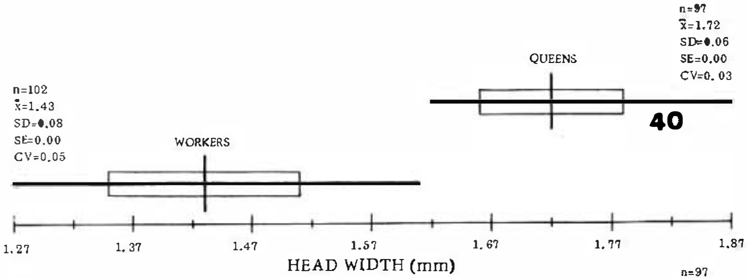
0
10
20
30
40
50
60
70
80
90
100
110
120
130
140
150
JANUARY
FEBRUARY
MARCH
APRIL
Number of cells
Depth of nest (cms)
Bee population
Depth of the first cell in use (cms)
Number of branches
Number of loops and arches

38



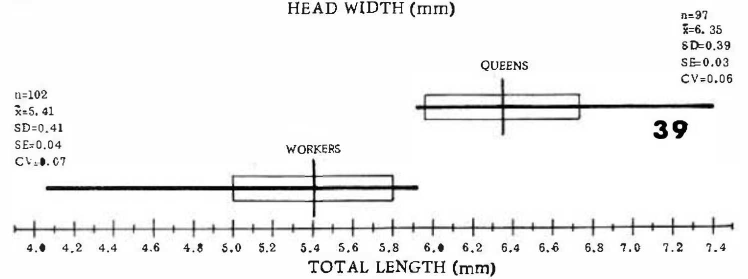
n=97
x̄=4.3
SD=0.18
SE=0.01
CV=0.04
QUEENS
n=102
x̄=3.58
SD=0.31
SE=0.04
CV=0.08
WORKERS
2.9 3.0 3.1 3.2 3.3 3.4 3.5 3.6 3.7 3.8 3.9 4.0 4.1 4.2 4.3 4.4 4.5 4.6 4.7
WING LENGTH (mm)

41



n=97
x̄=1.72
SD=0.06
SE=0.00
CV=0.03
QUEENS
n=102
x̄=1.43
SD=0.08
SE=0.00
CV=0.05
WORKERS
1.27 1.37 1.47 1.57 1.67 1.77 1.87
HEAD WIDTH (mm)

40



n=97
x̄=6.35
SD=0.39
SE=0.03
CV=0.06
QUEENS
n=102
x̄=5.41
SD=0.41
SE=0.04
CV=0.07
WORKERS
4.0 4.2 4.4 4.6 4.8 5.0 5.2 5.4 5.6 5.8 6.0 6.2 6.4 6.6 6.8 7.0 7.2 7.4
TOTAL LENGTH (mm)

39