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Nesting Biology and Immature Stages of the Bees *Centris caesalpiniae, C. pallida,* and the Cleptoparasite *Ericrocis lata* (Hymenoptera: Apoidea: Anthophoridae)

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ABSTRACT

The nesting biologies of two species of the bee genus *Centris* are described and compared with one another and with information in the literature regarding other Centridini. Information about *Centris* (*Paracentris*) *caesalpiniae* Cockerell was obtained from examination of an extensive emergence aggregation in southern Arizona. Data concerning *C.* (*Xerocentris*) *pallida* Fox came from investigations of several nesting sites, also in southern Arizona. Both species nest shallowly in nearly horizontal desert soils and have similarly shaped brood cells. Nest site requirements, nest architecture and structure, cocoon constructions, larval defecation patterns, provisioning, some aspects of development and adult emergence, and nest parasitism are described and significant interspecific differences pointed out. Biological information on *Ericrocis lata* (Cresson) (Ericrocini), a cleptoparasitic anthophorid from the nests of *C. caesalpiniae,* is documented and confirms the suspected association of *Ericrocis* with *Centris.* The mature larvae of these three bee taxa are described taxonomically as are pupae of *C. caesalpiniae* and *E. lata.*

INTRODUCTION

We report on the nesting biologies of *Centris* (*Paracentris*) *caesalpiniae* Cockerell and *C.* (*Xerocentris*) *pallida* W. Fox (Centridini) and *Ericrocis lata* (Cresson) (Ericrocini), a cleptoparasite of *C. caesalpiniae.* JGR also includes taxonomic descriptions of mature larvae of the three species and of the pupae of *C. caesalpiniae* and *E. lata.*

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Centris caesalpiniae is a relatively large member of the genus found from western Texas to Arizona and northern Mexico (Snelling, 1974). Its males are strongly dimorphic in color, morphology, and size, and the largest males are much larger than the largest females. *Ericrocis* has long been suspected of parasitizing *Centris* (Snelling and Zavortink, 1984), no doubt for reasons of sympatry, synchrony, and similarity in size. This study confirms the association for one species of *Centris.*

Nesting information regarding *Centris caesalpiniae* and its cleptoparasite has not been published before. Data presented here refer only indirectly to nesting, for the site discovered was an emergence site where males and females of *C. caesalpiniae* were leaving last year's (spring 1988) nests, feeding, and mating. No new nests were being constructed and provisioned. Another emergence site of the same species was observed (but not studied) by JGR on August 29, 1968, at 1 mi east of Douglas, Cochise Co., AZ. Both occurrences were characterized by the loud buzzing of numerous territorial males flying low over the site in search of emerging receptive females.

Centris pallida, in the Southwest and northern Mexico, is also a large species with dimorphic males. Its mating behavior has been treated extensively (Alcock, 1976, 1979; Alcock et al., 1976b, 1977), and its nests have been described before (Alcock et al., 1976a). We here add additional nesting information, comparative with that of *C. caesalpiniae.* No cleptoparasites have been associated with *C. pallida.*

During the last 30 years nesting data on the centridine genera *Centris, Ptilotopus,* and *Epicharis* have accumulated to the point that the nesting biology of this large, essentially Neotropical group is coming into focus. Michener and Lange (1958) reviewed the early literature and contributed new information about several species of *Centris.* More recently Coville et al. (1983) provided a detailed study of *Centris segregata* Crawford, summarized all previous literature contributions regarding *Centris* and *Ptilotopus* to date, and attempted to sort out differences in nest architecture and variability of nesting substrate preferences on the basis of subgeneric placement. To this information should be added the investigations of Camargo et al. (1975) on *Epicharis* (*Epicharana*) *rustica flava* (Olivier), of Roubik and Michener (1980) on *E.* (*Parepicharis*) *zonata* Smith, and of Coville et al. (1986) on *Centris* (*Trachina*) *heithausi* Snelling. Nothing is known about the nesting biology of the species of *Caenonomada,* the fourth genus within the Centridini.

Specimens (including cells and cocoons) collected in association with this study are stored in the American Museum of Natural History and at the Carl Hayden Bee Research Center.

Acknowledgments

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NESTING BIOLOGY OF *CENTRIS CAESALPINIAE*

Description and Density of Site: The emergence site of *Centris caesalpiniae* was approximately 5.8 mi east of Sahuarita, Pima Co., AZ (UTM grid coordinates: Zone 12, N3536320 E513480), at an elevation of 2905 ft. It first came to the attention of SLB when a receptionist for the Intercontinental Electric Corp. called on the morning of April 19, 1989.

A field crew, installing a 27 mi long line of high-tension towers south of Tucson toward Nogales, had driven across the site and were concerned about stings from the thousands of bees flying over the site. Because they had driven back and forth several times per day along the north/south unpaved powerline access road before they first noticed the bees on April 19, that date must have been very close to the first day of male emergence.

SLB visited the site late on the afternoon of April 19, at which time the weather was hot (>30°C), males were inactive, but the outline of the site was evident due to the thousands of emergence holes and new excavated pits dug by males. Two days later SLB captured females and identified the species on the basis of their bright red eyes and pile color and of the dimorphic males. Roy Snelling later confirmed the identification as *Centris caesalpiniae.*

SLB carried out preliminary observations on nesting biology on several occasions after that, and especially with regard to mating behavior. Both authors spent most of the week of May 1 investigating the bee in the field and laboratory. During this week, adult activity (mate searching and mating) was near its zenith. Thereafter, one or the other of us visited the site approximately once a week until bee activity ceased (last mating observed on June 8). JGR revisited the site on August 16, 1989, at which time it was inactive.

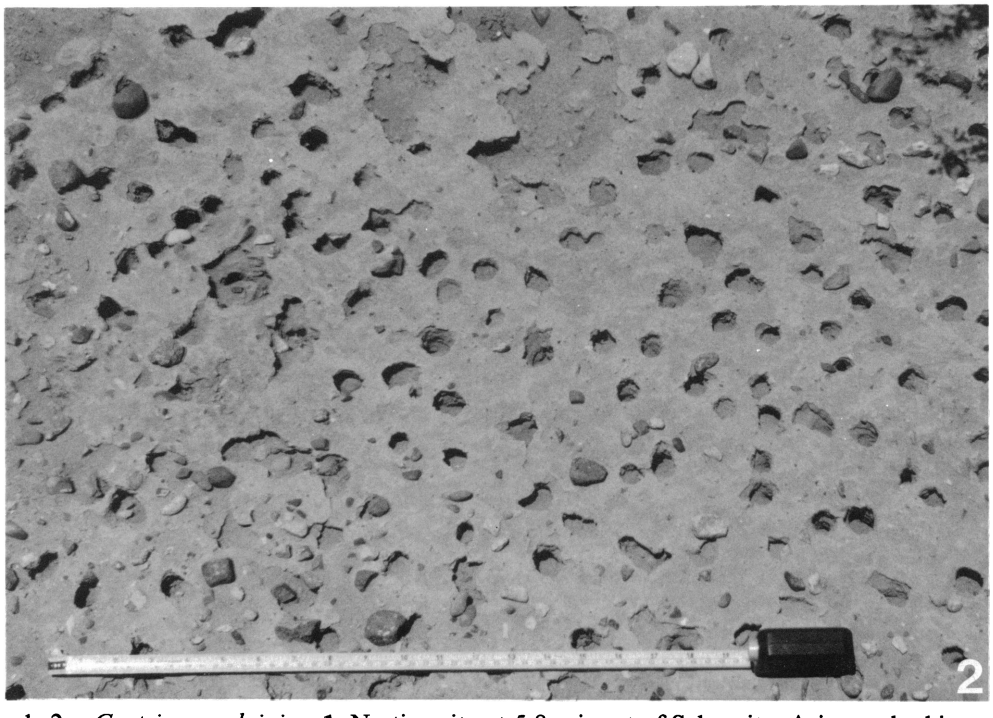
The site was on a gently sloping bajada extending from low mountains to the southeast. The site itself was almost entirely dominated by *Larrea tridentata* (fig. 1). The surrounding vegetation within flight range of these bees was a "creosotebush flat," classified as the Creosotebush-Bursage Series of the Arizona Upland Subdivision of the Sonoran Desertscrub (Brown, 1982). The dominant perennial plants adjacent to the site were creosotebush (*Larrea tridentata*), triangle leaf bursage (*Ambrosia deltoidea*), and, in the washes, velvet mesquite (*Prosopis velutina*), foothill palo verde (*Cercidium microphyllum*), catclaw acacia (*Acacia greggii*), white thorn acacia (*Acacia constricta*), sweet acacia (*Acacia farnesiana*) along with scattered individuals of the columnar saguaro cactus (*Carnegiea gigantea*) and barrel cactus (*Ferocactus wislizeni*).

The 1989 emergence site, chosen by *C. caesalpiniae* females as a nesting site presumably in 1988, was on a flat geomorphic surface with large gravel as well as well-drained silty soils. A particle size analysis revealed its loam nature with a percentage composition of 11 percent clay, 43 percent silt, and 46 percent sand. Another sample consisted of 12 percent clay, 34 percent silt, and 54 percent sand. The soil was Yaqui fine sandy loam (technically, a fine-loamy, mixed, thermic fluventic camborthids). It was a two-tiered soil with about a 0.5–1.0 m fine sandy portion overlaying a buried relict soil. Soil pH at the cell level was 8.30. Soil moisture was 2.7 percent at cell depth when excavated in May 1989.

The top soil layer, approximately 5 cm thick, was unconsolidated, but the substrate was firm beneath so that bee burrows could be traced easily. Deeper yet, the soil gradually became less consolidated so that it could not be excavated in clods. The lower soil was more easily sifted for cells than that above, and it was in this layer that most of the cells still containing unemerged *Centris* were concentrated.

The site was mapped on May 27, 1989, with a plane table, alidade, and stadia rod to produce the topographic map shown in figure 3. To calculate the area of the site we cut out a paper polygon (traced from the original field map) of the emergence area onto typing paper which was then weighed to the nearest 0.1 milligram on a Sartorius balance. Its weight (4.47 g) was substituted into a linear regression equation for three calibrations squares of known area. The equation for the straight line, $y = a + bx$ (where $a = 0.6011$ and $b = 288.3216$) exhibited a perfect correlation with area ($r^2 = 1.0$). Thus measured the site occupied 1290 m^2.

Emergence holes (fig. 2) were approximately equally dense throughout the site, whether at the periphery or center of the area, indicating that these bees nested contiguously. Only under the bases of the *Larrea* plants were there fewer openings. On one 0.25 m^2 plot near the center of the site, we counted 82 emergence holes and retrieved 325 *Centris* cells (table 1). If this sample was representative for the entire emergence site, then the nesting site was established by approximately 423,000 female *Centris* assuming that a fe-



Figs. 1, 2. *Centris caesalpiniae.* **1.** Nesting site at 5.8 mi east of Sahuarita, Arizona, looking north-northeast across transmission line access road from point on dirt road near southwest boundary of site (see map, fig. 3). **2.** Emergence holes near center of site. These holes had been enlarged by males digging to find emerging females below surface. Tape measure extended 0.5 m.

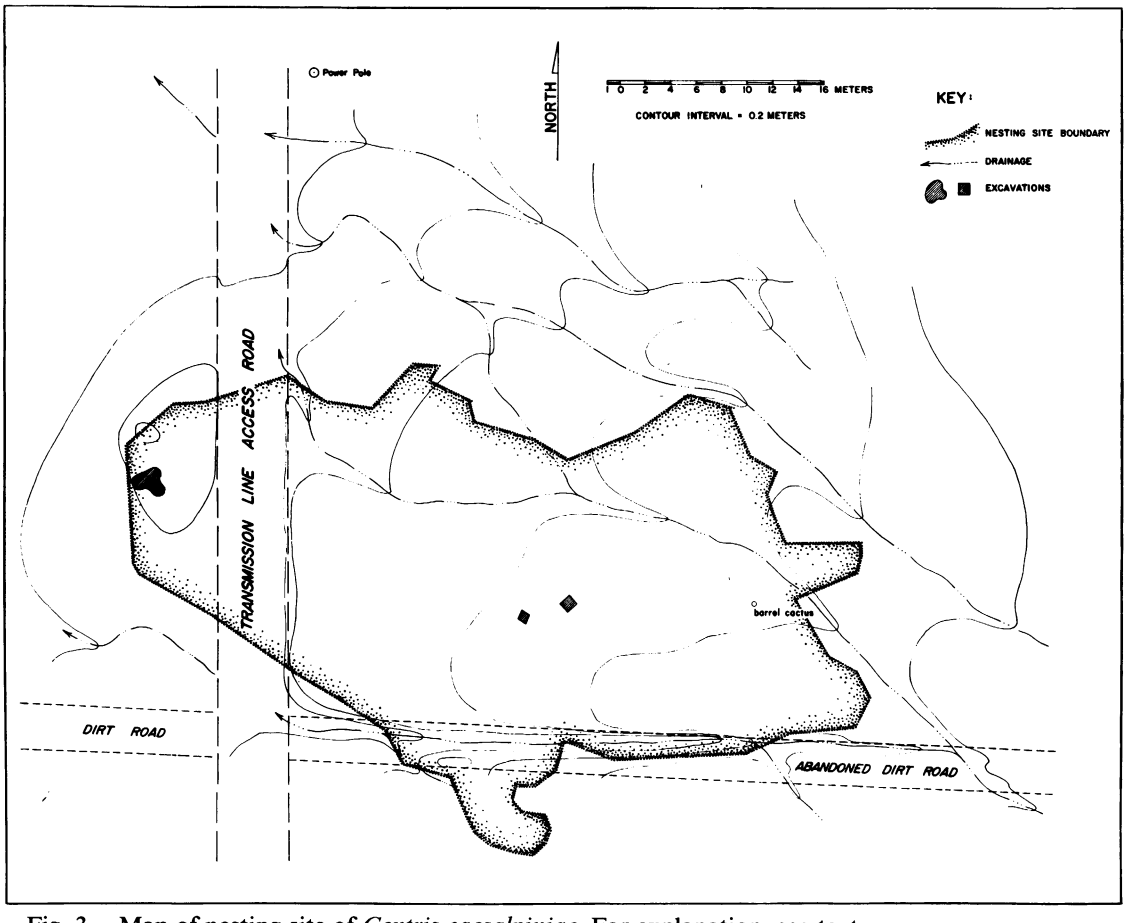


Fig. 3. Map of nesting site of *Centris caesalpiniae*. For explanation, see text.

male establishes only a single nest during her life (which is possible for this species but untrue for some *Centris* such as *C. pallida*) and assuming that each emergence hole was a nest entrance (which seems likely). These females constructed 1,677,000 cells (our calculated value) at the average of 3.96 cells per female. Applying the same reasoning and using data from table 1, we estimated that 1,615,000 *C. caesalpiniae* adults emerged from the site as did 5160 *Ericrocis lata* (yielding a low percentage rate—0.3%—of parasitism by *Ericrocis*; see section on Parasitism). The site contained no cells from generations prior to 1988, indicating that the area had not been used as a nesting site before.

