Observations on Nests of Ceratina in Costa Rica* (Hymenoptera, Apoidea)

by

Charles D. Michener* and Kathleen R. Eickwort**

(Received for publication, August 19, 1966)

This paper is based on observations of seven nests and rearing of young of *Ceratina (Ceratinula)* sp. by K. R. E. and observations on five nests of *C. (Zadontomerus) ignara* Cressin 1878 by C.D.M. These observations provide the first information on nests of the subgenus *Ceratinula* and the only information known to us on nests of neotropical *Ceratina* other than the briet notes by FRIESE (2). Nevertheless, the most significant finding is the similarity between the nesting behavior of the Costa Rican species and that of the previously known species of the genus from North America, Europe, Asia and Australia.

Although at one time considered as parasitic, the nesting habits of the genus, involving provisioning series of cells in pithy stems, were made known by SPINOLA in 1807, and largely verified by DUFOUR and PERRIS in 1840.

Ceratina ignara Cresson

Nests were obtained in an old cofee plantation in a suburb (Los Yoses) of San José, Costa Rica, in March, 1966, and these data are supplemented by collections of specimens from flowers at other dates.

^{*} Contribution N° 1320 from the Department of Entomology, The University of Kansas, Lawrence. The data on *C. ignara* were obtained by C.D.M. thanks to the opportunity to serve as a faculty member for the Organization for Tropical Studies in Costa Rica. The data on the *Ceratinula* were obtained by K. R. E. whose work in Costa Rica was possible thanks to the Organization for Tropical Studies and to the facilities provided by the Instituto Interamericano de Ciencias Agrícolas de la O. E. A. at Turrialba.

^{**} Department of Entomology, The University of Kansas, Lawrence, Kansas.

During March, 1966, an occasional specimen of *C. ignara* was found visiting flowers of *Gomphrena dispersa* (Amaranthaceae). Pollen was being carried on the tibial scopae of females. On March 30 nests were found in erect, dead, dry, pithy weed stalks, all within 10 meters of the patch of *Gomphrena*. The nest burrows entered broken ends of the stalks and had evidently been excavated in the pith by the bees. FRIESE's (2) record of this species (under the synonymous name *cuprea* Friese; for synonymy see MICHENER, 10) and of two species of the subgenus *Calloceratina* nesting in bamboo where they would not excavate their own burrows requires verification in view of our observations and the numerous records of *Ceratina* elsewhere excavating in pith.

The nest excavations of *C. ignara* were straight cylindrical burrows through the pith, 3.0 to 4.0 mm in diameter, 17.0 to 60.0 cm deep. There was no evidence of a constricted entrance or of an enlargement (sentry box) inside the entrance as reported for *C. callosa* (MALYSHEV, 7, 8). Furthermore, there is no evidence of barrel-shaped cells as are sometimes made by *C. chalcites* (PONOMAREVA, 12). In other species whose nests are known, and usually in *chalcites*, the burrow walls are parallel.

Nests being constructed and provisioned were each inhabited by only a single adult female, although several recently emerged adults were present in old nests.

Nests in all stages were found on March 30. One was a burrow 18.0 cm deep with about 4.0 mm of loose pith particles in the bottom. Apparently this was a new nest, being constructed or ready for provisioning of the first cell.

Nest 2, 25.0 cm deep, contained 17 cells, the uppermost in the process of being provisioned, the several lowermost with prepupae, with all growth stages between. Nest 3, 17.0 cm deep, with 12 cells, contained all stages from larvae about two-thirds grown in the upper cells to white pupae with black eyes in the lower cells. About 3.5 mm above the uppermost cell a second partition suggested that the cell series was complete, an idea supported by the considerable age of the youngest larvae. Nest closure of this sort is irregular in the genus; within the same species nest closure may be present or absent, and the last cell may never be closed even though the mother remains in the nest entrance (MALYSHEV, 7; MICHENER, 11). Particularly extensive nest closure is illustrate by GRANDI (4, 5).

