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OBSERVATIONS ON THE NESTING BEHAVIOR OF WASPS OF THE TRIBE CERCERINI[1]

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ABSTRACT

Data on the nesting behavior of the following species are presented: *Cerceris fumipennis* Say, *C. echo* Mickel, *C. crotonella* Viereck and Cockerell, *C. r. robertsonii* Fox, *C. halone* Banks, *C. n. nigrescens* Smith, *C. atramontensis* Banks, *C. b. bicornuta* Guérin, *C.* (*Didesmus*) *binodis* Spinola, and *Eucerceris zonata* (Say). The larva of *E. zonata* is described. It is concluded that all Cercerini are very similar in their nesting behavior but that host-specificity is marked, in many cases permitting several species to nest side-by-side without competing for limited food resources.

Cercerine digger wasps have attracted the attention of students of insect behavior particularly because of the relatively high degree of host-specificity exhibited by most species. Scullen and Wold (1969) have reviewed much of the literature on the North American species. From time to time, in the course of studies of other wasps, I have collected data on various species of Cercerini, and I now feel that despite the desultory nature of these observations I can add a number of significant facts to current knowledge of the tribe. The following points are of particular interest:

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[1] Hymenoptera: Sphecidae. Accepted for publication May 23, 1971.

[2] Many of these studies were conducted while the author was in residence at the E. N. Huyck Preserve, Rensselaerville, Albany Co., N. Y., during the summer of 1970.

1. Considerable new information is presented on the well-studied *Cerceris fumipennis*, including details of nest structure, cell size as correlated with sex of offspring, and data on parasites and inquilines.

2. Beetles of the family Phalacridae are reported as prey of *Cerceris* for the first time, having been taken from nests of both the eastern and western subspecies of *C. echo*.

3. A record is presented of *C. crotonella* preying on a beetle of the family Nitidulidae. This record and the preceding increase the number of families known to be utilized by North American *Cerceris* from 5 to 7.

4. A striking instance of competitive exclusion among species preying upon weevils is presented.

5. The nesting behavior of a species of *Didesmus* is reported for the first time. This group is variously ranked as a full genus, a subgenus of *Cerceris*, or no more than a species-group of that genus.

6. The nesting behavior of *Eucerceris zonata* is reported for the first time, and the larva of this species is described. This is the only representative of its genus in eastern United States.

The wasps were identified by Herman A. Scullen or by myself with the aid of Scullen's keys. Professor Scullen also brought the prey records for *Cerceris echo echo* and *C. crotonella* to my attention. Beetles were identified by several persons, as indicated in the text. Specimens of wasps, prey, and parasites, as well as my field notes, have been placed on permanent file at the Museum of Comparative Zoology, Harvard University.

Cerceris fumipennis Say

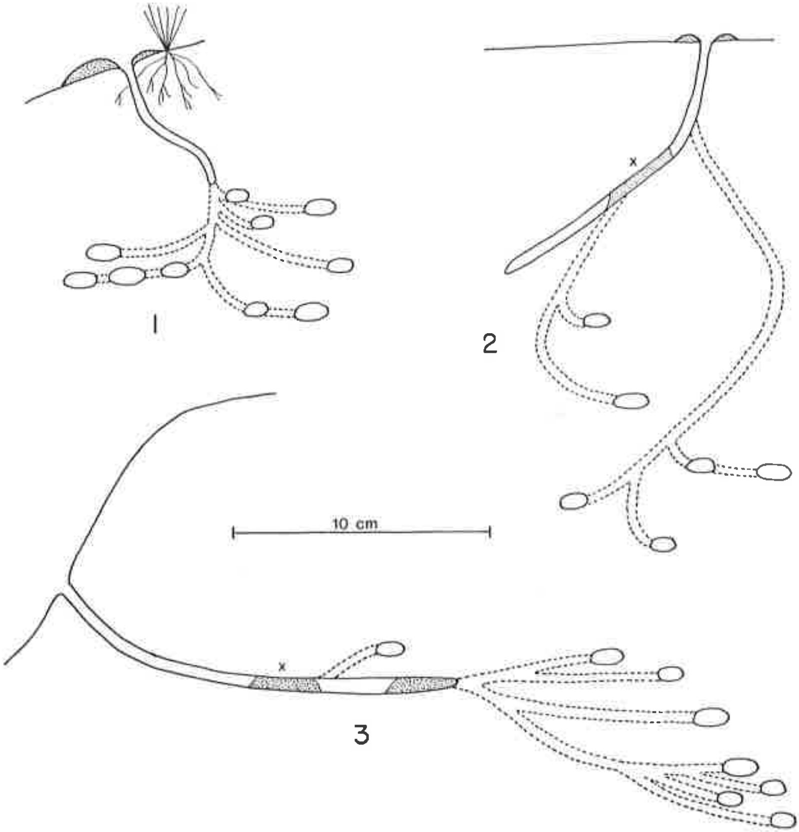
This species has a remarkably broad range, and I have studied it in localities as widely separated as Florida, New York, and Wyoming. Most of the published references have been listed by Scullen and Wold (1969) and I shall not attempt to review previous research. Those aspects of my studies that merely confirm previous work I shall cover very briefly; new data will be discussed in more detail. Although *C. fumipennis* nests in places where there is a considerable expanse of bare soil surrounded by trees or bushes where buprestid beetles are plentiful, there is much variation in the nature of the substrate: fine-grained, friable sand or hard-packed sandy clay or gravel seem equally acceptable. Nests usually occur on flat or nearly flat soil, but one nest in a vertical bank is described below. As usual in this genus, freshly dug nests have a circular mound of soil at the entrance, the vertical entrance burrow passing through its center and left open while the female is provisioning.

I first encountered this species in Arkansas Co., Ark., on June 9, 1956, when several females were seen carrying beetles into nests in friable sand along the Arkansas River (note no. 1158). One nest was excavated and found to have a vertical burrow in which four beetles had been stored at a depth of 10–13 cm. Five cells were found at depths of from 13 to 17 cm. Two contained 3–5 large buprestids, one contained 7 mostly smaller buprestids, and one contained 15 small ones; the fifth cell contained a large larva that had eaten the prey. One cell contained an egg laid longitudinally on the venter of the top beetle. The following beetles were represented in the numbers indicated: *Dicerca spreta* Gory (1), *Cinyra gracilipes* Melsh. (12), *Chrysobothris azurea* Lec. (1), *C. purpureavittata* Horn (1), *C. sexsignata* (Say) (1), *Agrilus politus* Say (4) [det. H. Dietrich].

I next discovered several females nesting on a baseball diamond at Versailles, Indiana, where my studies of *Bembix nubilipennis* were conducted (Evans, 1966). From July 17 to 23, 1957, about ten nests were found in very hard-packed soil, well dispersed about the playing field and intermingled with nests of *Bembix* and *Astata* (note nos. 978, 1464). The prey here consisted of rather large buprestids, mainly *Dicerca caudata* Lec., but including at least one *Chrysobothris adelpha* Germ. and Hald. [det. J. N. Knull]. Only 3 such buprestids were used per cell (3 records). The one nest excavated had a vertical burrow 9 mm in diameter which soon became more oblique and led to a group of 5 cells at depths of from 11 to 15 cm. The cells were horizontal and smooth-walled, measuring 9 × 16 mm in size. The egg, about 4.5 mm long, was found to be laid longitudinally on the venter of the top beetle, attached near the second pair of coxae and reaching to the head.