Roubik and Michener (1980) noted that *Epicharis zonata* was also highly gregarious. They questioned what stimuli could attract so many bees to a small area, and concluded that it was not because the individuals were returning to their emergence site (no vacated cells). Hence, neither *E. zonata* nor *C. caesalpiniae* reuses the same nesting site year after year. A similar observation for *C. pallida* was made by Alcock et al. (1976a) although Alcock (personal commun.) now believes that a site may be reused at some interval though not necessarily in consecutive years. However, *Epicharis rustica* (Olivier), a large oil-harvesting centridine bee from Tabago Island off the Panamanian coast, does reuse nesting sites year after year (D. Roubik and Buchmann, unpubl. obs.). Similarly,

TABLE 1
Counts of All Cells of *Centris caesalpiniae* Taken from 0.25 m² Plot

Surviving *Centris*	
cells with adults or pupae	107
cells with *Centris* larvae	5
adults emerged in lab	10
vacated cells	191
total	313
Moldy cells	
with *Centris* cocoons	6
without *Centris* cocoons	5
total	11
Cell with *Ericrocis* larva	1
Cells with Mutillidae	0
Total cells found	325

Centris rufosuffusa Cockerell was reported to reuse the same site over many years (Callan, 1977).

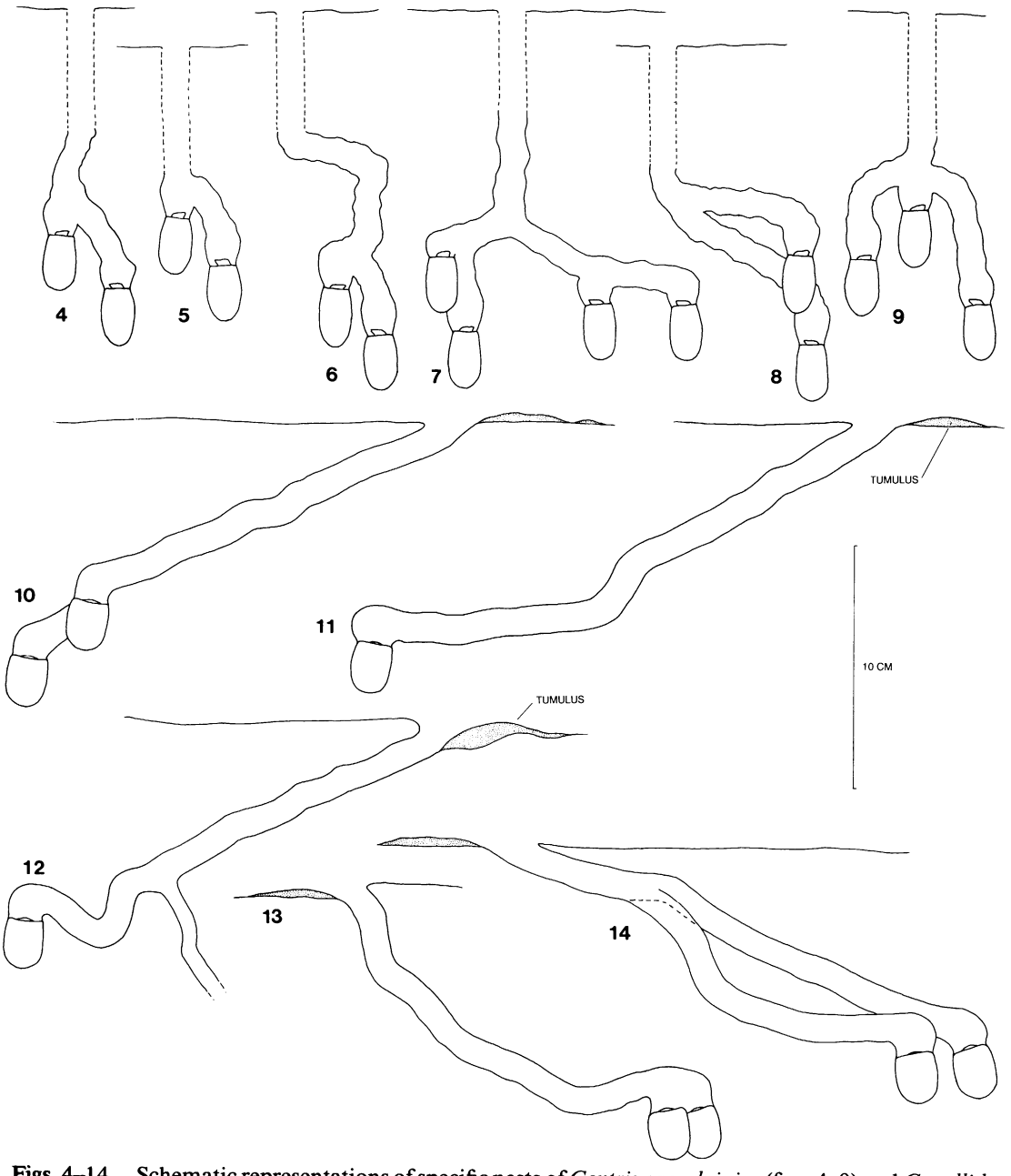
NEST ARCHITECTURE: Nests of *Centris caesalpiniae* were shallow, apparently characteristic of all *Centris* species nesting in horizontal surfaces. Cell depth ranged from 8 to 25 cm, and all cells occurred in the substrate beneath the top loose surface layer. Nests could not be excavated in their entirety because of confusion caused by nest density. Information regarding tunnels was derived from exit tunnels which in most cases seemed to be the same as the main burrows excavated in 1988 by nesting females. The tunnels contained very fine loose soil which may have been backfill from emerging adults as they crawled upward. Burrows immediately above unopened cells were filled with very soft soil loosely held together by fungal hyphae.

Surface openings (fig. 2) to most nests were marked by large, irregular holes created by males attempting to dig through the surface material to reach emerging or resting virgin females, as will be discussed elsewhere by Buchmann and H. Spangler (in prep.). The openings, pockmarking the surface, were filled with soil below a depth of several centimeters. In some areas of the nesting site the amount of digging by males in search of females had produced so much loose soil that all exits were hidden by a layer of loose soil overriding the surface.

Burrows (figs. 4–9) could not be traced through the top 5 cm layer of soft soil but were readily visible in the firm earth below where they descended more or less vertically. They usually branched 1 to 6 cm after penetrating the harder subsurface stratum. After branching, each ramus curved and descended downward and either branched again or ended in a cell. The rami were of varying lengths and in some cases a brood cell was found immediately below the bifurcation. Irregular in diameter (more so than is characteristic of those of most bees) and with rough walls, burrows were approximately 10 mm across. However, in all known cases a descending burrow widened to a diameter of 13 to 14 mm immediately above a cell and then started to curve inward 10 mm above the cell. Hence the burrow wall from the widest point to the cell top formed a funnellike structure. The funnel wall was very smooth (in contrast to the burrow wall above), lacked a visible special lining, and readily absorbed water.

All cells were oriented vertically with their entrances (closures) uppermost, and all were arranged singly (not in a cluster or linear series). Their walls were harder than the substrate even where the substrate was comparatively firm. After cocoon construction the reinforced wall was even more resistant; hence we were able to screen for vacated and occupied cells with a quarter-inch mesh screen.

Cell walls were approximately 1 mm thick although they tended to be thinner in places (e.g., they were 0.5 mm near the cell opening in some instances). Soil particles, adhering to the outer surfaces, could be washed away by submerging the cells in running water and rubbing them with our fingers. Cells remained intact even when left in water for 24 hours or longer. Beneath the softer soil was a slightly grayer, waterproof hard layer roughly 0.1–0.2 mm thick composed of soil particles cemented with a hardening material. Melded with this layer was an inner, slightly darker layer approximately 0.5 mm thick that was similarly hard and also composed of soil particles. It was separated from the outer layer by a dark gray boundary visible in cross section. The two hard layers and intervening gray boundary were inseparable. The inner surface of the cell was smooth (though not polished) and lined with a semitransparent shiny waxy material on all sur-



Figs. 4–14. Schematic representations of specific nests of *Centris caesalpiniae* (figs. 4–9) and *C. pallida* (figs. 10–14), side view. Tunnels drawn to show approximate size and direction, all cells as if walls and closure were intact. Narrow branch in figure 12 occupied (and presumably constructed) by female of *Diadasia*. All nests drawn to same scale.

faces (including the cell closure). The waxy material could not be peeled from the surface but could be scraped with forceps, which left a shiny channel. The shine of the wax tended to dull after cocoon construction but could be easily seen in those cells where the immatures had died before spinning.

The waterproof nature of the *Centris* cells

(including the closure), whereby they could be submerged in water for an extended period and even scrubbed without disintegrating, was remarkable (and constrasted sharply with the cells of *Centris pallida* described below). Considering the shallowness of the nests and the heavy monsoon rains in the Sonoran desert, we believe that waterproof cell walls and buoyant cells may be adaptive. We do not known the source of the waterproofing material, but note that females have strongly developed setal combs on the prothoracic and mesothoracic basitarsi in addition to coarse setae on the hind legs, as is characteristic of other *Centris* species (Neff and Simpson, 1981) that collect floral oils. Two ethanolic females, when dissected, revealed large tapering Dufours glands (11.5 and 18 mm long, respectively), the chemical secretion of which might also explain the waterproof nature of the cell wall.

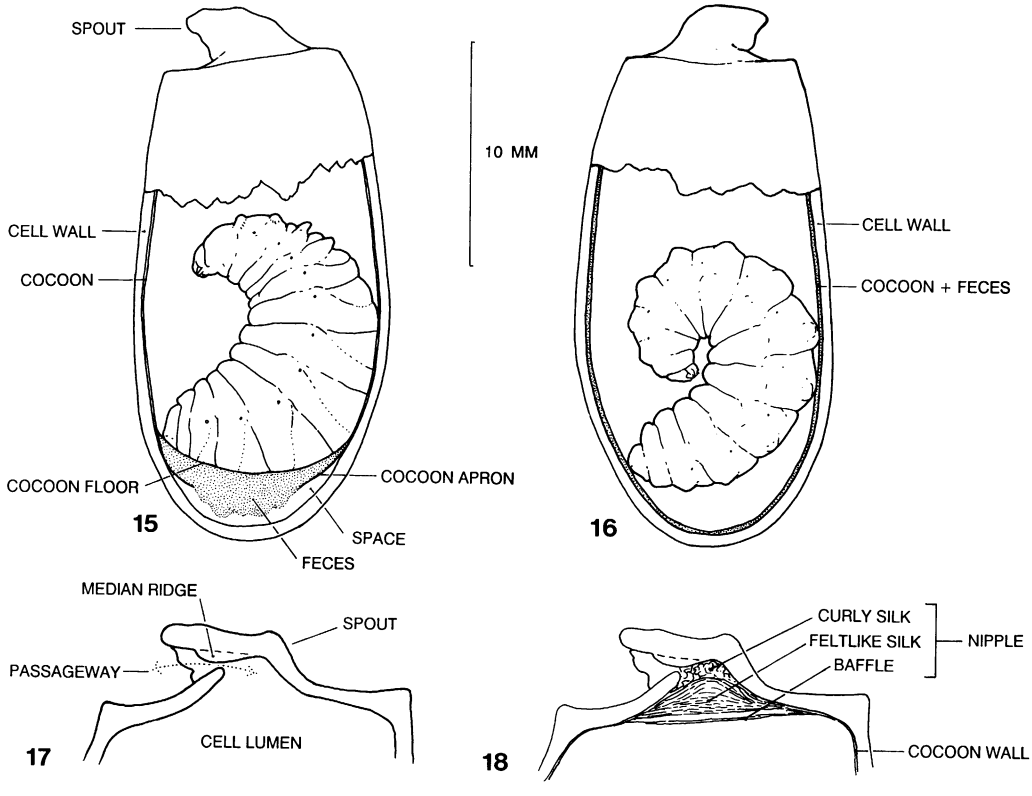
Roubik and Michener (1980) reported on the distinct waterproof nature of the cell walls of *Epicharis zonata* and attributed this to the fact that the species nested in seasonally swampy habitats. They also remarked that cell walls of other centridines were not generally separable from the substrate. The present study demonstrated that the cell walls of *Centris caesalpiniae* were both waterproof and easily separated from the surrounding soil. This new information, in conjunction with other studies (e.g., Alcock et al., 1976a; Batra and Schuster, 1977; Bennett, 1964; Coville et al., 1983; Coville et al., 1986; Vinson and Frankie, 1977), suggests that cell walls of ground-nesting centridines are always firm (although not always waterproof) and not usually intimately fused with the substrate.

Cells (figs. 15, 16, 19) were elongate ovals, rounded on the bottom, and truncate at the cell closure (top), as seems to be characteristic of all ground-nesting *Centris* bees. Cells varied extensively in size, probably correlated with the wide size range of the adult bees. Large male morphs undoubtedly occupied the larger cells. External dimensions of washed cells (N = 26) were 11.5–14.0 mm in maximum diameter and 22.0–31.0 mm in length from top rim to bottom. Inside dimensions (those usually recorded for bee cells) were obviously reduced by the width of the cell walls.