Nest 4, 60.0 cm deep, contained nine adults (both sexes) in the otherwise empty upper 36.0 cm of the nest. Below that level the burrows was largely filled (except for some rather large spaces) with a loose mixture of larval feces and pith particles from the intercellular partitions. One adult female was in an empty space obout 42.0 cm from the entrance. Three black pupae were more or less imbedded in the feces-pith mixture at a depth of 37.00 to 40.0 cm. These must have been in the last cells constructed by the mother. Emergence of older (lower) adults and their progress upward in the nest resulted in complete destruction of all cell partitions, but the pupae were in excellent condition with no damage from passage by them of numerous bees. Two of the pupae became adults the next day. Nest 5, 42.0 cm deep, contained six adults (both sexes), no immature stages, and the bottom centimeter of the burrow contained loose feces of larvae and intermixed pith fragments from the broken cell walls. Presumably one or more bees had removed much of the loose material resulting from destruction of cell partitions and mixture of the pith fragments with feces.

Information on cells is from nests 2 and 3. Nest 3 was inhabited by an adult female smaller than any of the others (5.5 mm long compared to 6.5 mm), and cell dimensions are correspondingly smaller; the figures in parentheses below relate to nest 3 while the other figures are from nest 2. Cells were 8.0 to 10.0 (7.0 to 9.0) mm long. There were no double partitions, empty cells, or very long cells as have often been reported in *Ceratina* (MALYSHEV, 7; RA-BAUD, 13; SAKAGAMI and YOSHIKAWA, 15; MICHENER, 11). Partitions dividing the burrow into cells were made of rather loose pith upper surfaces irregularly flat, their lower surfaces commonly concave. (Upper surfaces are concave in some species, see *Ceratinula* below and MICHENER, 11).

The pollen masses consisted entirely of the pale pollen of Gomphrena. Each pollen mass was 7.0 to 8.5 (5.5 to 6.0) mm long, at least twice as long as broad, roughly rectangular with rounded ends, parallel sides, convex on one surface which was more or less against the cell wall. It was not clear whether the pollen mass was supported only at one point, as in *C. callosa* (MALYSHEV, 1913, 1935), or more broadly attached to the wall of the cell. There is a broad longitudinal concavity along the full length of the inner surface, toward the center of the cell. The pollen masses are firm and dry, without the ornate margins found in *C. australensis* (MICHENER, 11); they are less rounded, more rectangular and more concave on the outer surface than in *C. curcurbitana* (GRANDI, 5) and the pollen mass could not possibly be described as semiliquid as has been suggested for certain species by SPINOLA (16), DUFOUR and PE-RRIS (1), and MALYSHEV (7).

The egg was not seen but when small, the larva lies in a vertical position in the lower part of the concavity of the pollen mass. Probably the egg occupies the usual position illustrated by MALYSHEV (7, 8), GRANDI (5), MICH-ENER (11), etc. The larva feeds from the inner, concave surface of the pollen, making the mass thinner. Larger larvae begin feeding from the top of the remaining part of the pollen mass, shortening it. As a large larva feeds, it curls its anterior region down to eat from the top of the reduced food supply, but at all times it is in an essentially head up position. Similar feeding progression is beautifully illustrated by GRANDI (5) and noted by other authors (e.g., MICHENER, 11) for various species. Both GRANDI (3) and TANO (17) have shown that prepupae and pupae may be directed either up or down in their cells. Grandi suggests that the lack of a rigorous orientation mechanism may be possible because the nest burrow is wide enough to allow the bees to turn around. All *C. ignara* seen were head upward.

Feces are first voided when the provisions are perhaps four fifths eaten, and defecation continues until the prepupal stage is attained.

Defecation beofre the end of the feeding stage appears to be characteristic

of the whole genus. The feces are pale yellow, dry, and fall to the bottom of the cell where they accumulate as loose dry material more or less below the food mass, as has also been noted by MALYSHEV (7, 8), but the posterior end of the larva, prepupa and pupa apparently rest on the layer of feces. Feces accumulate, often to a depth of 3.0 mm, in the bottom of a cell.

