NOTES ON NESTING AND FORAGING BEHAVIOR
OF *MEGALOPTA* (Hymenoptera: Halictidae)
IN COSTA RICA

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ABSTRACT
A nest of the nocturnal bee Megalopta centralis Friese is described from a nearly vertical, 22 mm-diameter dead stick along a road through primary lowland tropical wet forest. The cell substrate is wood fragmented by the bee; a single male was reared from a pupa in the nest. Solanum spp. and Calathea insignis are recorded as flower hosts of Megalopta.

The widespread neotropical genus Megalopta (based on Megalopta idalia Smith, see Moure, 1958) is one of the five night-flying genera of Halictidae. Of the other four, Sphecodesma of arid regions in temperate North America has been discussed most recently by Kerfoot, 1967a, 1967c; Megagination of lowland South America is presumed to be nocturnal based on its being found in the nests in the day, going to Ipomoea flowers before sunrise, and having very large ocelli (Michener and Lange, 1958; Jørgensen, 1912 as Megalopta ipomoeae); and Ariphanathra and Megaloptidia of lowland South America are presumed nocturnal by virtue of their large ocelli (see Moure, 1951 for a morphological discussion of the former genus). A single female of Megaloptina (a subgenus of Megagation) [Determination by Dr. G. C. Eickwort, now of Cornell University] was taken at Madden Dam, Canal Zone, while gathering pollen from a small, blue-flowered monocot at 6:15 AM (before sunrise, but light enough to see the bee clearly on the flower, July 9, 1967). Eickwort (1967) discusses the generic limits of the four tropical genera mentioned above. All records of Megalopta nest sites are arboreal (Sakagami, 1964; Sakagami and Moure, 1967) while Megagation and Sphecodesma nest in the ground. The nest in this paper is the third described in detail for Megalopta.

The biology of neotropical nocturnal bees is very poorly known, and Megalopta is no exception. In Central America, Megalopta and Ptiloglossa are the only two genera of bees commonly taken at light (incandescent and "black light"). Ptiloglossa (Colletidae) range from 20 to 30 mm in length and 7 to 14 mm in maximum width, are various combinations of yellow, brown, red, black, or black and gray, and come to light between 3:30 AM and about 30 minutes before sunrise. Megalopta range from 10 to 15 mm in length, have a yellowish brown abdomen with some darker brown banding and a metallic, greenish yel-

low to bronze thorax and head, and come to light throughout the night. Both genera may be distinguished from diurnal Central American bees of the same size by very large ocelli and compound eyes (see Kerfoot, 1967b, for a discussion of significance of large ocelli). Other crepuscular and matinal bees in Central America (e.g., the "squash bees" Peponapis and Xenoglossa, Anthophoridaceae [Hurd and Linsley, 1964, 1965a, 1967b], and the carpenter bee subgenus Notoxyllopora, Apidae [Janzan, 1964]), only very rarely come to lights. Two females of the rare halictid genus Rhinetula [det. G. C. Eickwort] were taken at black light in Panama (Cerro Campana, July 11, 1967); these small brown and hairy bees are quite unlike either Megalopta (which has an iridescent thorax) or Ptiloglossa (2 to 3 times as large as Rhinetula). The apparently equally rare subgenus of Caupolicana, Zikanapis (Colletidae), has on one occasion been collected at light in Mexico (Michener, 1967) but this bee is very similar to Ptiloglossa.

NEST OF MEGALOPTA CENTRALIS

The nest was found (Feb. 25, 1967) in the upper part of a dead trunk of Apeiba tibourbou Aubl. (Tiliaceae) among second growth from the bank of a dirt road that was made through primary forest in December, 1964 (mile 5, lowland road to the Pacific, S. of Rincon, Osa Peninsula, Puntarenas Prov., Costa Rica). The trunk leaned about 20 degrees from the vertical and was exposed to direct sunlight (insolated only from about 10 AM to 2 PM owing to the height of the neighboring trees) and direct rain (annual rainfall of 350-450 cm). All bark had rotted and fallen from the trunk; the top had been amputated by a slanting machete cut 190 cm above the ground. The nest was in a 22 mm-diameter side of a fork 25 cm below the trunk top (Fig. 1a); the other side of the fork and the main trunk (about 35 mm in diameter) were solid and without insect burrows.