Cell openings were approximately 8.0 mm in diameter. The cells were roughly symmetrical around their long axes. Although there was some variation in symmetry, we could not detect any consistent asymmetry with respect to the curvature of the sides in relation to the plane of the rim. Cells were rounded at the bottom, some more broadly so than others.

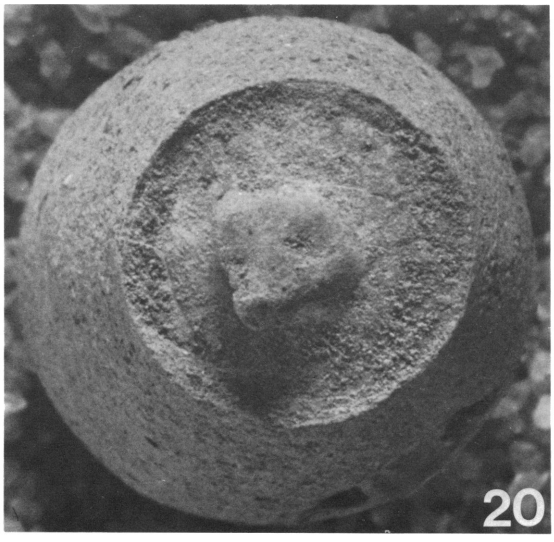
Females constructed the cell closures after provisioning and egg laying. The closure was built into the upper end of the cell wall so that a wall rim usually projected slightly above the closure. Closure material consisted of slightly grayish hardened soil essentially identical to the inner layer of the cell wall. Approximately 0.5 mm thick in most places, the inner layer was thicker where it joined the cell wall. The boundary between the closure and the wall was scarcely detectable, the two surfaces smoothly connecting to each other and the inner waxy coating of the two providing a continuous seal. The inner surface of the closure was smooth but, like the cell wall, was slightly irregular because of soil particles. There was no indication of a spiral, characteristic of most bee-cell closures.

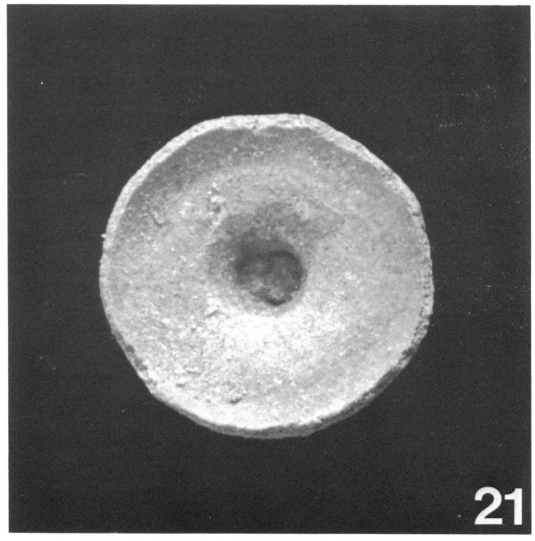
The closure (figs. 17, 18, 20, 21) was concave on the inside and less distinctly convex on the outside. Near the center there was a pronounced inner dimple corresponding to an exterior spoutlike projection that rose from the center and then bent horizontally. The structure of the spout was complicated and its method of construction unknown. The spout was an open tubelike passageway leading from the cell lumen to the outside. Its upper exterior surface was flattened and often exhibited a slight depression at the approximate center of the cell closure, and as seen from above (fig. 20) the apex of the spout usually was wider than its base. When one looked into the external opening of the spout from the side of the cell (fig. 22), a median ridge of closure material was seen to hang from above so that the opening appeared as two lateral holes connected below by a narrow crescentic opening or merely as two holes completely separated by the central septum. As seen from the inside (fig. 21), the connection of the spout passageway to the cell lumen was also crescentic with the extremities of the crescent being the main passageways leading

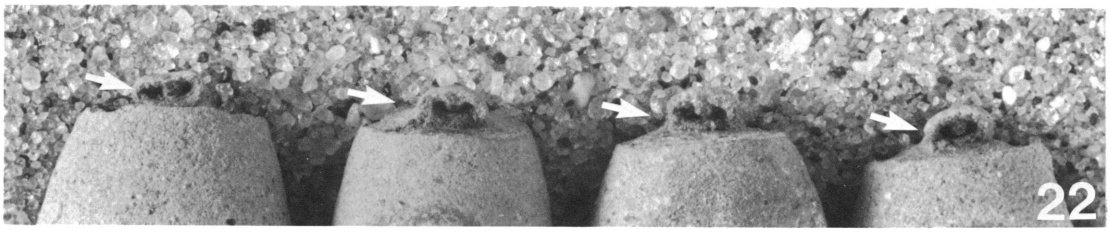


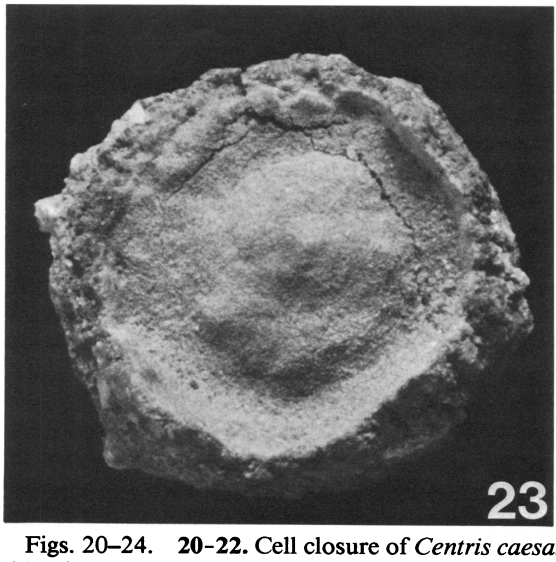
Figs. 15–18. **15.** Cell of *Centris caesalpiniae,* side view, containing cocoon, feces, and postdefecating larva of *C. caesalpiniae.* **16.** Same, containing cocoon, feces, and postdefecating larva of *Ericrocis lata.* **17.** Top of cell of *C. caesalpiniae,* in cross section, showing structure of spout. **18.** Same, including cross section of cocoon of *C. caesalpiniae,* showing structure of cocoon cap and how nipple fits into spout. Scale refers to figures 15, 16.

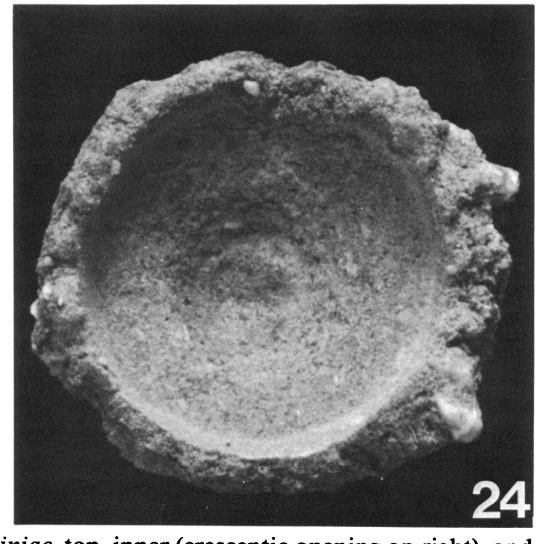
Fig. 19. Cells of *Centris caesalpiniae,* side view and with spouts also in side view, showing variation in form and size.





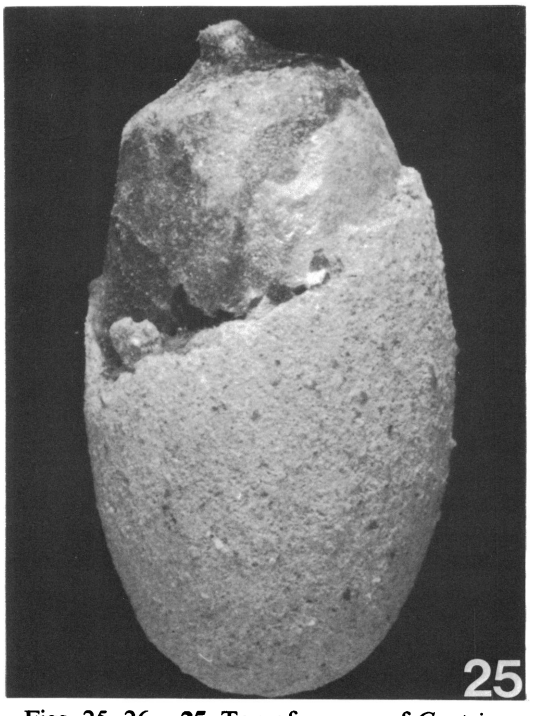


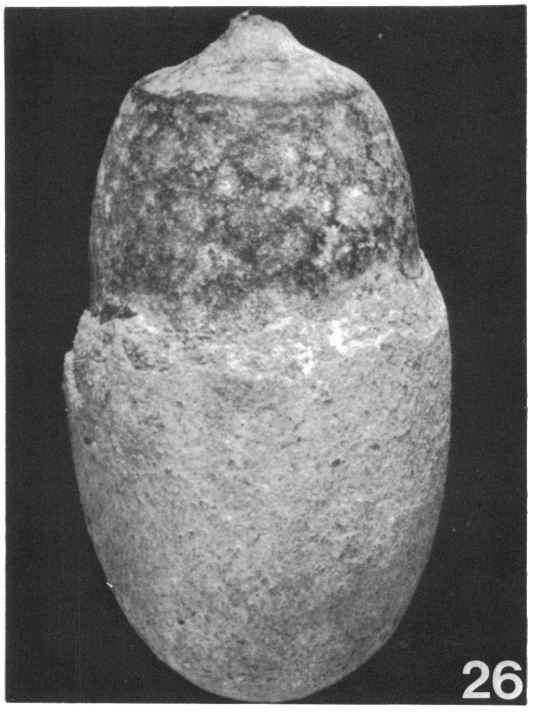




Figs. 20–24. **20–22.** Cell closure of *Centris caesalpiniae,* top, inner (crescentic opening on right), and side views. **23, 24.** Cell closures of *Centris pallida,* top and inner views.

to the two external openings. As seen in side view from the outside (figs. 15, 16, 19), the upper surface of the spout usually extended farther forward than the lower surface so that, when the closure was viewed from above (fig. 20), the external openings could not be seen.





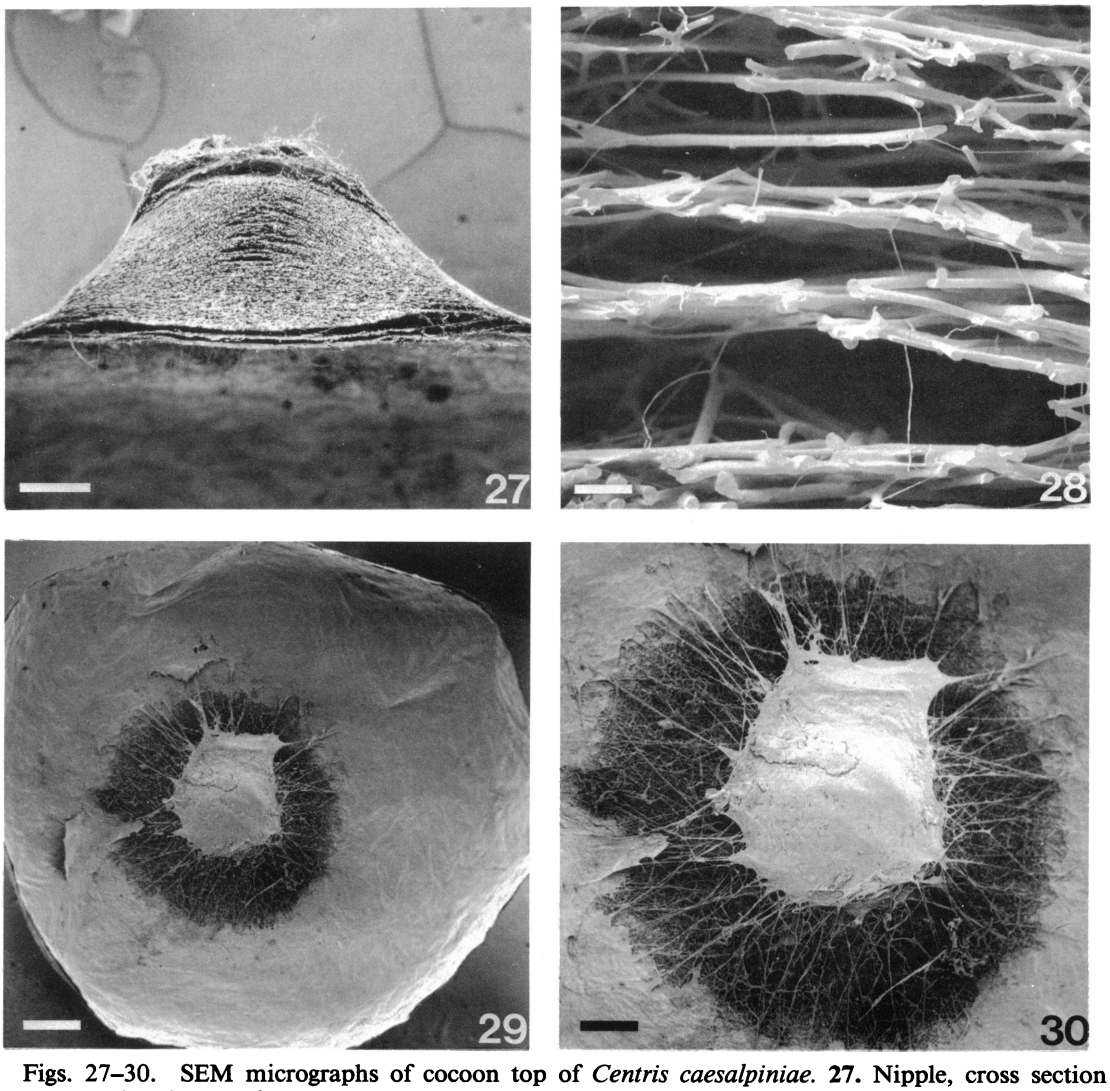
Figs. 25, 26. **25.** Top of cocoon of *Centris caesalpiniae,* side view, showing pronounced nipple. **26.** Top of cocoon of *Ericrocis lata,* side view, also showing nipple.