Arrangement of sexes in the nests seems not to follow the rule common in aculeate Hymenoptera that place their cells in series (males usually in outermost cells), for the three pupae at the bottom of nest 3 included a male, as did the three pupae which must originally have been at the top of nest 4. MALYSHEV (7) found that the lowest cells of C. callosa usually contained males and attributed this to the fact that females begin nests before mating. Above the lowest cells, he found the sexes mixed. TANO (17), however, shows a preponderance of males in cells near the nest entrances in C. flavipes and VERHOEFF's (18) limited data suggest the same thing. Adults emerging low in nests destroy cell partitions above them and escape without harming their siblings in the upper cells, at least if they have reached the pupal stage. Therefore placement of rapidly developing males near the entrances is unnecessary. Destruction of partitions by adults emerging from the bottom of the nest, and survival of prepupae and pupae in spite of such destruction, is well known in the genus, having been reported, for example, by MALYSHEV (7, 8), RAU (14), IWATA (6), and TANO (17). MALYSHEV emphasized the importance of double cell walls (i.c., spaces between cells) in nests of C. callosa to provide space for bees working their way past pupae and destroyed partitions, but in C. ignara similar emergence occurs even though the cells are separated by single walls.

Several cells in nests 2 and 3 contained prepupae of *Ceratina* parasitized by the eulophid, *Aprostocetus americanus* Ashmead. Dr. B. D. Burks, to whom we are indebted for identification of this chalcidoid, writes that this species is widespread as a parasite of *Ceratina* in North America. The mass of mature larvae and later pupae of *Aprostocetus* completely fills the transparent larval cuticle of the *Ceratina*.

As a note it may be added that a larva tentatively identified as a mutillid was found feeding on a pupa of *Ceratina* sp. at Turrialba by K. R. E.

Ceratina ignara has been taken on flowers in San José in June, July, August, November, and March; it seems likely that it is active throughout the year, with no inactive season such as occurs with temperate species of the genus. Several temperate species have shown to have only one generation per year (DUFOUR and PERRIS, 1; MALYSHEV, 7; MICHELI, 9; etc.). In a subtropical part of Australia, however, MICHENER (11) showed trat *C. australens* is starts nests and provisions cells from September to March and postulated that in the tropics the same species reproduces continuously. Continuous reproduction is indicated for *C. ignara* by the finding in March of nests in all stages, and by the presence of abundant pollen on the scopa of females taken in San José in June and August. March is in the dry season; June and August are in the wet. As would be anticipated, there is no evidence of storage of food by overwintering adults such as is observed in temperate areas.

Ceratina (Ceratinula) sp.

This Ceratinula is a feebly metallic species similar in size and appearance to C. (C.) rectangulifera Schwarz & Michener (see MICHENER, 10), with which it agrees in the weak mesepisternal punctation. The female differs from that species in the blackish femora and tibiae, the front tibiae each with a white stripe as in rectangulifera, but the middle and hind tibiae with only limited whitish areas basally instead of large white areas. The male (not known for rectangulifera) has facial markings similar to those of C. zeteki Cockerell. The seventh metasomal tergum is not distinctly bilobed as in zeteki, but is very feebly so, perhaps better described as broadly truncate with the margin of the truncation feebly concave. Voucher specimens are deposited in the Snow Entomological Musseum of the University of Kansas with the hope that when Ceratinula is revised, an accurate identification can be made.

Dry dead stems were collected along a shady bank on the grounds of the Instituto Interamericano de Ciencias Agrícolas de la O. E. A. at Turrialba, Costa Rica. Collections were made principally in the early morning and late afternoon; the stems were then brought into the laboratory and opened there, so that any adult bees in the nests could be captured as the stems were split. For this reason it is impossible to state how the nests are usually oriented. However, on one occasion a female was observed starting an excavation in an erect pithy stem. The bank was overgrown with weeds and tall grasses and was extremely moist due to runoff from the field above.