My third encounter with *C. fumipennis* was in a parking lot at Highlands Hammock State Park, near Sebring, Fla., May 12–23, 1961 (note nos. 1697, 1731). Here I was working on *Stictia carolina* and *Bembix texana*, studies reported in my book on sand wasps (Evans, 1966), where a photograph of this site is presented (Fig. 128, p. 227). Each nest entrance was surrounded by the usual rim of soil, and it was again found that freshly collected beetles were stored in the burrow (15–16 cm deep) before being placed in a cell. I observed one female being tailed closely to her nest by a miltogrammine fly, *Senotainia trilineata* Wulp. In another instance I observed a copulating pair of *Cerceris* on the ground, the male straddling the female, who was carrying a beetle. The following beetles were used as prey in this locality (all Buprestidae): *Buprestis lineata* Fabr. (1), *B. rufipes* (Oliv.) (1), *Chrysobothris femorata* (Oliv.) (2), *C. blanchardi* Horn (2), *Dicerca lurida* (Fabr.) (1), *D. punctulata* (Schön.) (3) [det. J. N. Knull].

On August 7, 1964, I discovered four females nesting near the other extremity of the range of the species, but behaving much as usual. This was on the rim of a mud pot at Imperial Geyser, in Yellowstone National Park, Wyoming. The nests were in fairly moist powdered geyserite, each near the base of a tuft of grass in slightly sloping soil



Figs. 1–3. Representative nests of *Cerceris fumipennis*, shown in side view as if all cells were in one plane. Burrows shown as dashed lines are hypothetical, as they had been filled and could not be traced. Points at which beetles were stored in the burrow are shown by "x." Fig. 1, nest 2036B, Yellowstone Nat. Park, Wyoming. Fig. 2, nest H26, near Albany, N. Y. Fig. 3, nest H50, near Rensselaerville, N. Y.

(note no. 2036). Three of the nests were excavated, and a sketch of one of these is presented here (Fig. 1). In each nest the burrow, about 1 cm in diameter, penetrated the soil perpendicularly to the slope, then tended to level off 4–8 cm deep. One nest had two cells when excavated, another 5, and another 10; the cells were in every case very shallow, from 7 to 12 cm deep. It was in these nests that I first became aware that cells and cocoons were of two sizes: small cells, about 12 × 20 mm, usually containing about 4 beetles, and eventually containing a cocoon

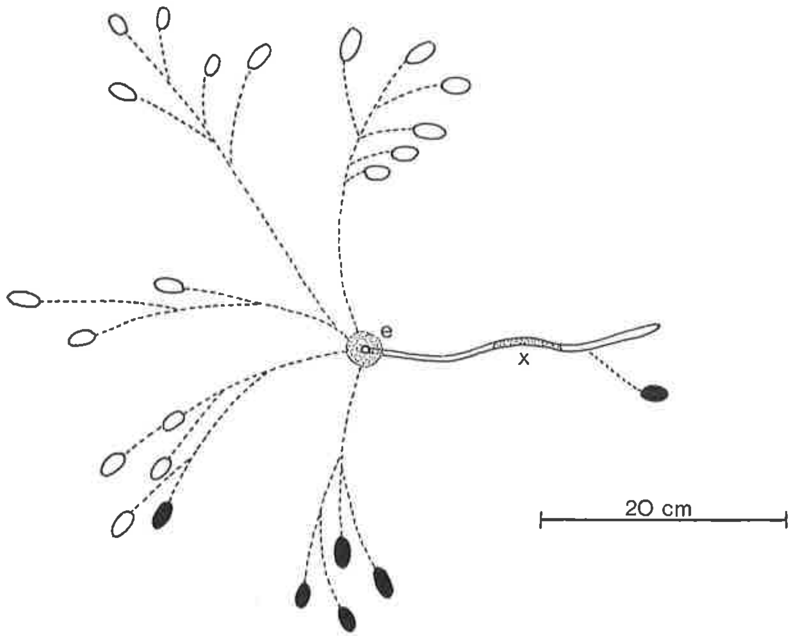


FIG. 4. Nest of *Cerceris fumipennis*, plan view, no. H55, near Rensselaerville, N. Y. Cells shown as solid black were recently made and contained an egg or larva; others were older cells, mainly with cocoons. X = point at which beetles were stored in the burrow; e = entrance of nest. Burrows shown as dashed lines were filled and could not be traced; hence these burrows are hypothetical.

about 14 mm long; and large cells, measuring about 12 × 30 mm, usually containing about 8 beetles, and eventually containing a cocoon 20–24 mm long. I studied this phenomenon further in the summer of 1970 at Rensselaerville, N. Y. (see below).

Storage of beetles in the burrow and oviposition on the venter of the topmost beetle in each cell were confirmed at this locality. One cell contained decomposing beetles, another several ants, *Solenopsis truncorum*, evidently feeding on beetle remains. All of the beetles found complete in cells or as fragments surrounding cocoons appeared to belong to the genera *Buprestis* and *Chrysobothris*. The following species were identified: *B. intricata* Casey, *C. blanchardi* Horn, *C. breviloba* Fall, *C. monticola* Fall, and *C. trinervia* (Kby.) [det. J. N. Knull].

In the summer of 1970 (July 17), a single nest was found in moderately compact sand having a hard surface crust, just west of the city of Albany, N. Y. (no. H26). A sketch of this nest is included here (Fig. 2). There were four beetles stored in the burrow, 6 cm deep.

The six cells formed a somewhat radial pattern from the burrow; they varied in depth from 11 to 22 cm. One of the cells contained a large dipterous maggot (not reared successfully), while three contained decomposed beetles. Another cell contained an egg on the topmost of ten beetles, the remaining cell a fresh cocoon. All the beetles employed were small Buprestidae: *Agrilus a. arcuatus* (Say) (4), *A. arcuatus fulgens* Lec. (1), and *Brachus ovatus* Web. (9) [det. J. N. Knull].

Near the village of Rensselaerville, 35 miles southwest of Albany, N. Y., *Cerceris fumipennis* nested in abundance at two different man-made gravel pits during the summer of 1970. At Snyder's Corners, 2 miles northwest of Westerlo and about 5 miles east of Rensselaerville, some 12 nests were active from July 18 through August 24 (note nos. H28, 29). On the property of O. Harry Olson, 2 miles south of Rensselaerville, at least 30 nests were active over the same period (note Nos. H37, 50, 55, 56, 79). In both cases the soil was a hard-packed sandy gravel, difficult to dig in with a trowel. Most nests were in flat soil, but one was near the top of a steep bank (H50; Fig. 3). Most nests were clustered, from 2 to 10 nests within a m^2, with some nest entrances only 4–10 cm apart. However, seven nests excavated were isolated nests, chosen so that the pattern of cell construction could be deduced without the possibility of confusing the cells of neighboring nests. In addition, one massive excavation was made of 7 nests clustered in approximately 1 m^2 (H79).