These external openings were normally clogged with soil particles but were easily cleaned so that light could be shown through them. The passageway in the spout was lined with the waxy material that coated the rest of the cell's interior surface.

The structure of the spout was such that parasites would likely have difficulty in ovipositing through the openings. The spout apparently permitted gas exchange between the cell and the loosely filled lateral tunnel because gases would probably not diffuse easily through the waxy cell lining. The spout's respiratory function was further suggested by the structure of the cocoon described below. However, questions remain such as how gases are exchanged in the spoutless cells of the related *Centris pallida* (see description below) and *Ptilotopus derasa* (Lepeletier) (Bennett, 1964).

According to Coville et al. (1983), the cell closure of *Centris segregata* was similar to that of *C. caesalpiniae* as it too was a bent tube permitting gaseous exchange. These authors suggested that its shape would make unlikely "entry of water or contaminants." The cell closure of *C. heithausi* is also similar (Coville et al., 1986). Information on *C.* (*Hemisiella*) *transversa* Perez provided by Batra and Schuster (1977), although not as complete, suggests a similar type of closure. However, closures of *C.* (*Centris*) *aethyctera* Snelling (Vinson and Frankie, 1977) are somewhat different, as are the cells of *C. pallida* first illustrated by Alcock et al. (1976a) and described and illustrated here (fig. 23).

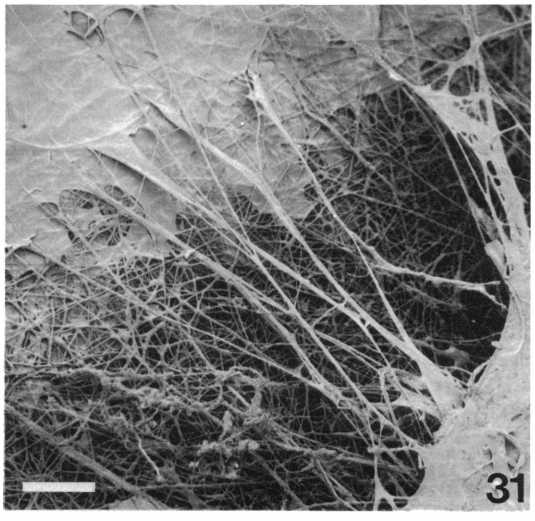
PROVISIONING: Because this was an emergence site and no new nests were under construction, we have no information regarding provisioning beyond the indirect composition of pollen loads as revealed by an analysis of a larval fecal deposit in a natal cell. Acetolysis of the intact fecal mass left inside of a cell from which an adult had emerged revealed that the 1988 larval diet consisted of pollen from 6 species of flowering plants. This average diet (based on a count and identification of 1064 pollen grains) contained pollen from: *Larrea tridentata* (58.7%); *Prosopis velutina* (36.0%); miscellaneous unidentified legumes (3.7%); *Acacia* cf. *constricta* (1.2%); unknown Polemonicaceae (0.3%); and *Chi-*

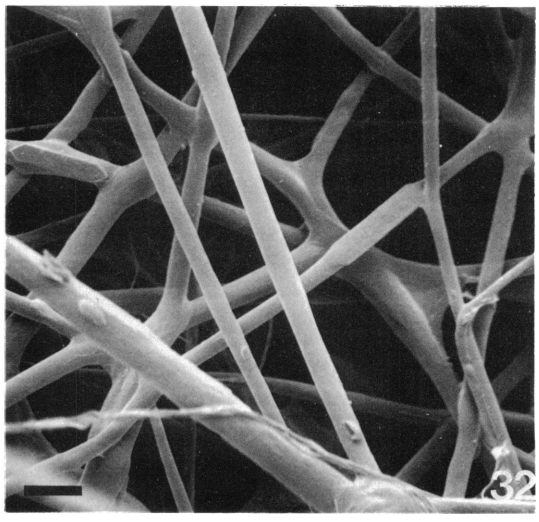


Figs. 27–30. SEM micrographs of cocoon top of *Centris caesalpiniae*. **27.** Nipple, cross section (compare with diagram, fig. 18) (scale = 500 μm). **28.** Cross section of feltlike layers, more highly magnified than in figure 27 (scale = 20 μm). **29.** Cocoon top, inner view (scale = 1 mm). **30.** Center of cocoon top more highly magnified than in figure 29, inner view (scale = 500 μm). Because of the metallic coating applied to the specimen photographed in figures 29 and 30, the central baffle is highly reflective and opaque, as is the periphery of the cocoon top; the dull circular band of fine reddish silk surrounding the baffle appears dark.

lopsis linearis (0.1%). Several spores from *Aspergillus niger* were also found in the feces. (Fecal material from 5 other cells, casually analyzed, showed a similar distribution of plant types.) These palynological data suggest that *Larrea* and *Prosopis* were the dominant pollen source for *Centris caesalpiniae* at this site in 1988. Other pollen types recovered probably represent nectar sources for females or very minor pollen source plants.

COCOONS AND DEFECATION: As is apparently true for all *Centris* species, *C. caesalpiniae* spun a cocoon that conformed to the cell surface and possessed a central projection (nipple) fitting into the spout (fig. 18). Evidence indicated that cocoon construction





Figs. 31, 32. SEM micrographs of cocoon top of *Centris caesalpiniae*. Increasingly magnified views (scale = 200 and 10 μm, respectively) of circular band of fine reddish silk which holds baffle in place and through which gases are presumed to pass, inner view.

commenced first, was interrupted by (or at least coordinated with) defecation, and was completed after the feces were fully voided.

The brownish cocoon was a thin, multilayer structure consisting of a specialized cap, the walls (sides), and the bottom which contained the feces. The walls were the simplest part, consisting of many layers of sheetlike, glistening transparent silk. The sheets were very thin, cellophanelike, closely appressed, but not fused together. The completed cocoon wall was semitransparent, and the outer surface dull because of minute irregularities of the cell wall and also apparently because the waxlike cell lining adhered to it at least in places. The sides of the cocoon were thin and weak such that a cocoon containing a pupa and feces could not be held without losing its shape. However, it was not easily torn.

The top of the cocoon (fig. 29), appressed to the cell closure, was a continuation of the cocoon walls. However, the center of the top (fig. 30) under the cell spout was very different. In spinning the cocoon, the larva first filled the recessed central part of the cell closure with a thick mass of curly reddish-brown threadlike silk (fig. 18) that covered the passageway to the outside. The larva then spun numerous layers of thick, feltlike silk one after another to form a hard core of material that completely filled the central concavity of the closure so that in a completed cocoon the core accounted for most of the central projecting nipple (fig. 18). As seen in cross section (figs. 29, 30), each feltlike layer of the nipple was attached to the periphery of the core. When viewed from within the cell, the center of the cocoon top was a reddish dull feltlike mass about 4.0 mm in diameter.

The larva then applied a circular multilayered shiny, sheetlike baffle of silk about 2.3 mm in diameter next to the core and attached it with radiating strands of threadlike silk extending from its periphery to the periphery of the core and to the inner edge of the outer ring of the cocoon cap. Hence, the completed cocoon cap when viewed from the inside consisted of a circular baffle (2.3 mm in diameter) of shiny silk in the center, surrounded by a dull circular band of fine reddish silk threads (figs. 29, 30, 31) about 0.8 mm wide on a side, and in turn this circular band was ringed by the rest of the cocoon cap consisting of a band of glistening sheetlike material roughly 2 mm wide.

The specialized central nipple of the cocoon cap may be a filter system (perhaps to exclude parasites), and gases pass through the core material and through the fenestrations

of the dull band of threadlike reddish-brown silk surrounding the central baffle.

We do not known when the nipple is spun in this species, but, in a cell of *Centris* (*Centris*) *flavofasciata* Friese collected by SLB in Guanacaste Prov., Costa Rica, the central nipple was spun and the larva removed before the rest of the cocoon was constructed. Hence the nipple may also be the first part of the cocoon deposited in *C. caesalpiniae.* JGR observed the horizontal cells of *Centris nitida* Smith in a trap nest at Chamela, Jalisco, Mexico. This species both spun the front end (including nipple) of the cocoon and deposited some feces at the rear end of the cell *before* the provisions were exhausted. Similar observations regarding timing of completion of food, defecation, and cocoon production for *C. caesalpiniae* and for other species in the genus should provide useful comparative information.

The rest of the cocoon of *Centris caesalpiniae* was constructed in two phases. The larva first applied a cellophanelike sheeting of silk to the wall but ended it before reaching the lowest point of the cell. The bottom of the cell was left uncoated with silk on all cocoons examined, so that an uncoated area 4–6 mm high always remained at the cell bottom (as seen in lateral view). Next the larva defecated the entire feces (fig. 15) into the bottom of the cell. Then during the second phase of the cocoon construction, it covered the fecal mass with a thick sheet of multilayered silk (the cocoon floor) that adhered closely to the mass and also extended up the sides of the cocoon to become an integral part of the cocoon wall.

The feces were dark brown to nearly black, and the cocoon floor where it covered them was a shiny dark brown to black, slightly concave, undulating surface. Feces at the time of our study were invariably hard, brittle and appeared completely dry. We believe that the moisture from the freshly deposited feces drains through the cell bottom into the substrate. Indeed, most, but not all, cell bottoms with cocoons showed a marked degradation of the cell lining, suggesting that an enzyme or other components in the fecal material may have caused a breakdown of the waxy lining. In the process of drying, the feces shrank, pulling the lower part of the cocoon (cocoon apron, fig. 15) away from the cell wall and creating an open space between the fecal material and the cell bottom. This space usually developed fungal hyphae where the feces were not covered by cocoon fabric.

Fecal deposition and cocoon production in *Centris pallida* is quite different (see below), but these processes have been generally ignored for other species of *Centris* and other Centridini, although Roubik and Michener (1980) offered an informative account of fecal deposition in *Epicharis zonata,* which does not spin a cocoon.

The bottom of the cocoon showed no mandibular scrapings to suggest that the larva perforated the cell lining as is the case with most diphaglossine bees (Rozen, 1984).

Mature larvae of *Centris caesalpiniae* were remarkably flaccid and slumped in the bottom of the cell with the anterior part of their body uppermost (fig. 15). Their posterior part was so formless that it merely conformed to the shape of the curvature of the larval chamber. They were covered with a thin layer of dark brown liquid or semiliquid, with an acrid phenoliclike odor, particularly in creases and wrinkles in the integument. This coating contrasted sharply with the white crusty coating on *Ericrocis* larvae, described below, although perhaps the function or functions of the coatings were similar. Although its source is unknown, this thin film may serve as waterproofing or as a barrier against microbial pathogens. A similar reddish-brown surface coating with an acrid odor has been noted in other bee larvae, especially *Nomia* and *Ptiloglossa* (Buchmann, unpubl. obs.) and in some halictines (G. C. Eickwort, in litt.).

ADULT EMERGENCE: As reported by Coville et al. (1983) for *Centris segregata,* adults of *C. caesalpiniae* bite their way through the cell closure as they emerge using their long, sharp mandibles. They make an incision in the cocoon at the periphery of the cell closure and then slice their way through the periphery of the closure itself.

We were able to recover from most vacated cells the excised cell closure to which the central part of the cocoon cap was attached. These disks (diameter 6 mm), with the spout on the outside and silk on the inside, rested in the bottom of the cell with loose backfill pushed into the cell as the adult emerged. *Centris* did

not use liquid to soften the cell cap as JGR has observed *Anthophora abrupta* Say doing in cells without cocoons.

We known of only two emergences of *Centris caesalpiniae*: this one in late April and May and one in late August 1968, perhaps suggesting that the species is double brooded.

We are unable to explain where the emerging adults went in the case of the recent finding. Careful walking inspections by us and five other individuals within a distance of 1.0–1.5 km from the site failed to locate a new nesting area used by females during the 1989 season. Not only did these robust fliers disappear from the site without starting new nests there (also true for the 1968 site), they were also out of synchrony with plant blooming, for all *Larrea* flowering had ceased by the middle of the emergence.

Some other large desert bees are known to move their nesting site every year (e.g., *Diadasia rinconis* Cockerell, Buchmann, personal obs.; *Diadasia diminuata* [Cresson], Eickwort et al., 1977) or every few years, presumably to avoid heavy parasitism from bombyliid flies, mutillid wasps, or cleptoparasitic bees. The extremely low parasitism (see below) found at this site supports this hypothesis.

MATING BEHAVIOR: Premating and mating behavior will be detailed separately from filmed copulations, sound recordings, and other data by SLB and H. Spangler (in prep.). The following is a general overview so as to complete the picture of nesting activity.

Centris caesalpiniae was protandrous with males tending to emerge from natal cells ahead of females. Females chewed their way free from cells but did not dig all the way to the surface. Instead they waited a few centimeters below the surface to be located, dug out, and mated later, as has been reported of *C. pallida* (Alcock et al., 1976b, 1977, and Alcock and Buchmann, 1985). The most striking feature of sexual selection operating on *C. caesalpiniae* was the dimorphism in males. The majority of the males, probably 95–98 percent, were large gray and light brown bees, usually larger or much larger than females, and possessed green eyes and yellow faces. These large males flew rapidly from 10–50 cm above the emergence site and only rarely departed to take nectar. Every few minutes they alighted to walk and antennate the soil surface. When they found a location, presumably by olfactory cues, they began a vigorous digging to uncover virgin females. The larger males were usually successful in finding and protecting a potential mate until the pair flew away.

The remaining few percent of the males were strikingly different since they were the same size as or smaller than most females. They also had dark brown/black coloration similar to that found in females. These smaller males were highly territorial and chased each other as well as other insects while patrolling flowering and nonflowering creosote bushes at the periphery of the emergence site. These males were observed capturing females at plants and mating. This alternative mating strategy may allow males to locate virgin females somehow escaping from the large digger males, or perhaps these males are the last to mate with females and thereby gain progeny through sperm precedence.

After a digger male unearthed a female, he usually flew the pair off to a safe site on a nearby plant. Pairs were in contact for long periods (1–5 minutes) with one to three or even six bouts of intromission and a characteristic rasping sound produced by the male.