The nest was discovered at 9:00 AM. A machete cut split off about one third of the stem wall, destroying the single lateral entrance and releasing at least three adult bees; they flew away very readily, apparently not confused by the sudden exposure to sunlight. A male pupa was in one cell; no eggs or larvae were present. When found, the pupa was creamy white with dark black compound eyes; it was very active within the cell, turning frequently even when the nest was not moved. The machete cut knocked about 2 mm off the top of its cell but this did not hinder development; it hatched on March 6, 1967 at the field station a few miles from the nest site. The species determination [det. G. C. Eickwort] is based on this male which is deposited with the nest in the Snow Entomological Museum at the University of Kansas.

As can be seen in Figure 1b, the nest is contained within the walls of the stem. Apeiba tibourbou has very soft wood (about like commercial balsa, Ochroma lagopus Swartz); the distinct rings (not annual, but nevertheless rings) are slightly harder than the xylem parenchyma between them. In excavating, it appears that the bee(s) cleaned out the

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FIG. 1. A. Entire nest of *Megalopta centralis* in dead trunk of *Apeiba tibou-bou*. Fragment in center formed wall of one half of main cavity but lacked cells. Cells in the photograph are identified by numbers immediately to the right of the ruler (see text). B. Central portion of nest. Coarse matrix is clearly distinct from virgin wood bounding nest. Cell numbers along right side correspond to those in A.

The entire nest cavity gives the impression of having been excavated and then rebuilt by the bees. The relatively finely comminuted and packed (?) material (matrix) in which the cells are situated is definitely not frass from some other insect or the wood of the stem in its original form, but it has the appearance of very fine sawdust that has been slightly moistened and packed into place. Small fibers and wood pieces are evident without magnification. Cells in what appears to be all stages of construction are present. These will be described in order below, from what appears to be the newest (1) to the one that contained the male pupa (6) (see Fig. 1a).

1) This hole cut into the virgin wood has a maximum diameter of 7 mm, and is 11 mm from the lower lip (lower edge of the entrance to the cell) to the bottom. As in all cells, except perhaps number 2, the entrance is at the top of the cell. This cell precursor is the bottom of a 5-mm tunnel that passes through or past the matrix of several more complete cells above it. Its long axis is about 5 degrees off the vertical when the trunk is in its original upright but leaning position. At 13 mm from the bottom, the cell narrows to the tunnel referred to above. Except for its obvious ovoid shape, this cavity would probably be regarded as the end of a tunnel. Judging from the appearance of neighboring cells, this cavity (perhaps after slightly more enlarging on one side) would likely have been lined with roughly chewed wood fragments from other excavations and then with a layer of particles of extremely finely comminuted wood to form the cell itself. The cavity could not be enlarged toward the center of the stem since it is already in contact with the thin matrix wall of an adjacent cell. If more of the virgin wood between these two cells had been removed, then they would have had a common matrix, as is the case with the older cells above. Since there are no particles of matrix in the walls of this cavity, it probably is not a re-excavation of a previous cell.

2) This cell is the uppermost end of a tunnel extending upward from the main chamber above the main mass of cells. Its maximum diameter is 5–6 mm, its entrance being set off from the rest of the tunnel by a deposit of coarse matrix slightly less than 1 mm thick which partially rings the tunnel and narrows it to about 4.5 mm diameter, 11 mm from its base (in terms of normal trunk orientation this is the top). The base and one side of this cell have an irregular patchwork of coarse matrix, ranging from 0.2 to 0.8 mm thick, but the other three-fourths of the wall are formed by the polished ring of the virgin wood. Despite the appearance of this tunnel end, it is called a cell only with some hesitation since Halictidae in general do not build cells with the entrances directed downward.

3) This cell, adjacent to cell 1, has a complete lining of matrix 0.2–1.5 mm thick. It is 14 mm from bottom to the upper lip of the entrance; the upper 3–4 mm is part of a constriction where it narrows to 6 mm. Its maximum width is 7.0 mm. Its long axis is about 10 degrees off the vertical when the trunk is in its normal position.