Each nest persisted through the season and had a single female associated with it; in no case were any new nests begun after the third week in July. Three nests excavated early in the season (July 18–22) each had four cells; two nests dug during the last week in July had 6–8 cells; while one nest dug on August 2 had 24 cells, possibly close to the maximum for this species. The simultaneous excavation of 7 clustered nests on August 19 yielded 95 cells (or 13.5 per nest), but some cells were almost certainly overlooked. In this excavation the nests varied in depth from 8 to 20 cm, but in the individual nests dug out earlier, the cells were in each case of roughly the same depth, e.g., 14–18 cm in the 24 cells of nest H55. In every nest the burrow was at first vertical, then became oblique or horizontal a few cm deep; the beetles were typically stored near the beginning of the oblique portion, 10–14 cm from the entrance. In a mature nest the cells form a somewhat radial pattern with respect to the nest entrance. Evidently only the more vertical, initial part of the burrow is permanent; this is extended obliquely or horizontally in one direction and several cells constructed from it, these cells often only 2–5 cm apart; after construction of 4–6 cells this section is closed off and a new oblique or horizontal burrow constructed in a different direction (see especially no. H55, Fig. 4). From time to time during the season, females push fresh soil from the entrance, restoring the circular mound at the entrance; these bouts of digging doubtless occur when the burrow is being extended in a new direction.

The one nest found in a steep bank (H50, Fig. 3) was near several in flat soil above the bank. In this instance there was no mound at the entrance, doubtless as a result of erosion. The burrow was at first perpendicular to the slope of the bank, then became horizontal. All the cells but one were fairly closely clustered beyond and below the end of the burrow. As in all nests excavated, the cells in any given cluster showed no particular pattern with respect to age; that is, there was no evidence that females made cells progressively deeper in the soil or progressively back toward the entrance.

In this firm but coarse soil, the smooth-walled cells stood out clearly, and it was again apparent that cells were of two sizes; large cells 25–30 cm long and small cells approximately 20 mm long (in both cases 9–10 mm in diameter). When provisioned with large buprestids (*Dicerca*), large cells typically contained 4, small cells 2; when provisioned with *Agrilus*, large cells contained 16–32, small cells 8–12. Large cells also eventually contained notably larger larvae that made larger cocoons. In any given nest, large and small cells appeared to be intermingled; that is, there was no evidence that the females made a series of large cells followed by a series of small ones, or vice versa.

Since many cells were broken into before they could be accurately measured, and since many cells contained cocoons when excavated, it was easier to obtain data on cocoon size than on cell size. The large excavation of seven clustered nests (H79) was made primarily to obtain as many cocoons as possible and to determine if cocoon size was indeed clearly bimodal. I obtained 71 cocoons, of which 34 were "small" (12–20 mm) and 37 "large" (20–30 mm), with a fairly distinct bimodal distribution (solid line in Fig. 5). It seemed probable that the small cocoons would produce males and the large ones females. The female *C. fumipennis* is considerably larger than the male, and there is relatively little overlap in size (dashed lines in Fig. 5). I reared the large and small cocoons separately, but as a result of an error in technique only four wasps emerged the following spring. These were all males, wing length 8.0–9.3 mm, and they emerged from cocoons 13–15.5 mm in length. Although a fuller confirmation had been hoped for, the evidence is reasonably clear that males and females are produced from cells of different size and containing differing amounts of prey. Evidence from this large excavation and from several individual nests suggests that males and females are produced in approximately a 1:1 ratio in this species.

Production of females in larger cells containing more prey is well established for twig-nesting wasps (Krombein, 1967) and is probably common in ground-nesters, though it has been clearly demonstrated only in *Sphecius speciosus* (Dow, 1942). *Cerceris* would seem an especially suitable genus in which to study this phenomenon further.

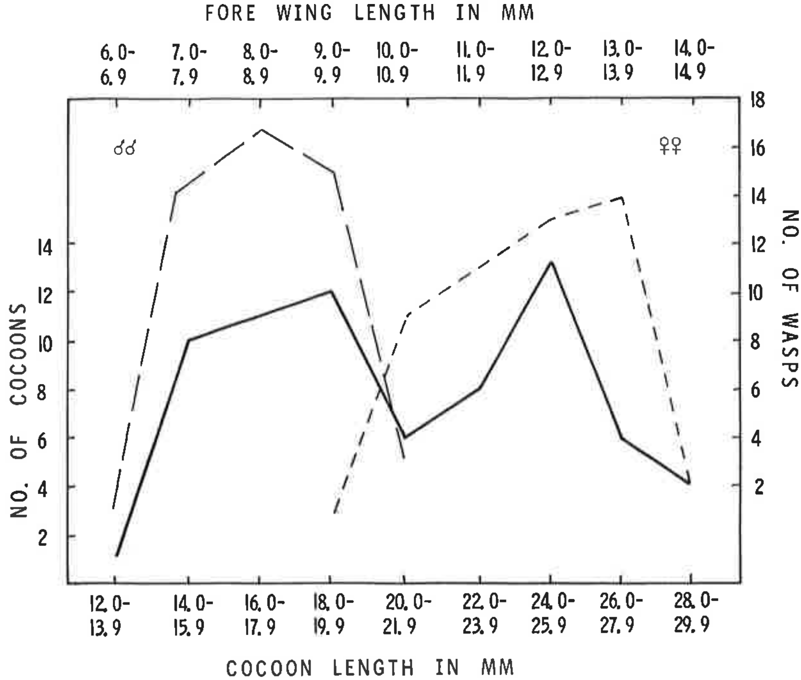


FIG. 5. Solid line: number of cocoons in various size categories from a sample excavation of several nests (H79) of *Cerceris fumipennis* (scale at left and bottom). Dashed lines: size (in fore wing length) of 50 male and 50 female *C. fumipennis* selected at random from diverse localities; long dashes: males, short dashes: females (scale at top and right).

There are, of course, some ground-nesters in which the males are about the same size as the females or even, on the average, somewhat larger (some Bembicini). In the latter case one would expect males to be produced in slightly larger cells. The mechanism and significance of this behavior are poorly understood.

In the course of these studies I took 310 beetles, all Buprestidae, from *C. fumipennis* nests in the vicinity of Rensselaerville. The majority of nests contained nothing but small species, chiefly *Agrilus*, and the use of the larger buprestids was mainly confined to a few females that took them in considerable numbers. Several *Dicerca divaricata* were found lying outside nest entrances (although *Agrilus* never were), suggesting that these beetles, which are actually larger than the wasps, sometimes cannot be taken successfully through the entrance hole. The following is a complete list of prey taken from nests in this locality, with the numbers of each taken [determinations by J. N. Knull].

Dicerca caudata Lec.	12
Dicerca divaricata (Say)	7
Dicerca lurida (Fabr.)	13
Poecilonotus cyanipes (Say)	9
Chrysobothris femorata (Oliv.)	1
Chrysobothris sexsignata (Say)	2
Eupristocerus cogitans (Web.)	2
Melanophila fulvoguttata (Harr.)	1
Brachus ovatus Web.	1
Agrilus anxius Gory	10
Agrilus arcuatus arcuatus (Say)	12
Agrilus arcuatus fulgens Lec.	1
Agrilus arcuatus torquatus Lec.	158
Agrilus bilineatus carpini Knull	1
Agrilus obsoletoguttatus Gory	29
Agrilus ruficollis (Fabr.)	1
Agrilus spp. (not identified)	50

On several occasions females were seen to be followed to their nests by miltogrammine flies, *Senotainia trilineata* (Wulp). However, the incidence of successful attacks appeared to be low. Of 52 cells in 7 separate nests excavated, only one contained an active maggot; 5 others contained beetle remains that may have been consumed by maggots, and 5 others contained molded contents. All of the other 41 cells contained viable eggs, larvae, or cocoons. The one maggot gave rise to a fly the following spring, a male *Phrosinella fumosa* Allen.