PARASITISM: The cells removed from the 0.25 m^2 sample plot indicated that the percentage of survival of *Centris caesalpiniae* in the nest was high (table 1). Of the 325 cells, 201 *Centris* adults had emerged and 107 cells contained live larvae, pupae, or teneral adults of *Centris* that presumably would have flown, so that only 17 cells produced no *Centris* survivors. Eleven of the 17 cells contained fungal hyphae, but we cannot determine whether the fungus was the cause or the result of the *Centris* not developing. Only one cell contained a live arthropod parasite of any sort, a larva of *Ericrocis lata.*

However, the 0.25 m^2 sample did not yield examples of all the nest parasites. From other cell samples taken at the nesting site, nine other *Ericrocis* larvae were recovered in the spring and two more in August. One, collected on April 22, pupated on May 6, and emerged as an adult 20 days later. Information on the biology and cocoons of *Ericrocis* follows as do descriptions of the larva and pupa. We observed and collected many males and females of an unidentified species of *Das-*

ymutilla at the site and reared a few adults of a sphaeropthalmine mutillid from other cells. A single coarctate meloid larva was also uncovered. Bombyliids were occasionally seen flying or resting on soil surfaces in the emergence area, but were never abundant and were not reared from any cells.

BIOLOGY OF *ERICROCIS LATA*

None of the cells containing *Ericrocis* larvae revealed how the cleptoparasite egg had been introduced into the chamber. Other ericrocines are known to insert eggs into closed cells (Rozen and Bennett, in prep.).

The 12 *Ericrocis* larvae uncovered were quiescent postdefecating forms in their cocoons with their anterior ends higher than the tip of the abdomen (fig. 16).

Cocoons (figs. 16, 25) of this cleptoparasite were immediately distinguished from those of the host and therefore permitted easy field recognition. Whereas *Centris caesalpiniae* cocoons were medium brown, soft (like tissue paper), and easily compressed, those of *Ericrocis lata* were dark brown, tough, leathery, and 0.3–0.4 mm thick throughout. By contrast the cocoon wall of *Centris* was less than 0.1 mm thick. Feces of *C. caesalpiniae* (fig. 15) always formed a hard platform beneath the larva; those of *Ericrocis* (fig. 16) were incorporated in the leathery cocoon fabric and surrounded the larva. However, like *Centris* cocoons, those of *Ericrocis* adhered to the cell wall, took on its contours, and possessed a nipple (figs. 26, 37) which fitted into the base of the closure spout.

The outer surface of the cocoon was composed of a dense mat of coarse reddish fibers without sheetlike silk. Feces were intermixed with these fibers, especially toward the inside of the cocoon. The inner cocoon surface may have consisted of some loose silk fibers, but details were obscured by mold hyphae that covered the inner surface.

The structure of the nipple (figs. 33, 34) was similar to that of *Centris caesalpiniae,* consisting of many feltlike layers of fuzzy tan silk, one applied beneath the other, making a filter 5 mm in diameter and 2.7–3.0 mm high. The interior part of the nipple was quite hard as was the case also with *C. caesalpiniae.* Unlike *C. caesalpiniae,* the hard nipple core projected downward as well as upward (fig. 33), although the downward projection was obscured by the underlying soft layers of pale tan, fuzzy, tissue-paper-like fabric of fine silk. These layers (figs. 35, 36) were denser in the middle and more open around the periphery of the cocoon top. Comprised of threadlike silk only, they did not form a well-defined baffle, but the more open periphery (fig. 37) suggests that most gas exchange occurred there rather than centrally. The fabric in the center of the cocoon top (fig. 38) contained abundant hyphae and mold spores, more so than at the periphery. There was no sheetlike silk in any part of the filter nor in the entire cocoon.

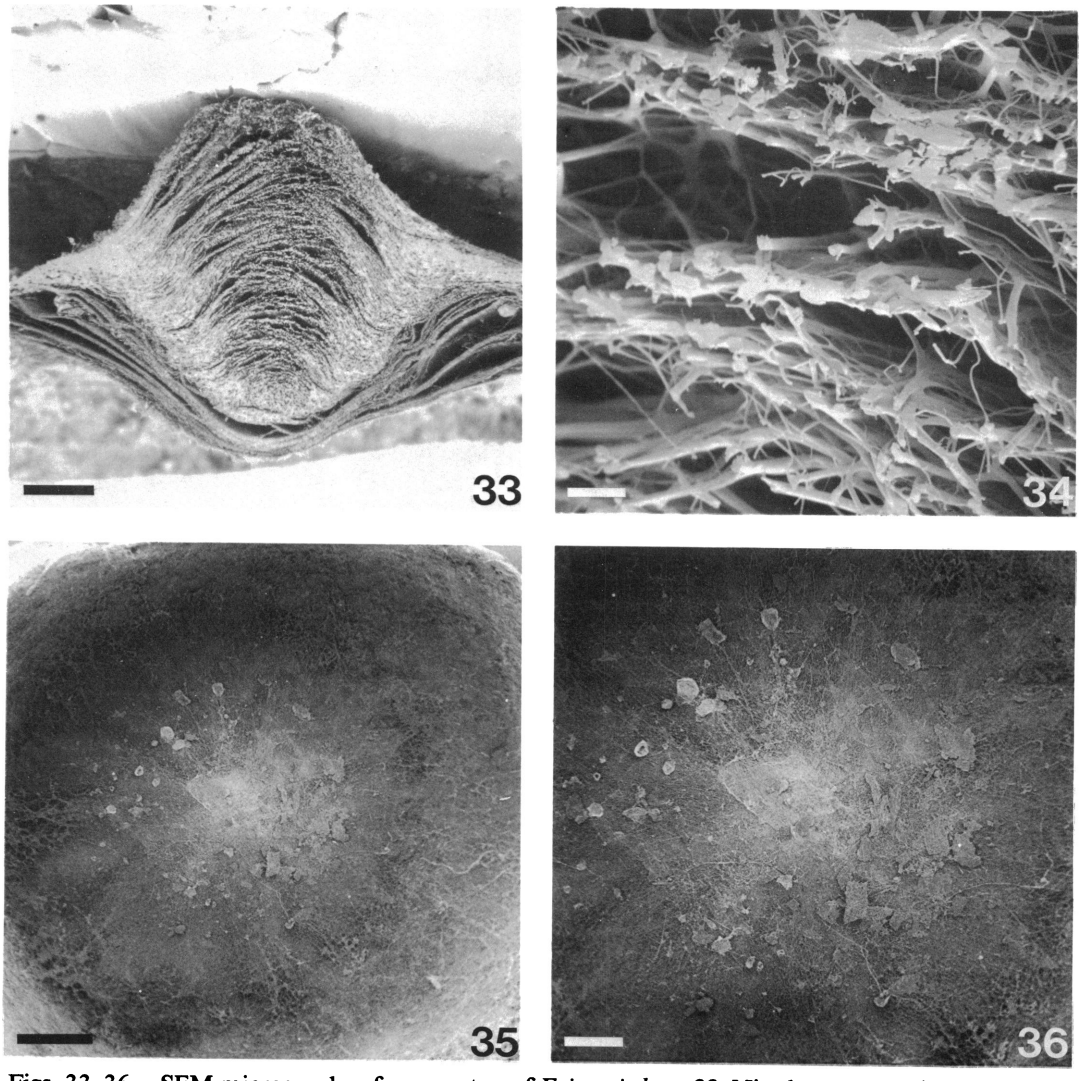
The distribution of fecal material (fig. 16) in the cocoon was substantially different from that of *Centris caesalpiniae* in that it was intermixed with silk fibers and covered the entire inner surface of the cell with the probable exception of the spout.

Coville et al. (1983) noted that the cocoon of another ericrocine, *Mesoplia rufipes* Perty, differed from that of its hosts *Centris segregata.* However, the *Mesoplia* cocoon was also markedly different from that of *Ericrocis* in that it consisted of two layers (not just one as in *Ericrocis*), a thin outer one and a thick, tough, ovoid inner one composed of densely fibrous, opaque, yellowish-brown material. The two layers were separated by a 1–2 mm space filled by loose matrix of silk threads.

Mature *Ericrocis* larvae were rigid and covered with a thin semitransparent white dry crustlike material that could be teased in flakes from the specimen. This crust, the interior surface of which was evenly papillate, conformed to the larva, but was slightly separated from it. The coating was probably a secretion, which perhaps reduced water loss or parasite attack. Beneath, the larval integument was yellow and soft, in general normal.

The interior of *Ericrocis* cocoons contained more mold than is generally found with other bee cocoons (Rozen, unpubl. obs.).

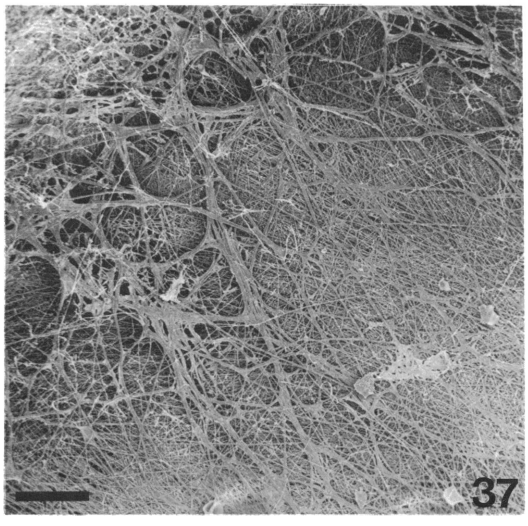
The synchrony of emergence of *Centris caesalpiniae* and *Ericrocis lata* is unclear. All individuals of the host bee emerged either during the spring study or shortly afterward. On the other hand, no adults of the cleptoparasite were encountered, and all 10 individuals excavated in the spring were post-

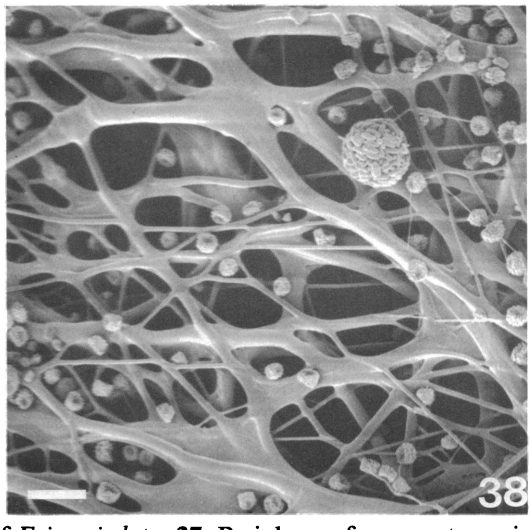


Figs. 33–36. SEM micrographs of cocoon top of *Ericrocis lata*. **33.** Nipple, cross section (scale = 500 μm). **34.** Cross section of feltlike layers, more highly magnified than in figure 33 (scale = 20 μm). **35.** Cocoon top, inner view (scale = 1 mm). **36.** Center of cocoon top more highly magnified than in figure 35 (scale = 500 μm). Irregular flakes in figures 35 and 36 are probably from the crusty coating of the larva of *E. lata*.

defecating larvae, only one of which pupated during the host emergence period. *Ericrocis lata* larvae removed to the laboratory remained unchanged during the following four months at the end of which most were preserved. Three remaining larvae had not pupated by the end of December. A single vacated cocoon of *Ericrocis* was encountered at the site in May, suggesting that a small fraction of the cuckoo bees had emerged. This cocoon had the top cut away, leaving a circular opening, 7 mm in diameter.

When JGR revisited the site on August 16, 1989, no adult *Centris caesalpiniae* were present although several other species of *Centris* were occasionally seen. A number of *Ericrocis* males were feeding at *Larrea* flowers. Excavating the site further, he recovered one vacated cocoon of *Ericrocis* with a circular opening 6.5 mm in diameter, two live post-





Figs. 37, 38. SEM micrographs of cocoon top of *Ericrocis lata*. **37.** Periphery of cocoon top, view comparable in position and magnification to that of figure 31 (scale = 200 μm). **38.** Fabric near center of cocoon top, inner view, showing mold spores and hyphae (scale = 10 μm).

defecating *Ericrocis* larvae in cocoons, and no live host immatures but numerous vacated cells or cells with dead *Centris*.

These facts indicate that *Ericrocis lata* is neither restricted to, nor firmly synchronized with, *Centris caesalpiniae* and that it will parasitize the nests of other available *Centris* species nesting in the area when it emerges. A cleptoparasitic bee with this strategy might be expected to have a distribution greater than any single host species and an extended flight period. We already know that *Ericrocis lata* ranges from California to Florida (Snelling and Zavortink, 1984) whereas *C. caesalpiniae* is restricted to Arizona, New Mexico, Texas, and Chihuahua (Hurd, 1979). Collection records over its range show that *E. lata* flies every warm month from March to October (Snelling and Zavortink, 1984).

NESTING BIOLOGY OF *CENTRIS PALLIDA*

We add the following information on the nesting of *Centris pallida* to that already presented by Alcock et al. (1976a) and Alcock (1979). Our observations agreed with theirs, except where noted. We studied one site behind the home of SLB on Liddell Drive, north of Tucson, Pima Co., AZ (UTM grid coordinates: Zone 12, N3579520 E500320) (fig. 39) on May 7, 1987, and another site at Shannon Road and Hardy Road outside of Tucson (UTM grid coordinates: Zone 12, N3580840 E4970260) on May 26, 1988.

DESCRIPTION OF SITES: At both sites nests were actively being constructed and provisioned at the time of study. Entrances were randomly distributed over nearly horizontal surfaces. A few entrances were as close as 10 cm apart, but most were much more distant. In the densest concentrations there were only approximately three nests per m^2. Surrounding vegetation included *Prosopis velutina,* food plants (*Cercidium floridum, C. microphyllum,* and *Olynea tesota*), several species of *Opuntia, Ambrosia, Larrea tridentata, Celtis,* as well as sparse typical Sonoran desert-scrub including annuals and grasses. Nest entrances were generally unshaded and often at the edge of slight depressions or near clumps of low grass or triangular leaf bursage (*Ambrosia deltoidea*).