Seven nests were found from July 26 to August, 3, 1965. They were noteworthy for the very few cells. One contained five cells, one four, but the others had from one to three. Some contained a cell still being provisioned or an egg or small larva and might have been extended to more cells, but one nest of one open cell contained only a large larva and a living adult bee (presumably the mother) in the outer part of the nest burrow. Another nest of one cell contained a pupa but no adult bee. If such small nests are the rule in the species, each female must make several nests, a not unlikely possibility since MALYSHEV (7) records individuals of *C. callosa* making small second nests of one to four cells after provisioning longer series of cells.

The nest excavations were straight, cylindrical burrows through the pith of small stems; the diameter of the burrows was about 2.5 mm. Immature bees of all stages (eggs to pupae) were found but due to the small number of cells per nest, young in any one nest were in about the same stage in spite of rapid growth.

To illustrate the rapid growth, data on the one individual (a female) reared from egg to adult are given, as follows: Cell with egg found July 29; hatched July 31; defecation began August 4; provisions all eaten August 6; pupation August 10; emergence of adult, August 21. Other individuals reared through parts of the growth period progressed at almost identical rates. These observations were made at room temperature which was similar to that of the shaded bank where the nests were found. The 22 days from egg hatching to

adult is somewhat less than the development period of over 25 days for *C. australensis* (MICHENER, 11), and 24 and 28 to 30 days for *C. ferghanica* and *C. chalcites* respectively (PONOMAREVA, 12), but such data probably mean little because of the presumed influence of temperature.

Only one nest had a closure in addition to the partition closing the last cell. Several had an empty space in the burrow below ' the lowest cell. Only in one nest was there an empty space between two cells; in other cases, as in *C. agnara*, a single partition served both to terminate one cell and begin the next.

Cells (eight measurements) ranged from 4.0 to 5.5 mm long. Partitions were 0.5 to 0.75 mm thick, slightly concave on both surfaces (perhaps more noticeably above), therefore thinnest medially. They are formed of bits of pith compactly cemented together and did not disintegrate even after months in alcohol.

The pollen masses, as in other *Ceratina*, are attached to one side of the cell. They are shorter than in other species, little longer than broad, somewhat rectangular but the corners much rounded. In other species they are elongate oval or rectangular (see illustrations of GRANDI, 5; MALYSHEV, 7; MICHENER, 11); PONOMAREVA (12) describes them as brick shaped. They are firm and rather dry in *Ceratinula*. The egg is laid at right angles to the long axis of the cell and principally on the lower part of the pollen mass.

SUMMARY

Ceratina ignara appears to be active and probably provisions nests throughout the year although all the nests studied were found in March. The principal features of the nest that differ from those of certain other species of *Ceratina* are as follows: no very long cells, empty cells or double partitions between cells; partitions concave below, not above; pollen mass firm, concave on outrer surface, with margins not arnate; thickness of pollen mass rather uniform.

The principal features of the nest of *C. (Ceratinula)* sp. that differ from those of certain other species are: very short cell series suggesting construction of two or more nests by each female; no very long cells, few empty cells or double partitions; partitions very thin and slightly concave on both surfaces; polien mass firm, scarcely longer than broad, margins rounded.

RESUMEN

Se describe los nidos y comportamiento de dos especies de *Ceratina* observadas en Costa Rica. *Ceratina ignara* parece mantener su actividad reproductiva todo el año; sus nidos se diferencian de los de otras especies en los aspectos si-

284

¹ "Below" is used for convenience because of the usual orientation of *Ceratina* nests with the entrances upward, although the actual orientation of nests in this species is unknown.

guientes: no tienen celdas muy largas, celdas vacías ni dobles tabiques entre celdas; los tabiques son cóncavos abajo, no hacia arriba; masas de polen firmes, cóncavas exteriormente, de grosor bastante uniforme, de márgenes sin adornos. Los nidos de *C. (Ceratinula)* sp. tienen como caracteres propios los siguientes: celdillas muy cortas, que sugieren la construcción de más de un nido por cada hembra; falta de celdas muy largas y muy pocas celdas vacías o tabiques dobles; tabiques muy delgados y algo cóncavos en ambas caras; masas de polen firmes, escasamente más largas que anchas, de márgenes redondeadas.