While excavating one nest (no. H50) I noted two rather large, pale mites in a cell with an apparently healthy, nearly full-grown larva. I failed to take these mites, but remembering that the European *Vidia concellaria* Cooreman is reported to be an obligate inquiline in the nests of *Cerceris arenaria* (Cooreman and Crèvecoeur, 1948), I made an effort to find mites in other nests. I was not notably successful, but one of the 95 cells found in my large excavation (H79) did contain three mites, again in a cell with a large larva. I examined all of the 71 cocoons collected under the microscope, and in the beetle fragments surrounding one of them I found several minute, immature mites. These mites were identified by Dr. George Eickwort of Cornell University as *Vidia* (*Crabrovidia*) n. sp., adult females, protonymphs, and hypopi. It appears that this mite has a life cycle very much like *Vidia concellaria.* That is, the mites reach maturity in the wasp's cell, feeding on pieces of the prey, but not harming the wasp larva; they oviposit here, and the newly hatched nymphs conceal themselves in the debris surrounding the cocoon; when the wasp emerges from the cocoon they attach themselves and in this way eventually reach a fresh cell, where they grow rapidly and reach adulthood in a few days. At least, what little is known of these mites is consistent with this pattern.

Cerceris echo Mickel

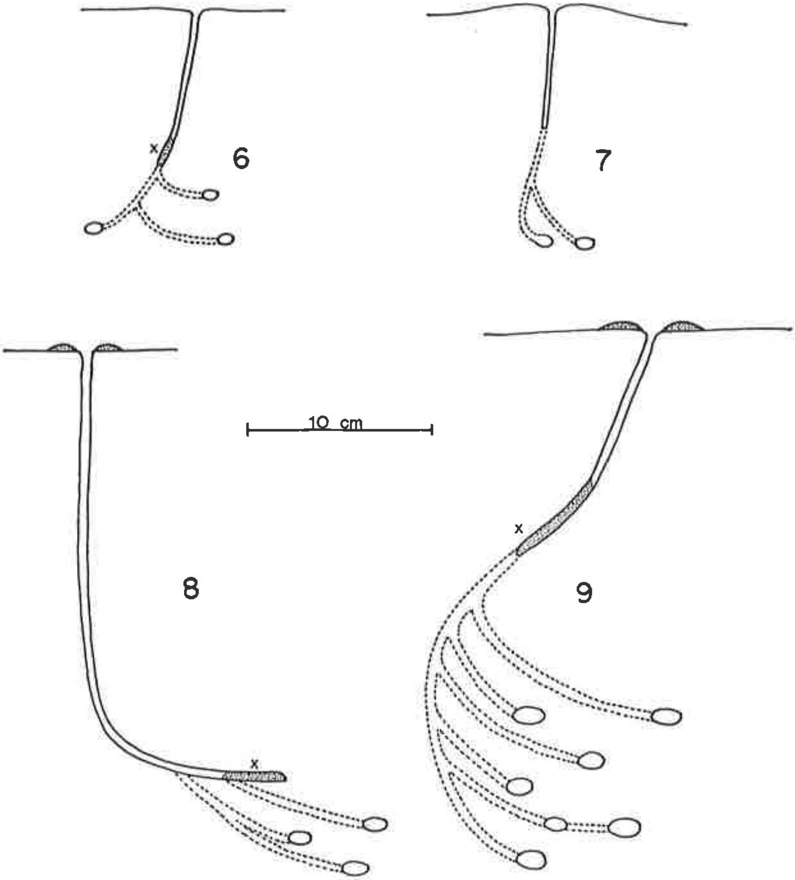
This small wasp is a member of Group I of Scullen (1965), a group of relatively diverse prey preferences, some species taking Curculionidae, others Chrysomelidae, and at least two taking Bruchidae. *C. echo* is the first member of the genus to have been found to prey upon shining flower beetles, Phalacridae. Records presented here apply both to typical *echo*, of western distribution, and to the eastern *echo atrata* Scullen, thus supporting the subspecific status of the latter form. It is interesting that this species resembles *C. rufinoda* so closely that the males cannot be distinguished; yet the latter species preys on weevils.

I first discovered *C. echo atrata* nesting on August 30, 1968, in bare, flat, fine-grained sand at Lexington, Mass. (note no. 2189). This nest contained 7 beetles that had been stored in the bottom of a vertical burrow, 6 cm deep. Six of these were *Olibrus* sp., a beetle only about 1 mm long, and the seventh was a slightly larger beetle, *Phalacrus* sp. [all Phalacridae; det. J. F. Lawrence]. Three cells were found somewhat below this, at depths of from 9 to 13 cm; each contained a cocoon surrounded by fragments of phalacrid beetles, almost all *Olibrus* sp. An effort was made to count the beetles adhering to one of the cocoons, and it was concluded that about 30 had been supplied in that cell. Specimens of *Olibrus* similar to those found in the nest were swept from flowers of goldenrod (*Solidago* sp.) in the vicinity, and it seems probable that the wasps were capturing them there.

A sketch of this nest is included here (Fig. 6), although it is probable that some of the cells were overlooked, as none were found containing eggs or larvae in what was obviously an active nest (the female was provisioning and was taken as she left the nest). The cells were very small, measuring only 6 × 9 mm. There was no mound at the entrance, and this apparently isolated nest was discovered only because intensive observations were being made on nests of *Philanthus lepidus* close beside it.

A second nest was discovered a year later (Aug. 17, 1969) about 4 m away, again in flat, fine-grained sand (note no. 2223; Fig. 7). Again there was no mound at the entrance, merely a vertical hole in a slight elevation. At a depth of 15 cm there were 9 phalacrid beetles, either stored in an incompletely provisioned cell or in the bottom of the burrow; two cm away and at the same depth there was a small cell containing a newly hatched larva and 39 phalacrid beetles. The 48 beetles all proved to be *Olibrus neglectus* Casey (Phalacridae) [det. J. M. Kingsolver].

The record for *C. echo echo* is based on specimens collected by Morteza Esmaili at Cornish, Utah, on July 27, 1963, and sent to H. A. Scullen for study. Dr. Esmaili observed a female carrying small beetles into a nest in open sand. He took the wasp and dug out the nest, finding



FIGS. 6–9. Nests of three species of *Cerceris*, shown in side view as if all cells were in one plane. Burrows shown as dashed lines are hypothetical, as these sections had been filled firmly. Points at which beetles were stored are shown by "x." Fig. 6, nest of *C. echo atrata*, no. 2189, Lexington, Mass. Fig. 7, nest of *C. echo atrata*, no. 2223, Lexington, Mass. Fig. 8, nest of *C. r. robertsonii*, no. H19, Colonie, N. Y. Fig. 9, nest of *C. halone*, no. 1852, Lexington, Mass.

13 beetles at the bottom of a short burrow. The beetles were all similar and were identified by G. B. Vogt as *Phalacrus* sp. (Phalacridae).

Cerceris crotonella Viereck and Cockerell

This small species also belongs to Scullen's Group I and is closely related to *echo*. It is therefore of interest to present a record of predation on still another family of beetles: Nitidulidae. This record is based on a specimen collected by J. E. Gillaspy on April 23–30, 1963, 1 mile west of Lajitas, Brewster Co., Texas. The wasp is pinned with the beetle *Carpophilus pallipennis* (Say) [det. J. M. Kingsolver] and bears the note "wasp caught beetle on *Opuntia* blossom."