NEST ARCHITECTURE: Tumuli of loose soil occurred at one side of entrances, all of which lacked turrets, the absence of which is characteristic of all known Centridini. Main burrows (figs. 10–14), 10–12 mm in diameter, were open and descended obliquely at an average angle of 30° from horizontal. However, their rate of descent was variable, and they angled and meandered (in contrast to the bur-

Fig. 39. Nesting area of *Centris pallida* on Liddell Drive, north of Tucson, Arizona. Nests were widely and sparsely scattered in flat foreground and middle ground.

row diagrammed by Alcock et al., 1976a: fig. 5). Burrow walls were rough, unlined, and of the same consistency as the substrate. Immediately above the cell the burrow expanded into a chamber, the wall of which was rough and not smoothed as is the case in *Centris caesalpiniae* (but see below). This enlargement presumably permitted the female to construct, provision, and close the cell.

Nests contained one or two cells (only single-celled nests reported by Alcock et al., 1976a, but Alcock, 1979, observed rare double-celled nests). When two cells were present, they were far apart or close together, there being no definite pattern.

Cells at a depth of 6–15 cm (N = 11) (measured from ground surface to cell top) were oriented nearly, but not exactly, vertically. The plane of the cell cap was 10–15° from horizontal. Internal cell shape was similar to that of *Centris caesalpiniae* but more uniform in size. Cell walls, made of soil, were conspicuously harder and denser than the substrate, and they were approximately 2 mm thick. On closed cells the walls projected a short distance above the closure, and on open cells they extended 3–5 mm above the narrowest part of the cell opening and flared outward. Hence this upper part of the cell may correspond to the funnel above the cell of *C. caesalpiniae*. Unlike those of *C. caesalpiniae*, the cell walls of *C. pallida* disintegrated when submerged in water (even though they were lined with waterproof material). The nature of the hardening substance is unknown but might be either a glandular secretion or material (such as *Cercidium* nectar) brought into the nests. This species, unlike *C. caesalpiniae*, lacks modified basitibial oil scraper setae (Buchmann, 1987), a difference that may reflect the dissimilar substances used by two species in hardening their cell walls.

The inner cell surface was smooth but not shiny, and possessed a thin, waterproof lining. The smoothness, contrasting with the uneven inner surface of the burrow walls, extended to the topmost part of the open cell, although its lining (and water retardant nature) did not extend onto the flared cell rim. The lining was difficult to detect, but when a

piece of cell wall was placed in water, the wall crumbled and the lining remained intact as a thin, soil-coated film.

Inside cell dimensions were: diameter at top 10–13 mm (N = 4); diameter at narrowest constriction (mouth, closure attachment) 7.5–9.0 mm (N = 9); maximum diameter 10.0–12.0 mm (N = 9); and length from constriction to bottom 15.0–19.0 mm (N = 6). Outside dimensions were: maximum diameter 16.0–18.5 mm (N = 6); and outside length (from top of rim to bottom) 19–23 mm (N = 5).

Cell closures (figs. 23, 24), 2.0 mm thick, were also different from those of *Centris caesalpiniae.* Their upper surface bore a nearly central low mound that corresponded to a pit on the under surface, as pointed out by Alcock et al. (1976a). This structure did not possess a passageway connecting the cell lumen with the burrow, as is characteristic of *C. caesalpiniae* and some other species (see section on *C. caesalpiniae*). However, as with other known *Centris* species, there was no indication of a spiral structure on the inside. The closure seemed to be constructed of the same material as the cell wall, and, when tested with a water droplet, was not waterproof on either the upper or lower surfaces. Because the closure of *C. pallida* bears no spoutlike opening, gas exchange is apparently possible through the nonwaterproof cell closure.

PROVISIONING: As described also by Alcock et al., (1976a), provisions were very moist, sticky, mostly liquid on top, and with more pollen below. They filled the lower part of the cell and their meniscus curved upward at the cell wall. One cell, only partly provisioned, contained the sticky mixture of pollen and nectar only 3.0 mm deep at the bottom, but the liquid extended up the sides to within 5.5 mm of the cell constriction.

DEVELOPMENT: One egg, 4.0 mm long and 0.8 mm in maximum diameter, was curved and had a rounded anterior end and a more tapering posterior end. Its chorion was opaque white, highly hydrofuge, and matte, presumably because of submicroscopic sculpturing. Eggs were placed on the center of the provisions and touched the food only with the anterior and posterior ends.

First instars remained within the chorion, which was split in a line on each side along the spiracles. Still curved and touching the provisions only at the front and rear ends, they fed on the food mixture; the orange pollen was visible in their guts and their tracheae were filled with air.

The structure of the cocoon and pattern of defecation of *Centris pallida* are based on a vacated cocoon and on three cocoons that were spun after the cells containing them had been collected, all from the sites identified above. However, the information was supplemented by examining cells (collected from 1972–82) of the same species from South Mountain Park near Phoenix, AZ. Cocoons of *C. pallida* differed in a number of significant ways from those of *C. caesalpiniae.* Cocoons of both were identical in shape, in that they conformed to the inner surface of the cell and had a nipple centered on the top that occupied the invagination of the lower surface of the cell closure. Also, just as in *C. caesalpiniae,* the nipple of the cocoon of *C. pallida* projected only upward (thereby differing from that of *Ericrocis lata*) and consisted of multiple layers of feltlike silk. However, the baffle on the inner surface, instead of being constructed of sheetlike silk, was formed from pale tan threadlike silk with some hardening substance (perhaps feces) smeared on the center of the inner surface. The ring of soft fiber surrounding the baffle was similar to that of *C. caesalpiniae* in that it was apparently open enough to permit exchange of gases between the inside of the cocoon and the burrow. The remainder of the cocoon cap was mostly silk although irregular smears of very dark material (feces?) were sparsely incorporated in it. The external silk of the cap extended onto the walls of the cocoon but ended or became much thinner several millimeters down the sides.

Feces of *Centris pallida* were applied to the sides and bottom of the cell and provided the completed cocoon with a pronounced rigidity over the entire surface. By contrast, the feces of *C. caesalpiniae* were placed only at the bottom of the cocoon as a thick stratum so that the sides of its cocoon, without feces, were weak and easily compressed. With both bees the feces were very dark brown, almost black, and dried into a hard, tough mass. The larva of *C. pallida* apparently incorporated

some silk into the feces and certainly applied a layer of fibrous dark silk over the entire inner cocoon wall. The inner surface, almost black, glistened as if it were composed of threads of silk covered with shellac. Whereas the larval chamber of *C. caesalpiniae* was truncated on the bottom (as seen in side view, fig. 15) because of the stratum of feces, that of *C. pallida* curved very much as did the cell surrounding it. The outside bottom of the cocoon was irregular in shape and lacked an outside layer of silk, as was also the case for *C. caesalpiniae.* On the sides the cocoon and feces of *C. pallida* were 0.2–0.3 mm thick; at the bottom 1.0 mm thick. The cocoon of this species was similar to that of *Ericrocis lata* in its toughness and superficial appearance although the cocoon of *C. pallida* did not have so many silk fibers on the outside except for those extending down from the cell cap a short distance. Whereas the cocoon bottom of *Ericrocis lata* was evenly rounded, conforming to the cell bottom, those of *C. pallida* and *C. caesalpiniae* were irregular because of the uneven bottoms of the meconial masses.

Because the cell wall of *Centris caesalpiniae* was hard and waterproof, the cell might float when washed from the soil by heavy rains and thereby enable the larva to survive. Although cell walls of *C. pallida* would be destroyed under similar stress conditions, the tough, waterproof cocoon of *C. pallida* would provide the same protection afforded by the cell wall of the other species.

MATURE LARVAE OF *CENTRIS*

As illustrated in Rozen (1965), mature *Epicharis* larvae are easily distinguished from larvae of other known centridines, because *Epicharis* larvae do not spin cocoons and therefore lack a projecting labiomaxillary region. They also exhibit dorsal transverse rows of pigmented spines on most body segments, unlike any other bee larvae. The key to other centridines presented by Rozen (1965) is now unsatisfactory, because of the taxa treated here. The larva of *Ptilotopus derasa* (Lepeletier) (described in *Centris* by Rozen, 1965) does not seem significantly different from larvae of known *Centris.*

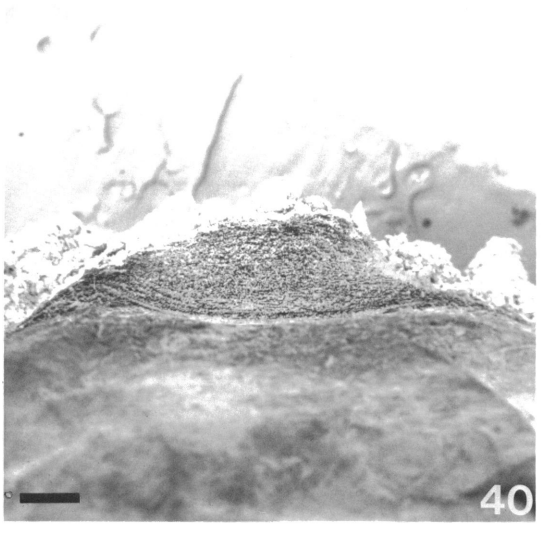
The following descriptions are comparative with the description of the mature larva of *Centris* (*Hemisiella*) *tarsata* Smith (as *C. lanipes* [Fabricius] fide Padre J. S. Moure, in litt.) (Rozen, 1965). However, they include additional features now thought to be taxonomically important for anthophorids and other long-tongued bees. Consequently they follow the format and terminology adopted for *Paratetrapedia swainsonae* by Rozen and Michener (1988).

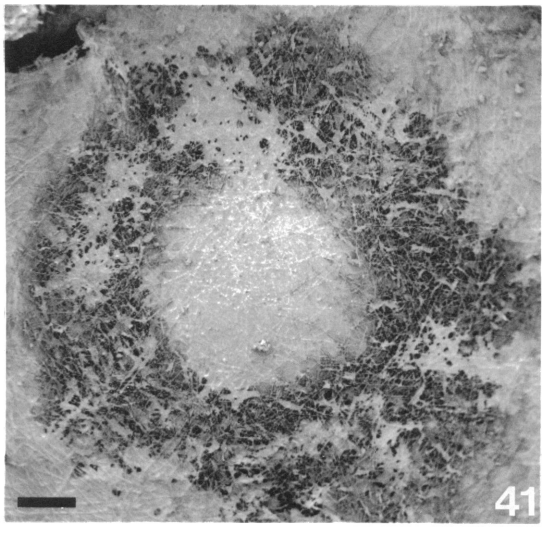
POSTDEFECATING LARVA OF *CENTRIS CAESALPINIAE*
Figures 43–48

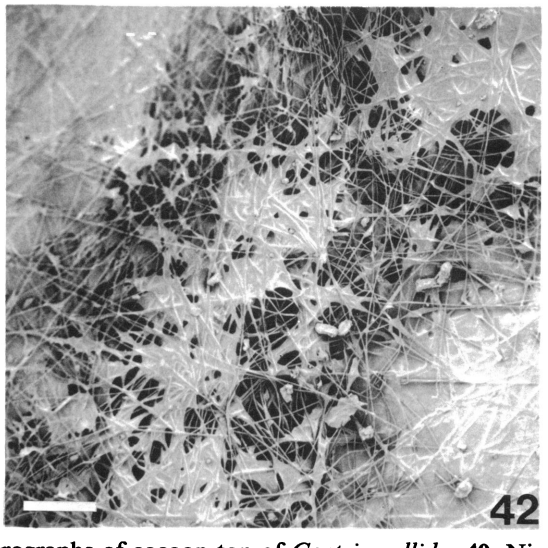
DIAGNOSIS: The mature larva of *C. caesalpiniae* differs little from other *Centris* larvae. The dense spiculation at the apex of the epipharynx, the very wide salivary lips, and the shiny but unpigmented integument on the dorsal tubercles will separate this species from *C. pallida* and perhaps most other members of *Centris* and *Ptilotopus.*

HEAD (figs. 44, 45): Integument with scattered sensilla, those of maxilla and labium long and strongly setiform; dorsal surface of maxilla spiculate; dorsal surface of labium as well as plate subtending salivary lips irregularly and weakly spiculate; epipharyngeal surface thickly beset with long sharp spicules; hypopharynx weakly spiculate. Mandibular apices, mandibular articulations, bases of mandibular apodemes, and articulating arm of stipital sclerite pigmented; other sclerotized areas at most faintly pigmented.