4) This cell has the appearance of being completed, except perhaps needing slightly more of the very finely comminuted lining matrix. From base to the well-defined highest lip of the entrance, the cell is 14.5 mm deep. It is 11 mm deep from the opposite (and lowest) side of the entrance. The 5-mm-diameter entrance lies in a nearly vertical plane. This cell is slightly above cells 1 and 3, and has a vertically oriented axis. It is imbedded in a coarse matrix 0.1–2.0 mm thick and is surrounded by cells or tunnels on three sides. While the inner lining is
exceedingly smooth, it is not as thick (0.1-0.2 mm) as that of the apparently completed cell 5; further, it is the same light beige color as the coarse matrix rather than white as is cell 5. In one place, differential shrinkage of the two kinds of matrix while drying has resulted in a separation, clearly indicating their difference in composition.

On first glance it appears that this cell might have been excavated in a mass of solid coarse matrix. However, the presence alongside the cell of a tunnel partly plastered with a matrix of wood particles bigger than those associated with the cell, makes it appear that at least that side of the cell was against virgin wood that was later excavated in tunnels. Otherwise, one has to assume that the bee built an independent cell wall of wood matrix of at least 18 mm² and not over 0.8 mm thick (in places considerably thinner), or else built a thicker wall and then pared it to its present thickness.

(5) This cell is virtually identical to cell 4 except that a glistening white, waxlike material has been deposited over the entire surface up to the lip. The cell is 14.5 mm deep from the uppermost lip of the entrance and 11 mm deep from the lower lip. The entrance is 4.5 mm diameter and very round; the maximum inside cell diameter is 6.0 mm. At 45x magnification, the white liner, 0.1-0.2 mm thick, looks like opaque fiberglass. At its edge it has the appearance of a material laid down in a fluid state, later solidifying. This cell has coarse matrix 0.2-4.0 mm thick on all four sides. Its long axis is about 30 degrees off the vertical in the normal (original) upright position of the trunk. It appears that the original cavity for another cell is being excavated into the coarse matrix above it. There is no pollen in the cell.

(6) This cell is the next one below number 5 and contained the pupa. The maximum diameter is 6.5 mm and the maximum depth before the top was broken off appears to have been 14 mm. The top was approximately 0.8 mm thick and both a layer of fine and of coarse matrix were in the cap. Details of its morphology were not recorded. The walls are very smooth (as in cell 5) but beige in color and slightly stained with dark brown. In the base of the cell, cemented in a 5-mm-diameter circular patch at the bottom, are about 125 fecal pellets measuring 1 mm by 0.5 mm. There is no evidence of any type of cocoon having been spun and the pupa was naked (head upward). There are scattered bits of what might have been fungal hyphae or silk on the walls, but they are so dispersed that they are unlikely evidence for rudiments of cocoon spinning behavior. This cell is bounded on one side by virgin wood (with a very thin layer of coarse matrix lined by an inner layer of fine matrix) and on three sides by other cells or tunnels. Its axis is essentially vertical. The coarse-matrix walls are 0.1-1.5 mm thick; one of these walls has clearly been thinned by tunneling between the cell and the virgin wood.

The cells in this nest, in view of the apparent series of cells 1-4, were probably made by building up the sides of an irregular shaped cavity with coarse matrix, and then adding fine matrix. An undeterminable amount of the material removed for this cavity was virgin wood. There is no evidence of old cells being only partly torn away and then rebuilt. The three essentially completed cells (4, 5, 6) are slightly flattened on their ventral sides (in respect to a sagittal section and as compared to the dorsal side) but apparently circular in cross section at any point.

This nest differs from that described by Sakagami (1964) for an undetermined species of Mealopta in a few points. There were neither as many adult bees (3 vs 11) nor as many cells (8 vs 23). The entire inner surface of Sakagami's nest was covered with coarse matrix while the Costa Rican nest has numerous patches of virgin wood. While the larval fecal pellets are deposited on the upper side of the deepest part of the cell in Sakagami's nest (and in the one described in Sakagami and Moure, 1967), in the one Costa Rican cell with fecal pellets they are rather uniformly deposited over the lowermost part of the cell. Sakagami feels that the lack of a lower blind passage under the nest was likely due to the hardness of the wood, but in the Costa Rican nest, absence of this passage cannot be attributed to this cause. While such a passage is commonplace in ground-nesting halictid bees (Sakagami and Michener, 1962), Stockhammer (1966) gives no evidence of it in Augochlora nests in rotten wood in Kansas. Sakagami and Moure (1967) place emphasis on the hypothesis that the cells in their Megalopta nest were excavated in, rather than built with, decayed matter; it is however noteworthy that the cell walls were "consolidated together" and thus could be removed intact from the decayed matter. This would indicate original excavation of a large cavity and later lining of this cavity, as, in other halictines, with wood particles "cemented" (salivary secretions?) together. This appears to be the case with the nest described in the present paper.