Cerceris robertsonii robertsonii Fox

Scullen (1965) places this in his Group III, the members of which, so far as known, prey on Chrysomelidae. I shall present only a few notes here, as this form as well as the Floridian *C. robertsonii emmiltosus* Scullen have been well studied by Krombein (1953a, 1953b, 1964).

Several years ago I found three nests of this species at Ithaca, N. Y. (nos. 1113, 1574) and described larvae from one of these (Evans, 1957, 1959). The nests were found in rather coarse sandy gravel in July and August, 1955 and 1958. All three were provisioned exclusively with *Rhabdopterus picipes* Oliv., the cranberry rootworm (about 20 specimens) [det. H. Dietrich]. Beetles were stored in the burrow, as usual in this genus; cells measured 8 × 20 mm and varied in depth from 20 to 30 cm.

I encountered this species again on July 7, 1970, in an extensive artificial sandpit in Colonie, N. Y. (no. H16). There were several nests in flat, fine-grained sand, each with a mound about 7 cm across pierced by a vertical burrow. One nest was excavated and is illustrated here (Fig. 8). There were 6 beetles stored in loose soil at the bottom of the burrow, 23 cm deep. The three cells were from 25 to 27 cm deep. One fully provisioned cell contained 8 beetles and had an egg longitudinally on the venter of the top beetle. In all, 18 beetles were taken from the nest, and all proved to be *Tymnes tricolor* Fabr. (Chrysomelidae) [det. J. Wilcox].

Cerceris halone Banks

This and the following three species were all listed as "Ungrouped Species" by Scullen (1965). All four species are known to prey on Curculionidae, and the records presented here confirm this fact. *C. halone* has been well studied by Byers (1962) and others and my notes on it will be brief. This is a common species in the Boston area during September. I excavated two nests in Lexington, Mass., September 16–23, 1962 (nos. 1851, 1852), and two in Bedford, Mass., September 21–25, 1970 (nos. 2230, 2232). Three nests were in fine-grained, friable sand, but one was in coarse, hard-packed sandy gravel. Mounds at nests entrances were conspicuous and measured about 6 cm across. Weevils were stored in the burrow at depths of 7–8 cm, but the cells were much deeper (17–29 cm). A sketch of a 7-celled nest is included here (Fig. 9). All the weevils from these nests, as well as several others taken from provisioning females (57 in all) belonged to the genus *Curculio*, including *C. sulcatulus* (Casey) (12 records) and *C. proboscideus* Fabr.

(7 records) [det. R. E. Warner]. All previous records for *C. halone* involve weevils of this same genus; they are from localities as diverse as Virginia, Minnesota, and Illinois.

Cerceris nigrescens nigrescens Smith

This common eastern species has also been studied by Krombein (1936, 1938), who found it preying upon weevils of the genera *Hyperodes*, *Sitona*, and *Gymnaetron*. I found several females nesting at Bedford, Mass., in hard-packed, stony, sandy loam within the limits of a nesting aggregation of *Philanthus gibbosus*. Females were seen arriving at their nests flying low, only 3–6 cm high, carrying small weevils in their mandibles, and requiring only 5–10 minutes for each hunting trip. Each nest was surrounded by a small rim of soil, about 3 cm across. Burrows were vertical, but as usual tended to level off a few centimeters down. A nest excavated August 15, 1969 (no. 2220), had two weevils stored in the burrow at a depth of 7.5 cm; there was one cell at 10 cm containing 23 weevils and an egg. Of the 25 weevils, 22 proved to be *Calomycterus setarius* Roelofs and 3 *Sitona scissifrons* (Say) [det. R. E. Warner]. A nest excavated September 17, 1970 (no. 2225), had two cells, both at 10 cm depth; one contained 14 weevils and an egg, the other 16 weevils and a small larva. The 30 weevils from these two cells, plus one other taken from another female, all proved to be *Sitona hispidula* (Fabr.) [det. R. E. Warner].

The four genera of weevils reported as prey of this species are diverse taxonomically, but all are superficially similar and probably occur in much the same habitat. *Sitona hispidula*, the clover root curculio, apparently constitutes the major prey in several localities. Adults of this and other species of *Sitona* feed on the leaves and stems of clover and related legumes.

Cerceris atramontensis Banks

I located one nest of this species on September 17, 1970 (no. 2226), only 1.5 m from one of the *nigrescens* nests described above. The burrow was vertical and close to the base of a tuft of grass. Four weevils were found in the burrow at a depth of only 3 cm. I was unable to trace the burrow further because of the many stones in the soil. The weevils proved to be *Conotrachelus posticatus* Boh. [det. R. E. Warner].

At this particular locality three species of *Cerceris* nested within the limits of a *Philanthus gibbosus* colony in an area about 2 × 4 m, for one of the *C. halone* nests reported above (no. 2232) was also located here. Each species restricted itself to one particular complex of weevils, and records from other areas indicated that these differences in prey preference persist elsewhere. In the case of *atramontensis*, there are records from New Hampshire and Virginia for the use of weevils of the genus *Conotrachelus* (Scullen and Wold, 1969). There is also a series in the collections of the Museum of Comparative Zoology, taken in Reading, Mass., in July, 1931, by Richard Dow. Pinned with the wasps, as prey, are 27 specimens of *Conotrachelus nenuphar* Hbst., 1 *C. anaglypticus* Say, and 5 *Hyperodes sparsus* Say.

Cerceris bicornuta bicornuta Guérin

Scullen and Wold (1969) list many prey records for this species, all for the genus *Sphenophorus* (= *Calendra*), from localities as diverse as New York, the Carolinas, Ohio, and Missouri. Specimens in the Museum of Comparative Zoology indicate that weevils of this genus also are utilized as prey in Connecticut; Richard Dow collected a series at Old Saybrook in August, 1937, with the following: 16 *Sphenophorus cariosa* (Oliv.), 9 *S. venatus* (Say), and 1 *S. zeae* (Walsh) [det. Satterthwait]. All three species have been reported as prey in other localities.

Cerceris (*Didesmus*) *binodis* Spinola[3]

On June 1, 1959, I discovered 5 females of this wasp nesting in a hillside 3 miles north of Taxco, Guerrero, Mexico (no. 1604). The nests were in an area about 2 m^2 in an opening among short *Acacia* trees. The soil consisted largely of pulverized limestone, and was sparsely covered with short grass. Although the soil was hard and chunky on the surface, below 15 cm it was somewhat moist and of more uniform texture. Each nest had a high rim of fresh soil at the entrance, the burrow penetrating the center of the mound.

Females arrived at their nests carrying prey well forward beneath them, probably holding it with their mandibles. Each female descended slowly, making a humming sound, then dropped directly into the open nest entrance. As soon as she entered, the entrance was closed from the inside and left closed as long as the wasp remained in the nest.

I took two beetles from provisioning females and found 31 beetles in the one nest I excavated. All were Chrysomelidae, and all but two were of one species, *Anomoea mutabilis* Lac., a beetle common on *Acacia* in the vicinity. The remaining two each belonged to a different species, 1 *A. sphacelata* Lac. and 1 *Coscinoptera mucida* (Say) [det. D. M. Weisman].