Head size small (fig. 43) in relation to robust body; head capsule about as wide as long. Tentorium incomplete on specimen examined but probably complete and well developed on specimens not about to molt; anterior tentorial pits low on face, nearly adjacent to anterior mandibular articulations; posterior tentorial pits normal in position; posterior thickening of head capsule well developed, only slightly bending forward medially as seen in dorsal view; longitudinal thickening of head capsule well developed dorsally but fading well before halfway point to level of antennae; hypostomal ridge well developed and without dorsal ramus; pleurostomal ridges well developed; epistomal ridge well developed laterad of anterior tentorial pits but less developed, though distinct, mesad of pits. Parietal bands faintly developed. An-



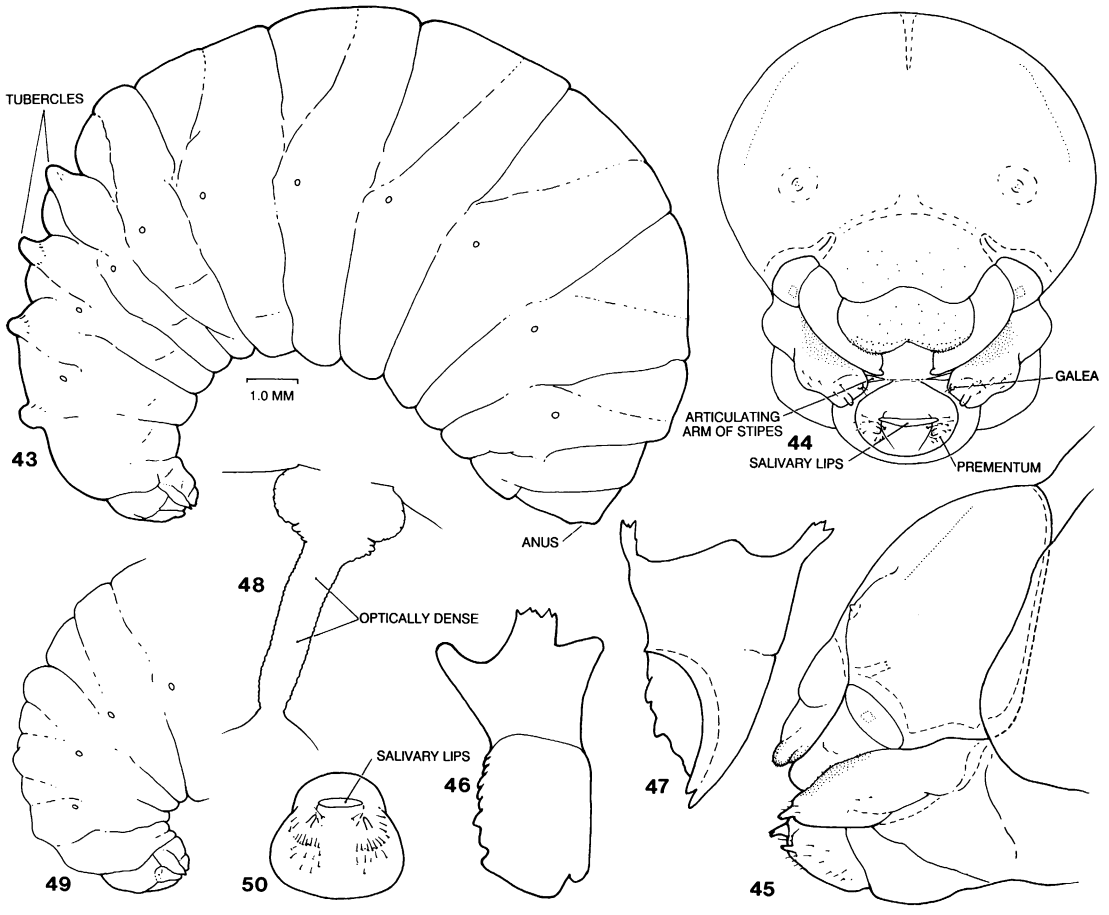




Figs. 40–42. SEM micrographs of cocoon top of *Centris pallida*. **40.** Nipple, cross section (scale = 500 μm). The compressed condition of the nipple was due, at least in part, to difficulties in cutting the fabric to which sand particles adhered. **41.** Center of cocoon top, inner view, showing central baffle and surrounding silk strands holding it in place (scale = 500 μm). **42.** More highly magnified view of silk strands holding baffle (lower left) in place, comparable to figure 31 (scale = 200 μm). The irregular shiny areas seeming to glue these strands in some places in figures 41 and 42 are actually dark smears (possibly feces) that become reflective when coated in SEM preparation.

tennal prominences weakly developed, each without distinct depression above antenna; each antennal papilla small, little projecting, bearing three sensilla. Vertex evenly rounded, as seen from side, without unusual projections or tubercles; clypeus narrow in frontal view; frontoclypeal area normal in lateral view, not projecting beyond labrum. Labrum not projecting strongly beyond clypeus; labral sclerite not evident; forward-directed labral tubercles absent; anterior labral margin bilobed but without swellings.

Mandibles (figs. 46, 47) massive, broadly rounded apically, with pronounced apical scoop-shaped concavity; dorsal spiculation near apex; outer surface without conspicuous



Figs. 43–48. *Centris caesalpiniae,* postdefecating larva. **43.** Entire larva, lateral view. **44, 45.** Head, frontal and lateral views. **46, 47.** Right mandible, inner and ventral views. **48.** Spiracle, side view. Figs. 49, 50. *Centris pallida,* postdefecating larva. **49.** Anterior part of larva, lateral view. **50.** Prementum and salivary lips, frontal view. Scale refers to figures 43 and 49.

seta-bearing tubercles but with a few setae on small tubercles; apex broadly rounded and bearing ventrally single rounded subapical tooth, as is characteristic of all known *Centris* and *Ptilotopus*; dorsal edge of concavity irregularly toothed, with teeth not as distinct as those of *Centris tarsata*; concavity without spines or pits; mandible lacking denticulate, defined dorsal adoral surface in contrast to that of *Paratetrapedia* (Rozen and Michener, 1988). Labiomaxillary region (fig. 45), as is characteristic of cocoon-spinning larvae, produced and not greatly fused. Maxillary apex not produced or bent mesad; cardo and stipes sclerotized although not deeply pigmented; articulating arm of stipes distinct; palpus apical, elongate; galea distinct, bearing two elongate setae. Labium strongly projecting, divided into prementum and postmentum, and bearing wide slitlike salivary opening apically; premental sclerite not pigmented or defined in other ways; area beneath salivary lips nearly flat, platelike, faintly pigmented, defined laterally by grooves, and bearing conspicuous seta immediately beneath lips on each side; labial palpus somewhat smaller than maxillary palpus. Salivary lips projecting and, in contrast to those of *C. pallida,* lips about two-thirds maximum width of prementum as seen in frontal view (fig. 44). Hy-

popharynx normal in size, bilobed, exceeded by labiomaxillary region; hypopharyngeal groove deeply impressed.

BODY: Integument finely granulate in some areas, mostly nonspiculate except for very fine spicules above anus, and with widely scattered, fine setae, especially on abdominal segment 10; body without sclerotized spines (as in *Epicharis*); integument of dorsal tubercles of thorax and abdominal segment 1 unpigmented but smoother and shinier than surrounding integument. Form (fig. 43) robust; intersegmental and intrasegmental lines of thorax and abdominal segment 1 well incised but those of following segments far less so because of flaccid nature of rest of body; thoracic segments and caudal annulet of abdominal segment 1 each with pair of low transverse dorsal tubercles, these tubercles becoming wider on each successive segment; other abdominal segments without tubercles; most abdominal segments divided dorsally into cephalic and caudal annulets; venter of abdominal segment 9 not produced; abdominal segment 10 short; anus dorsal. Spiracles (fig. 48) normal in size, without spiracular sclerites; peritreme flat or nearly so; atrium projecting, with rim; atrium shallow in relation to diameter; atrial wall indistinctly ridged and granulate, without spines; primary tracheal opening without distinct collar but opening obscured by the fine annulations of subatrium below and ridges at bottom of atrium; subatrium composed of numerous, even but indistinct, fine annulations (perhaps 30–40); subatrium wide at attachment of atrium but narrowing immediately below attachment apparently due to longitudinal folding of integument which is subgranulate; because of granulations and folding, subatrium appearing optically dense under compound microscope.

MATERIAL STUDIED: 5 postdefecating larvae, 5 mi east of Sahuarita, Pima Co., AZ, May 3, 1989 (J. G. Rozen, S. L. Buchmann).

MATURE LARVA OF *CENTRIS PALLIDA*
Figures 49, 50

DIAGNOSIS: Unlike in other *Centris* and in *Ptilotopus*, the thoracic segments and abdominal segment 1 of the mature larva of this species are not produced into dorsal transverse tubercles covered with shiny, sclerotized, or pigmented integument.

HEAD: As described for *Centris caesalpiniae* except for following: Spiculation greatly reduced so that only lateral parts of epipharynx distinctly spiculate.

Head capsule clearly wider than maximum length from top of vertex to lower clypeal margin. Tentorium complete and well developed; longitudinal thickening of head capsule ending approximately midway to level of antennae; midsection of epistomal suture well developed. Each antennal prominence with distinct, shallow depression dorsomesad of antenna.

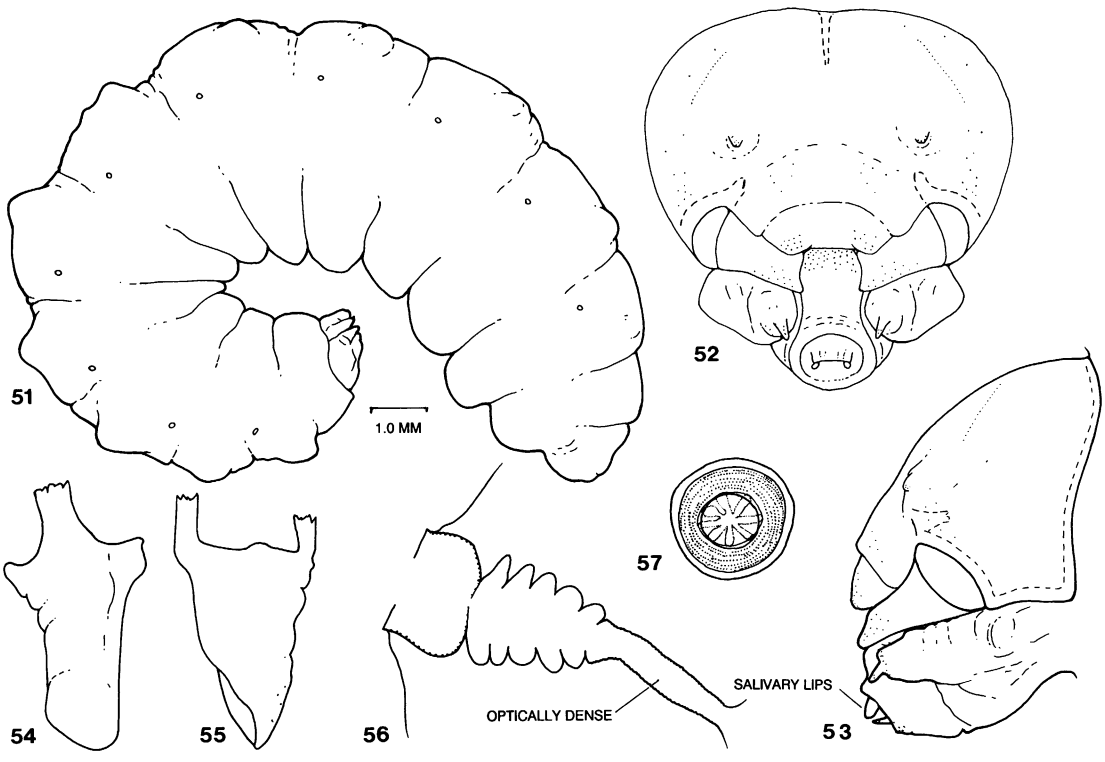
Area beneath salivary lips normally curved, unpigmented, defined only faintly laterally by grooves, but bearing conspicuous seta on each side beneath lips. Salivary lips (fig. 50) narrow by comparison with those of *C. caesalpiniae*, about one-third maximum width of prementum as seen in frontal view.

BODY: As described for *Centris caesalpiniae* except for following: Integumental spiculation apparently reduced; integument of thorax and abdominal segment 1 uniformly wrinkled dorsally, without shiny tubercles (fig. 49). Intersegmental and intrasegmental lines of thorax and abdominal segment 1 less deeply incised than those of *C. caesalpiniae* so that lines of these segments less contrasting with those of following segments; thoracic segments and abdominal segment 1 (fig. 49) without distinct paired tubercles.

MATERIAL STUDIED: 3 larvae, Hardy Rd. and Shannon Rd., north of Tucson, Pima Co., AZ, collected May 26, 1988, preserved as postdefecating larvae August 8, 1988 (J. G. Rozen, S. L. Buchmann); 1 larva same except collected May 25, 1988, preserved as predefecating larva June 15, 1988.

POSTDEFECATING LARVA OF *ERICROCIS LATA*
Figures 51–57

The following description is comparative with that of *Acanthopus splendidus urichi* Cockerell (Rozen, 1969), but we use the description format employed above for *Centris* larvae.



Figs. 51–57. *Ericrocis lata,* postdefecating larva. **51.** Entire larva, lateral view. **52, 53.** Head, frontal and lateral views. **54, 55.** Right mandible, inner and ventral views. **56, 57.** Spiracle, side and top views. Scale refers to figure 51.

DIAGNOSIS: The larva of this species shares many unusual features with that of *Acanthopus splendidus urichi,* as mentioned below. Some of the same features agree with what is known of the larva of *Mesoplia rufipes* (Perty) (Rozen, 1969). These facts suggest that larval Ericrocini may be both homogeneous and distinctive. (Although Pickel, 1928, described a larva identified as that of *Acanthopus excellens* Schrottky, his description is obviously not of a bee and probably refers to a meloid.) The larva of *Ericrocis lata* can be distinguished from *A. splendidus urichi* because the former lacks an epistomal ridge between the anterior tentorial pits, its atrium is less heavily denticulate, and its clypeus is less protuberant.

HEAD (figs. 52, 53): Integument with scattered sensilla, most of which are nonsetiform; integument nonspiculate except for hypopharynx which bears distinct, regularly spaced, but not dense spicules. Mandibular apices very dark; much of rest of integument brownish.

Head size normal in relation to body; head capsule wider than maximum length from top of vertex to lower clypeal margin. Tentorium complete, well developed, and with dorsal tentorial arms; anterior tentorial pits low on face, nearly contiguous to dorsal mandibular articulations, in contrast to those of *Acanthopus splendidus urichi* which are somewhat higher; posterior tentorial pits normal in position; posterior thickening of head capsule moderately developed, not bending forward medially as seen in dorsal view; longitudinal thickening of head capsule well developed dorsally, fading out about two-thirds distance from vertex to level of antennae; hypostomal ridge well developed, without dorsal ramus; pleurostomal ridge moderately developed; epistomal ridge well developed but short laterad of anterior tentorial pits; ridge absent mesad of pits; in con-

trast, epistomal ridge of *A. splendidus urichi* with longer lateral sections and with distinct, upward-arching median section. Parietal bands faint. Antennal prominences not developed; each antennal papilla, like that of *A. splendidus urichi,* moderate in size, projecting downward, and bearing numerous sensilla apically. Vertex evenly rounded as seen from side, without projections or tubercles; clypeus moderately narrow in frontal view; frontoclypeal area normal, not projecting beyond labrum in lateral view; clypeus not so strongly projecting as in *A. splendidus urichi.* Labrum not projecting strongly beyond clypeus; labral sclerite not evident; as in *A. splendidus urichi,* labrum unusually short; forward-directed labral tubercles absent; apical labral margin weakly bilobed. (When the mature larva of *A. splendidus urichi* was described, Rozen, 1969, interpreted its apical lobes as being homologous to labral tubercles. This now seems unlikely because first instars of ericrocines do not have labral tubercles as do both the first *and* last instars of the Nomadinae. Hence, in the Ericrocini these lobes are believed to be the bilobed apical labral margin, and perhaps are homologous with the weakly bilobed apical margins of many Centridini.)