Several other records of Megalopta nesting or resting under arboreal conditions have come to my attention. Dr. H. R. Roberts, Sr., while looking for twig-inhabiting Orthoptera in hollow stems of sea grape [Coccoloba uvijera (L.) Jacq.] at the beach at Portete (about 5 miles NW Limon, Limon Prov., Costa Rica), found female Megalopta in several of them. At the I1CA station at Turrialba, Cartago Prov., Costa Rica, Dr. G. C. Eckworts received Megalopta adults that were reported to have been found in hollow stems.

It should be emphasized that present knowledge of nesting behavior of Halictidae that use wood as a substrate is intensive (e.g., Augochlora pura in rotten logs, Stockhammer, 1966) but not extensive (Sakagami and Michener, 1962), making further detailed records of nest structure well worthwhile.

Foraging

Virtually nothing has been reported of the hosts of Megalopta. On May 16, 1965, at 7:10 PM, a single female Megalopta was observed entering flowers of a white-flowered, shubby Solanum (cf. Solanum
torvum Swartz) (Playa Coco, Guanacaste Prov., Costa Rica). It was so dark that she could only be observed in silhouette against the sky. This open-flowered Solanum which lacks floralnectaries is normally visited and pollinated by matinal and diurnal bees that "buzz" the pollen out of the anthers (Michener, 1962; Wille, 1963). By late evening the petals had partly closed over the anthers; the Megalopta female pushed down between these petals and was in the flower for periods of 16 to 45 seconds. She did not audibly buzz the anthers and there was no pollen on her scopae. The most striking thing about her behavior was her extremely slow flight between flowers. She used 5-10 seconds to cross a space of 10-20 cm. This slowness was not due to hovering but rather that her forward rate was slow. However, when a flashlight was turned on her, she flew much more rapidly until captured.

One record each for nectar and pollen hosts are available from the area near the airstrip at Rincon, Osa Peninsula, Costa Rica. A female Megalopta centralis was collected while taking nectar from Calathea insignis (Marantaceae) at dawn when it was just light enough to barely see the bee at a distance of 50 cm (4:48 AM, July 21). She had no pollen in her scopae and flew very slowly, somewhat resembling a small moth in flight. A female of the same species was collected at the same light intensity as it flew from flower to flower of a shrubby, white-flowered Solanum (cf. Solanum torvum) (5:00 AM, July 29, 1967). Both scopae of this bee had many grains of Solanum pollen among the hairs. She was not buzzing the anthers. The latter two records are from the rainy season. All three records were for plants within 3 m. of the ground.

Under primary forest conditions, these bees probably forage and nest in the canopy. A twig- or branch-inhabiting deviation from the usual ground nesting habit of Halictidae would eliminate problems of ground predators since it is considerably more vulnerable to vertebrate and invertebrate predators than is a nest in the soil.

A considerable number of Central American solitary bee species appear to have their flight period during the dry season (December or January through late April or early May; see Janzen, 1967), so it is of interest that Megalopta have been taken at black lights at various localities in Central America during both the rainy and the dry season. At Barro Colorado Island, Canal Zone, Panama, C. W. Rettenmeyer (in litt.) has found them to be common at lights from February through August, especially after midnight (most frequently between 4:30 and 7:00 AM).

Since the taxonomic status of bees in the genus Megalopta is still in a somewhat chaotic state, the bees discussed in this paper have been labeled as follows and deposited in the Snow Entomological Museum of the University of Kansas. Megalopta centralis from the nest: 1001 Megalopta centralis from the Calathea insignis: 1002 Megalopta centralis from the Solanum on the Osa Peninsula: 1003

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