The nest is shown in Fig. 10. The burrow was open for 20 cm, reaching a storage area where 5 beetles were found in loose soil. There were 3 cells, separated by 6–10 cm, varying in depth from 28 to 30 cm. The cells were ovoid and smooth-walled, measuring 12 × 18 mm. The beetles were packed in them tightly, venter-up, 8 or 9 beetles per cell. The egg was 4 mm long and was laid somewhat obliquely on the venter of one of the topmost beetles in the cell (Fig. 12).

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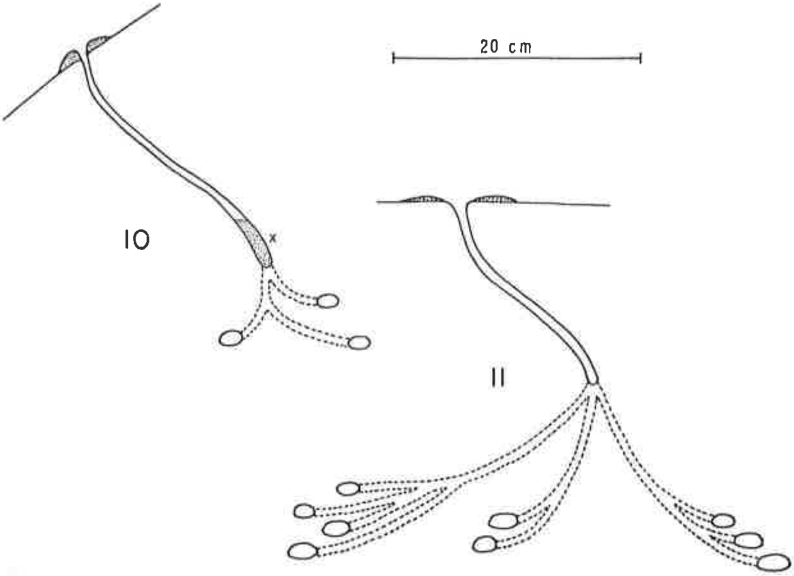
[3] Professor Scullen regards *Didesmus* as a genus separate from *Cerceris*, but others regard it as a subgenus or merely a species-group of *Cerceris*.



FIGS. 10–11. Nests of Cercerini, shown in side view as if all cells were in one plane. Burrows shown as dashed lines are hypothetical, as they had been filled and could not be traced. "X" indicates a point at which beetles were stored in the burrow. Fig. 10. *Cerceris* (*Didesmus*) *binodis*, nest no. 1604, near Taxco, Mexico. Fig. 11. *Eucerceris zonata*, nest no. H93, near Westerlo, New York.

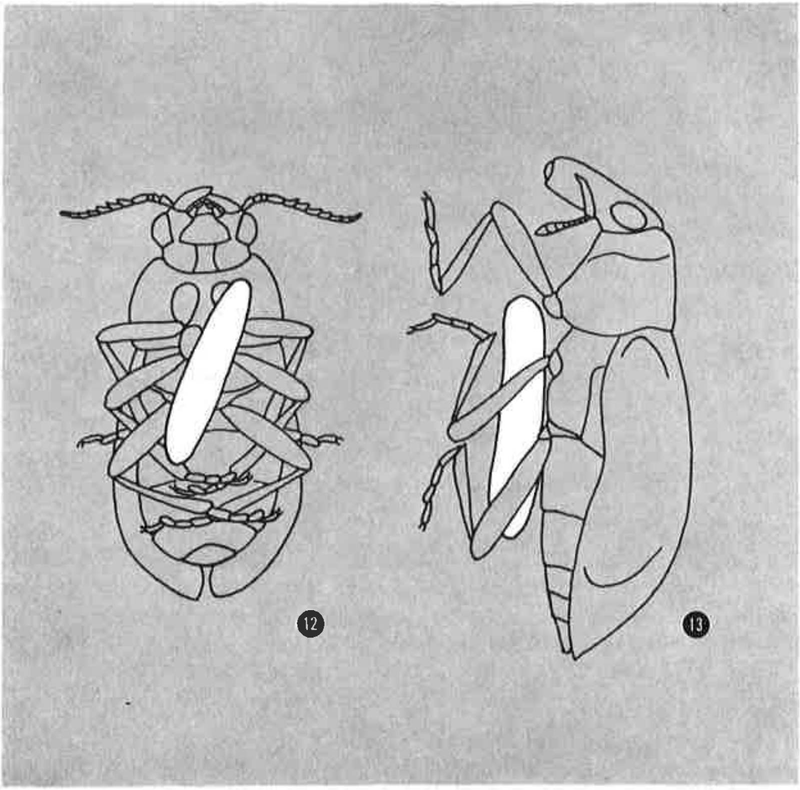
Eucerceris zonata (Say)

This is the only eastern species of *Eucerceris*, ranging across the northern United States from Colorado and the Dakotas to New England. It has not been studied previously, but several western species have been studied, all of them (like *zonata*) preying upon weevils (see Scullen and Wold, 1969, for references).[4]

The present studies were conducted during July and August, 1970, 2 miles north of Westerlo, Albany Co., N. Y., in one of the gravel pits in which I studied *Cerceris fumipennis*. Whereas the latter species nested in a gravel roadway and in hard soil nearby, *E. zonata* nested in fine-grained, friable sand several meters away. Eight nests were situated in flat soil, amongst sparse herbs, in an area measuring about 1 × 3 m. Three of the nests were closely clumped, their entrances only 10–30 cm apart.

I discovered these wasps accidentally on July 19, when I was

[4] More recently I have published on *E. fulvipes* Cresson and presented additional data on *E. flavocincta* Cresson (Evans, 1970). *E. triciliata* Scullen, the larva of which I described in 1964, is properly known as *E. pimarum* Rohwer (Scullen, 1968).



Figs. 12–13. Eggs of Cercerini on beetle prey. Fig. 12. Egg of *Cerceris* (*Didesmus*) *binodis* on *Anomoea mutabilis*, near Taxco, Mexico (no. 1604). Fig. 13. Egg of *Eucerceris zonata* on *Cleonus plumbeus*, near Westerlo, New York (no. H75).

digging out a nest of *Philanthus politus*, which nested in great abundance here (H33). During the excavation I uncovered 8 cocoons, 3–7 cm apart, at depths of 15–20 cm. These cocoons were brown in color, parchment-like in texture, and strongly tapered toward one end; they measured 9–10 × 20–30 mm in size and were surrounded by weevil fragments. They were obviously cocoons of Cercerini, and on the next day a male *Eucerceris zonata* emerged from one of them; on July 28 two females also emerged.

On August 2, I noted four active nests, all near the excavation I had made on July 19. Each was marked by a small mound of soil, 5–7 mm across, with the hole in the center. Females were seen arriving with prey, flying in low and quietly, often landing on vegetation

FIG. 14. Female *Eucerceris zonata* carrying its prey, *Cleonus plumbeus*. This female has paused on a vertical bank before proceeding to her nest in flat sand about a meter away. Note that she holds one of the front legs of the weevil in her mandibles.

surrounding the nesting site before proceeding to their nests. Rather than plunging directly into the open holes, they invariably landed 2–8 cm away and walked in with their prey, holding it in their mandibles by a front leg (Fig. 14). When prey-laden females first landed on plants or on the ground, they held their wings at about a 35 degree angle with the body for a few seconds, then lowered them parallel to the body. On August 6, I noted a male in the nesting area, flying about and landing on the ground here and there, also holding his wings in the same manner. The male made one attempt to mount a female carrying prey, but she flew away and returned to her nest a few minutes later.