As in *Acanthopus splendidus urichi,* mandibles (figs. 54, 55) massive, short, obliquely truncate apically as seen in inner view, with pronounced apical scoop-shaped concavity; this concavity in both species appearing to accommodate very large bilobed hypopharynx when mandibles are closed; dorsal mandibular spiculation absent; outer surface with scattered short setae especially apically, without tubercles; obliquely truncate apex without teeth other than acute angle of truncation; concavity without spines or pits; mandible lacking denticulate, defined adoral surface in contrast to that of *Paratetrapedia swainsonae* (Rozen and Michener, 1988). Labiomaxillary region strongly produced. Maxillary apex not produced mesad; cardo and stipes weakly defined, poorly sclerotized; articulating arm of stipes not evident (also true for *A. splendidus urichi*); palpus elongate, apical; galea absent. Labium strongly projecting, divided into prementum and postmentum, bearing slitlike salivary opening apically; in contrast to *A. splendidus urichi,* premental sclerite scarcely defined; labial palpus smaller than maxillary palpus. Salivary lips projecting and apparently arising from labial apex that is retractable so that lips can be directed either forward or downward (fig. 53). Hypopharynx large, projecting both dorsally and laterally, bilobed, exceeded by labiomaxillary region; hypopharyngeal groove obliterated by enlarged hypopharynx which grades into dorsal surface of labium as in *A. splendidus urichi.*

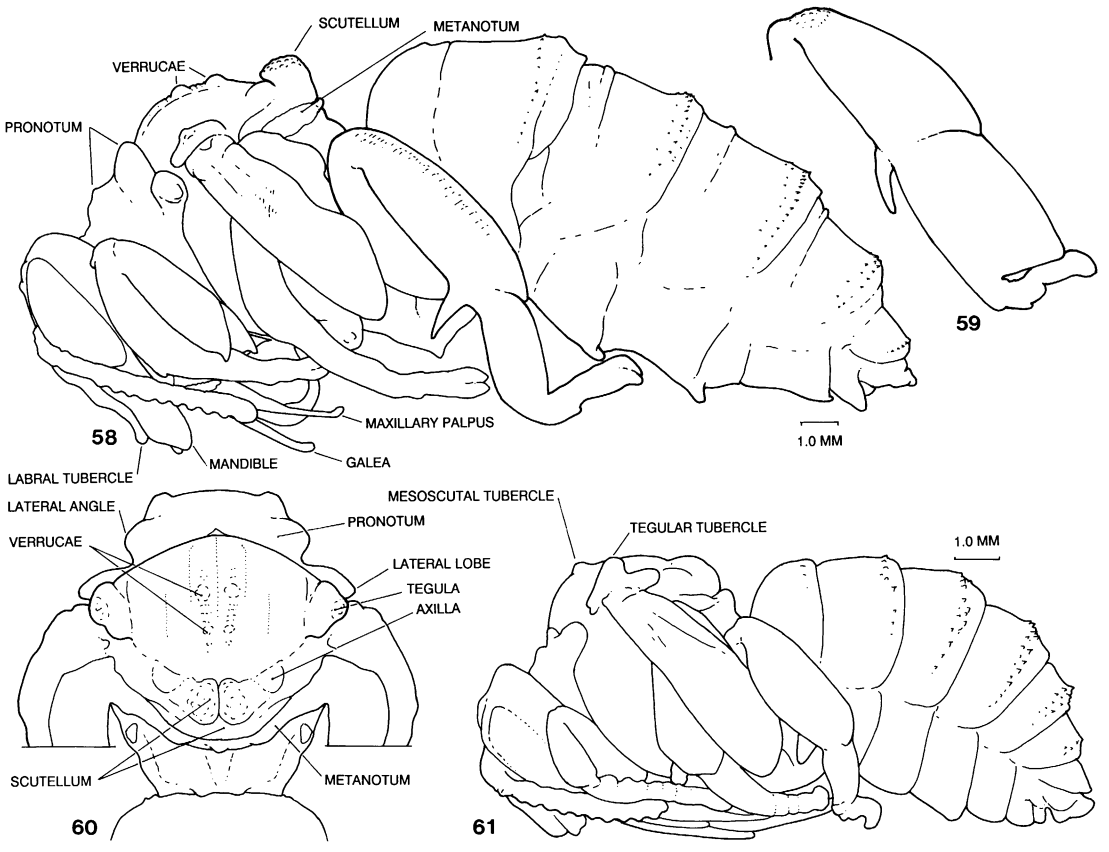
BODY: Integument finely granulated in some areas, nonspiculate, and without setiform sensilla; body without sclerotized spines; integument of paired dorsal tubercles nonsclerotized although anterior tubercles sometimes slightly pigmented. Form neither robust not slender; intersegmental lines moderately deeply impressed; intrasegmental lines very faint, scarcely evident; hence most abdominal segments not clearly divided dorsally into cephalic and caudal annulets; thoracic segments and abdominal segments 1–9 with low transverse tubercles which are on caudal annulets of abdominal segments; venter of abdominal segment 9 appearing protuberant because segment 10 small in lateral view and attached to body dorsally; anus apical in position. Spiracles (figs. 56, 57) normal in size, not surrounded by sclerites; peritreme flat; atrium projecting, with rim; atrium normally globose; wall with small, regular, distinct denticles arranged in concentric rows; primary tracheal opening guarded by fringed projections, similar to situation in *Acanthopus* and *Mesoplia* (Rozen, 1969: figs. 48, 53); subatrium consisting of about 5 distinct chambers to which is attached equally long, optically dense, finely annulated section (this inner section nearly identical to subatrium of *Centris caesalpiniae,* described above).

MATERIAL STUDIED: 5 postdefecating larvae, 5 mi east of Sahuarita, Pima Co., AZ, May 17, 1989 (J. G. Rozen), from cells of *Centris caesalpiniae*; 1 postdefecating larva, same except May 3, 1989 (J. G. Rozen, S. L. Buchmann).

PUPAE

PUPA OF *CENTRIS CAESALPINIAE*
Figures 58–60

DIAGNOSIS: Among the Centridini, the pupa of only *Epicharis rustica flava* has been de-



Figs. 58–60. *Centris caesalpiniae,* pupae. **58.** Male, lateral view. **59.** Hind leg of female, lateral view. **60.** Mesosoma of male, dorsal view. Fig. 61. *Ericrocis lata,* female pupa, lateral view. Scales refer to figures 58–60 and to 61, respectively.

scribed (Camargo et al., 1975). Because pupae of other centridine taxa are represented in the collections of the American Museum of Natural History, additional comparisons can be made. The pupae of *Centris caesalpiniae,* two other species of *Centris,* and *Ptilotopus derasa* lack strongly projecting paired mesoscutellar tubercles that are characteristic of *E. r. flava* (Camargo et al., 1975: fig. 8) and three other *Epicharis* species. Two of these *Epicharis* species as well as *E. r. flava* also have strongly projecting mesoscutal tubercles. *Ptilotopus derasa* is nearly identical to *C. caesalpiniae* but has strongly raised axillae which project nearly as far as the mesoscutellar projections. Other *Centris* species agree closely with the one described below, but differences in the size of the mesoscutal verrucae, extent of axillary projection, and other features will almost certainly be useful in distinguishing between species in the genus.

Male
Figures 58, 60

Except for body size and degree of swelling of the hind leg (discussed below), pupae of both large and small male morphs were identical.

Head: Integument nonspiculate; setae absent. Antenna without tubercles except for usual tuberclelike swellings on each flagellomere. Vertex without tubercles except for vague ocellar tubercles; frons and clypeus without tubercles; genal tubercle absent. Labrum bearing conspicuous rounded elongate median tubercle apically; mandible moder-

ately swollen subapically as seen from side; mandibular apex faintly pigmented; all paired mouthparts without large or small tubercles, except for apex of labial palpus which bears small inner tubercle making palpal apex appear bilobed in dorsal and ventral views.

MESOSOMA: Integument nonspiculate, nonsetose, verrucous in certain areas identified below. Lateral angles of pronotum conspicuously and acutely produced; lateral lobes also conspicuously and acutely produced as seen from above; mesepisternum with longitudinal linear series of rounded verrucae on each side of median line; midline groove faint; axilla produced, rounded, not projecting dorsally as far as scutellum; scutellum broadly produced dorsally and anteriorly on each side, so that midline deeply incised; produced areas verrucous; metanotum with transverse swelling on each side, but not medially, as seen in dorsal view. Tegula with vague rounded verrucous swelling but without distinct tubercle; wings with low verrucous swelling in middle of forewing but without tubercles. Forelegs with coxa bearing very large, sharp tubercle on inner apex; trochanter with moderate-size apical tubercle; femur with narrowly rounded basal tubercle; tibia without tubercles. Midleg with coxa bearing moderate-size apical tubercle; trochanter with small apical tubercle; other leg segments without conspicuous tubercles. Hind leg with coxa, trochanter, femur, and to lesser extent tibia greatly enlarged on large morph, corresponding to swollen hind leg of adult and contrasting with pupal hindleg of small male morph; coxa and trochanter each with small apical tubercle; femur with small but distinct, rounded apical tubercle on outer surface; tibia verrucous along basal dorsal edge, with small but distinct apical tubercle.

METASOMA: Integument nonspiculate, nonsetose. Tergum I without tubercles; tergum II with apical row of small tubercles, most evident laterally rather than medially; terga III–VII, each with apical band of distinct but small tubercles; these tubercles acute but not sharp-pointed, often apically pigmented; sterna without transverse bands of small acute tubercles, but sterna II–IV, each with single, posteriorly directed, median tubercle arising from apical edge; sternum V with similar but smaller median tubercle; apex of abdomen not bearing apical spine.

FEMALE
Figure 59

As described for male except for following: Midlegs with femur bearing small basal tubercle; tibia bearing small apical tubercle; basitarsus with apical projection. Hind leg (fig. 59) with verrucous area of tibia restricted to basitibial region. Metasomal terga I, II as described for male; III–VI each with apical band of distinct, small acute tubercles like those of male; sternum V with median tubercle absent.

MATERIAL STUDIED: 3 large male morphs, 2 small male morphs, 11 females, 5 mi east of Sahuarita, Pima Co., AZ, May 3, 1989 (J. G. Rozen, S. L. Buchmann).

PUPA OF *ERICROCIS LATA*, FEMALE
Figure 61

DIAGNOSIS: Because the pupae of a number of other parasitic anthophorids have been described and figured, the pupa of this species can be distinguished from them: *Zacosmia maculata* (Cresson) (Torchio and Youssef, 1968) and other pupal melectines (Thorp, 1969) possess a pair of large vertical, flattened mesoscutal tubercles that bear heavily sclerotized spines in contrast to the small, rounded, spineless paramedian mesoscutal tubercles in *Ericrocis lata.* The absence of tegular tubercles of *Protepeolus singularis* Linsley and Michener (Rozen, et al., 1978) sharply contrasts with the large tegular tubercles of *Ericrocis. Isepeolus viperinus* (Holmberg) (Michener, 1957) has two pairs of mesoscutal tubercles whereas *Ericrocis* has but one. Pupae of the Nomadinae (sensu Rozen, in prep.; i.e., excluding Isepeolini and Protepeolini) generally lack rounded mesoscutal tubercles (although they may have numerous small sharp-pointed scutal tubercles) and often have sharp-pointed large or small tubercles mesad of their compound eyes (Rozen and McGinley, 1974), as is also characteristic of *Zacosmia maculata.* In contrast, *Ericrocis* has distinct rounded mesoscutal tubercles, but no sharp-pointed tubercles on the top of its head. According to Camargo et al. (1975) the pupa of *Rhathymus* possesses a pair of large conical tubercles on the mesoscutellum although it lacks tubercles on the mesoscutum; *Ericrocis* has no mesoscutellar tubercles.

Hence, it is probably reasonable to say that the pupae of the parasitic Anthophoridae seem to possess many obvious diagnostic features for recognizing taxa. However, they are still too poorly known to be used as a source of characters for phylogenetic analysis.

HEAD: Integument nonspiculate, nonsetose. Scape and front without tubercles; vertex without tubercles; genal tubercle apparently absent; clypeus without tubercles. Labrum apically bilobed although lobes not pronounced; mandible without swelling on ventral surface; its apex darkly pigmented; paired mouthparts without tubercles.

MESOSOMA: Integument nonspiculate, nonsetose. Lateral angles of pronotum not produced; posterior lobe of pronotum not produced; mesepisternum without tubercle. Mesoscutum with single pair of rounded, small but distinct paramedian tubercles; mesoscutal midline a groove; axilla slightly swollen but not tuberculate; mesoscutellum slightly swollen on each side; metanotum without tubercles. Tegula with large dorsal projecting tubercle; wings without tubercles or swelling. All coxae apparently without tubercles; foretrochanter with small apical tubercle; femora without tubercles; tibiae without tubercles except midtibia with apical protrusion, too rounded to be called tubercle; midtibial spur apically truncate (corresponding to apical bifurcation of adult).

METASOMA: Integument nonspiculate, nonsetose. Tergum I without apical tubercles although surface at apex is somewhat irregular; tergum II with single apical row of small tubercles which are not apically sclerotized or pigmented; terga III–VI each with apical band of tubercles, some of which are sharp-pointed but none of which is apically sclerotized or pigmented; tergum VII without tubercles; sterna without tubercles; terminal spine lacking.

MATERIAL STUDIED: 1 male, 5 mi east of Sahuarita, Pima Co., AZ, collected as larva April 22, 1989 (S. L. Buchmann), pupated May 5, 1989, described as live pupa May 6, 1989, emerged as adult May 26, 1989.

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