LITERATURE CITED

- DUFOUR, L. & E. PERRIS 1840. Mémoire sur les insectes Hyménoptères qui nichent dans l'intérieur des tiges sèches de la ronce. Ann. Soc. Entom. France, 9: 5-53.
- 2. FRIESE, H.
 - 1925. Neue neotropische Bienenarten, zugleich II. Nachtrag zur Bienenfauna von Costa Rica (Hym.). Stettiner Entomol. Ztg., 36(2): 1-141.
- 3. GRANDI, G.
 - 1935. Contributi alla conosenza degli imenotteri aculeati XV. Boll. Inst. Entomol. R. Univ. Bologna, 8; 27-121, pls. I-IV.
- 4. GRANDI, G.
 - 1957. Contributi alla conoscenza degli imenotteri aculeati XXVII. Boll. Inst. Entomol. Univ. Bologna, 22: 307-398.
- 5. GRANDI, G.
 - 1961. Studi di un entomologo sugli imenotteri superiori. Boll. Inst. Entomol. Univ. Bologna, 25: xv+1-659.
- 6. IWATA, K.
 - 1938. Habits of some bees in Formosa, III (Ceratina). Trans. Nat. Hist. Soc. Formosa, 28: 257-262 (in Japanese).
- 7. MALYSHEV, S. I.
 - 1913. Life and instinct of some Ceratina-bees (Hym., Apidae), a comparative and experimental study. Horae Soc. Entomol. Rossicae, 40(8): 1-58, pl. 1.
- 8. MALYSHEV, S. I.
 - 1935. The nesting habits of solitary bees (a comparative study). Eos, 11: 201-309, pls. III-XV.
- MICHELI, L.
 1936. Note biologiche e morfologiche sugli Imenotteri (IV serie). Atti Soc. Ital. Sci. Nat. Mus. Civico Storia Nat. Milano, 75: 5-16.
- 10. MICHENER, C. D. 1954. Bees of Panamá. Bull. Am. Mus. Nat. Hist., 104: 1-176.

- 11. MICHENER, C. D.
 - 1962. The genus Ceratina in Australia with notes on its nests (Hymenoptera: Apoidea). J. Kansas Entomol. Soc., 35: 414-421.
- 12. PONOMAREVA, A. A.
 - 1958. Nesting habits of certain species of higher bees (Hymenoptera, Apoidea) in south-western Turkmenistan. Entomol. Obozrenie, 37: 616-629 (in Russian).
- 13. RABAUD, E.
 - 1923. Sur la n'dification de Ceratina callosa F. Ann. Soc. Entomol. France, 91: 277-280.
- 14. RAU, P.
 - 1928. The nesting habits of the little carpenter-bee, Ceratina calcarata. Ann. Entomol. Soc. Am., 21: 380-396, pl. xxvii.
- 15. SAKAGAMI, S. F. & K. YOSHIKAWA
 - 1961. Bees of Xylocopinae and Apinae collected by the Osaka City University Biological Expedition to Southeast Asia 1957-58, with some biological notes. Nat. Life S.E. Asia, 1: 409-444.
- 16. Spinola, M.
 - 1807. Mémoire sur les moeurs de la Ceratine albilabre. Ann. Mus. Hist. Nat. [Paris], 10: 236-248.
- 17. TANO, T.
 - 1964. Biology of Ceratina flavipes Smith. Life Study [Fukui, Japan], 8(1): 1-6 (in Japanese).
- 18. VERHOEFF, C.
 - 1891. Biologische Aphorismen über einige Hymenopteren, Dipteren und Coleopteren. Verhandl. Naturbist. Ver. Preussischen Rheinlande u. Westfalens [Bonn], Jahrg. 48, 8: 1-80.