I dug out one nest on August 2, finding 7 weevils in the bottom of the burrow, surrounded by loose soil, at a depth of 14 cm (H54). The burrow was 8 mm in diameter and was vertical for the first 2 cm, then at about a 70 degree angle with the surface to near the bottom, where it became horizontal. I found no cells.

On August 9, I found 7 active nests. Females proved to be slow provisioners, bringing in a weevil every 20–90 minutes, always landing on the ground a short distance from the open burrow and walking in. I dug out one nest on that date (H75), finding three cells at depths of from 17 to 25 cm. One contained an egg on the topmost of five weevils. The egg was 4.5 mm long and was glued lognitudinally on the venter of the abdomen (Fig. 13). Another cell contained a fresh cocoon, the third cell several weevils that appeared to be decomposing.

My final observations were made on August 14. On that date I observed one female for several hours, then made a careful excavation of two nests in the late afternoon. This female (H94) was first seen looking out the entrance of her burrow at 1000 hours (it had rained heavily the night before). At 1020 she made several circling flights and disappeared. At 1150 she returned with a weevil, landing first on a *Melilotus* plant, then on the ground 5 cm from her nest before walking in. She remained in the nest 45 seconds, then flew off directly, returning with another weevil at 1212. In 40 seconds she reappeared, scraping a little soil into the hole from the rim of the entrance, then flew off. I left the area for one hour, and when I returned she was again seen bringing in prey at 1325 and 1405. At this time I took her and dug out the nest. One of the weevils was stored in the burrow at a depth of only 2.5 cm. I found only two cells in this nest, at 22 and 25 cm deep.

The second nest dug out on this date had nine cells (H93; Fig. 11). These appeared to be in three clumps within which the cells were separated by 2–6 cm; the cells varied in depth from 23 to 30 cm. The cells appeared to be of two sizes, as in *Cerceris*, the smaller ones measuring about 9 × 20 mm and containing 3–5 weevils, the larger ones about 10 × 30 mm and containing 5–7 weevils. Several larvae were collected from this nest, and a description of the full-grown larva is appended below.

I took about 40 weevils from these two nests as well as 15 additional weevils from other nests or from provisioning females. In every case they represented one species: *Cleonus* (*Stephanocleonus*) *plumbeus* Lec. (Curculionidae) [det. R. E. Warner]. I also found five fresh cells accidentally on September 26, while digging a nest of *Philanthus lepidus* in this area, and in every case the cocoons were surrounded by fragments of this same species of weevil. Also, on August 30, 1969, Dr. George Eickwort, of Cornell University, collected a female in this same gravel pit carrying a weevil of this same species. Study of fragments found in the last-year's cells dug out on July 19, 1970 (H33) revealed that they, too, all represented *Cleonus plumbeus*. Thus it seems safe to assert that during two successive summers this population of *Eucerceris zonata* restricted its predation to this one species of weevil.

The larva of *Eucerceris zonata*. The larvae of only two species of *Eucerceris* have been described (Evans, 1957, 1964), and since there has been some question as to valid larval characters for separating this genus from *Cerceris*, I append here a description of the larva of *zonata*, based on four fully grown specimens collected in the course of the studies described above (H93). It does appear that the shape of the anal segment is the best feature for separating these two genera, as I suggested in 1964. The head of *zonata* is unusually long and slender, as in the other described species of this genus, but at least one species of *Cerceris* shares this feature. The head of *zonata* is more narrowed above and the spinnerets more elongate than in either of the previously described species, but in all other features the resemblance is very close. A detailed description follows.

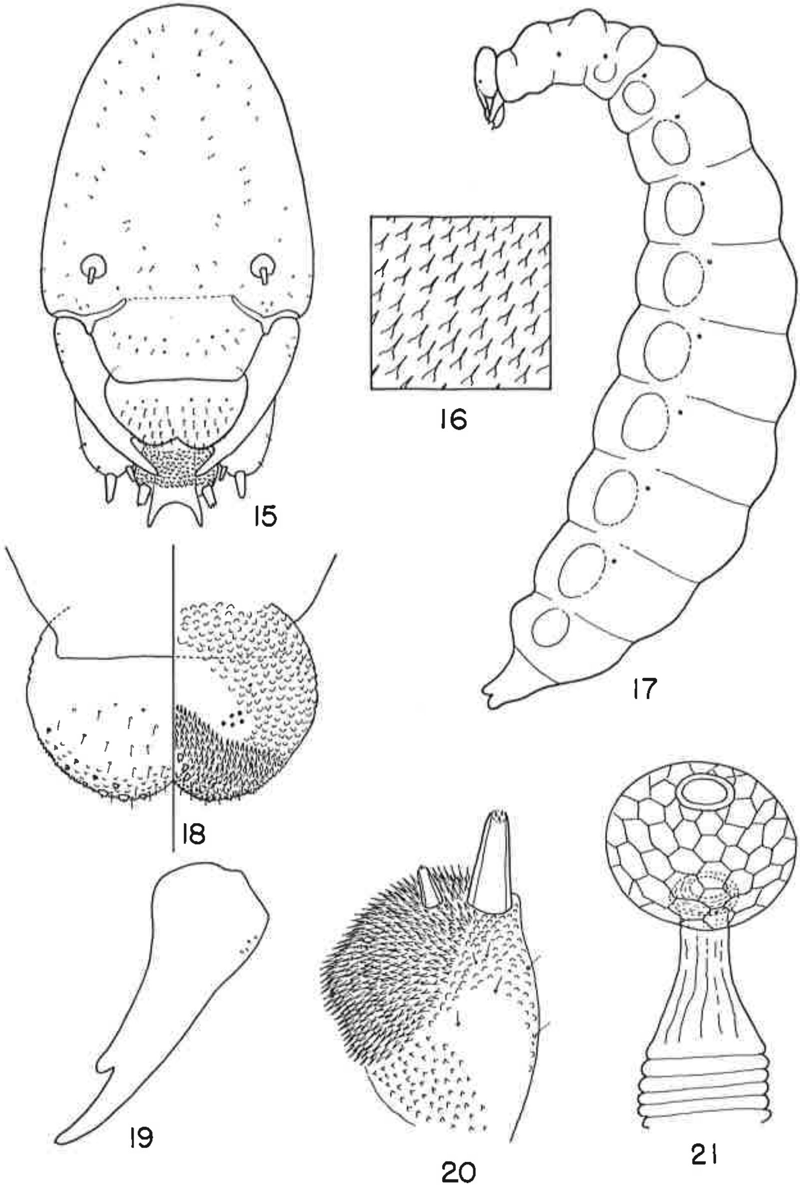
Body length 24 mm; maximum width 5 mm; strongly curved and tapered anteriorly; pleural lobes strongly developed but segments not divided into annulets dorsally; anal segment protuberant, supra-anal and subanal lobes about equally developed (Fig. 17). Integument very densely covered with short spinules (Fig. 16). Spiracles inconspicuous, largely unpigmented, under high power seen to have an unusually small opening; walls of atrium lined with fairly regular hexagons; opening into subatrium simple, unarmed, the subatrium gradually expanded to the trachea (Fig. 21).

Head 1.0 mm in maximum width, 1.4 mm high (exclusive of labrum and mouthparts); sides of head converging above to a rather narrowly rounded vertex; coronal suture long; parietal bands barely visible, unpigmented (Fig. 15). Antennal orbits large, circular, the membrane of the orbits conically elevated, giving rise to a large papilla, measuring nearly 100 μ in length. Head with scattered punctures, some of which give rise to minute setae, the longest measuring only about 20 μ. Labrum strongly bilobed, bearing numerous setae, margin slightly bristly and bearing several large sensory cones; epipharynx also with several large sensory cones near the midline subapically, as well as several large pores on each side toward the base; epipharynx strongly spinulose medio-apically (Fig. 18). Mandibles very slender, bidentate, 2.6 times as long as their maximum width; base with 4 minute setae (Fig. 19). Maxillae densely spinulose and slightly produced on their inner margin; maxillary palpi very large, measuring about 150 μ in length, galeae much smaller, about 50 μ in length (Fig. 20). Labium papillose above, palpi robust, 75 μ in length, much exceeded by the pointed spinnerets.

DISCUSSION

This study has demonstrated little diversity in the nesting behavior of Cercerini. This remains true when one includes published data on species not covered here, e.g., Linsley and MacSwain's study of *C. californica* Cresson (1956) and Krombein's work on *C. blakei* Cresson (1963) and several other species.[5] Extralimital *Cerceris* that utilize beetles also make very similar nests, including several Asiatic species

[5] Krombein (1959, 1964) found, however, that both the nominate and Floridian subspecies of *C. flavofasciata* Smith nest in vertical sand banks. Linsley and MacSwain (1954) reported that *Eucerceris ruficeps* Scullen utilizes abandoned burrows of halictid bees, making a lateral burrow from the vertical shaft of the bee.



FIGS. 15–21. Fully grown larva of *Eucerceris zonata*. Fig. 15. Head, anterior view. Fig. 16. Portion of integument of prothoracic dorsum, high magnification. Fig. 17. Body, lateral view. Fig. 18. Labrum (left) and epipharyx (right). Fig. 19. Mandible. Fig. 20. Maxilla. Fig. 21. Prothoracic spiracle, high magnification.

(Tsuneki, 1965) and several Australian species (Evans and Matthews, 1970). Common elements in the nesting behavior of most if not all Cercerini are as follows: (1) the burrow is at first vertical or nearly so, but deeper in the soil becomes oblique and finally nearly horizontal; (2) the soil is removed from the burrow by pushing it out with the strongly developed pygidial plate (Olberg, 1959), forming a circular rim around the entrance; this rim may be refreshed when soil is pushed out following rain or when a new major branch of the burrow is constructed; (3) the nest entrance is left open during periods of provisioning; (4) prey is carried well forward beneath the body in flight, holding it with the mandibles and embracing it in flight with some or all of the legs; probably one of the front legs of the beetle is grasped in every case (see Fig. 14 in the present paper, Fig. 29 in Evans and Eberhard, 1970, p. 365 in Olberg, 1959); (5) during bouts of provisioning, the beetles are left in the burrow, surrounded by loose soil which is scraped from the sides of the burrow or entrance; (6) cells in any one branch of the burrow may be closely grouped, and any one nest may eventually have several groups of cells from successive branches of the lower part of the burrow; (7) cells are of two sizes, small ones containing less prey and producing males, and cells averaging about 1.5 times as large and as much prey and producing females; (8) females typically maintain a single nest for their entire active period.

Most of the diversity in behavior in this group is related to prey selection. In the Old World a major segment of the genus *Cerceris* preys on bees (see, e.g., Tsuneki, 1965). In the New World, all species utilize beetles, and there is considerable concordance of species-grouping on structural grounds with type of beetle used. Thus, all members of *Eucerceris* use Curculionidae, as do many *Cerceris*; members of Scullen's (1965) *Cerceris* Group II so far as known use Buprestidae; all known members of his Group III use Chrysomelidae, all known members of Group IV, Tenebrionidae. This implies major differences in hunting behavior and in the way in which the prey is handled. It is also probable that the differences in the form of the female clypeus, used extensively by Scullen in his classification, are somehow related to handling of the prey, but hypotheses as to the nature of this relationship had best await data on the prey preferences of additional species (only about a quarter of the species in America north of Mexico have been studied).

Members of Scullen's Group I of *Cerceris* are, however, diverse in their host relationships. Scullen reports them as taking Curculionidae, Bruchidae, and Chrysomelidae (rarely Tenebrionidae), and I have added Phalacridae and Nitidulidae to this list in the present paper. Scullen left more than 30 species of *Cerceris* unassigned to any group; it happens that all the unassigned species that have been studied prey on weevils, but I gather that all do not seem closely related on the basis of structure.

It should be pointed out that on the basis of prey and nesting behavior, so far as studied, neither *Didesmus* nor *Eucerceris* appears separable from *Cerceris*. While the larvae of *Eucerceris* do seem distinctive, at least one *Cerceris* has a very long head capsule as in *Eucerceris*, and there is no assurance that the difference in the shape of the anal segment, discussed above, will hold up when more species have been studied. Scullen (1968) has listed the structural characters of the adults used to separate the two genera. I am not proposing that *Eucerceris* be reduced to the rank of a subgenus or species-group; but I fail to find the prominent behavioral differences that distinguish so many genera of Sphecidae.

The most prominent feature of the behavior of Cercerini remains their host-specificity. All records presented above either confirm previous records of specificity or include new records, the most striking of which is the exclusive use of one species of seemingly rare weevils by two successive broods of *Eucerceris zonata*. Experience with other species leads one to doubt whether *zonata* will be found to prey upon this same weevil throughout its range; but I feel safe in predicting that it will be found to prey on weevils of similar size and habitat, and probably of the same subfamily (Cleoninae) in other parts of its range. Studies from new localities have in the past almost always demonstrated a preference for the same or similar beetles; see, e.g., the records for such species as *Cerceris echo, halone,* and *bicornuta* presented above. A high degree of host-specificity may permit several species to nest essentially side-by-side, each exploiting a limited source of food without interference from other species. An instance of *C. halone, nigrescens,* and *atramontensis* doing just that has been presented above. I suggest that these wasps are not necessarily "good taxonomists," but that they are programmed to hunt in certain situations and to respond to prey of a certain size and behavior; in some instances there may be only one genus or only one species that fills these requirements, while in others there may be several species, sometimes of unrelated genera. In the case of the three species mentioned above, the evidence suggests that *atramontensis* hunts primarily in trees (taking mainly *Conotrachelus*), *nigrescens* mainly in herbs (taking mainly *Sitona*), while *halone* is a specialist on nut weevils (*Curculio*).

The case of *C. fumipennis* deserves special mention. This species is a predator on Buprestidae of many different kinds. There are only 5 members of its species-group, and *fumipennis* is the only one ranging throughout eastern North America. Hence it faces no competition from other buprestid-hunters and has been under no pressure to specialize further. There is one record of *fumipennis* taking a chrysomelid and one of it taking a curculionid (Scullen and Wold, 1969). Use of beetles of these families must be exceedingly rare, as I have presented above nearly 400 records from 7 separate nesting aggregations, and without exception the prey consisted of Buprestidae. Presumably when normal prey is scarce there is a lowering of the female's threshold of acceptance, such that other beetles are taken. Under conditions of continued prey scarcity, this may result in a permanent switch-over to a different type of prey, following the model I have presented elsewhere (Evans, 1966, p. 498). As is common in biology, it is often the exceptions that help explain the rule.

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