

Nesting Biology of the Solitary Bee *Epicharis* *albofasciata* (Apoidea: Apidae: Centridini)

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ABSTRACT

This paper describes the extensive nesting site and the nesting behavior of a large population of the solitary, ground-nesting bee *Epicharis* (*Epicharoides*) *albofasciata* Smith, found in Trinidad in association with its cleptoparasite *Mesoplia* (*Mesoplia*) *rufipes* (Perty). In addition to describing nests and their cells, it provides information about provisioning, egg deposition, and larval eclosion.

While pursuing an investigation comparing the larval anatomy of *Centris* (*Heterocentris*) *bicornuta* Mocsáry with that of *Epicharis* (*Epicharoides*) *albofasciata* Smith, I became aware that nothing had been reported on the nesting biology of that species of *Epicharis*. These two species belonging to related genera had been selected for study because of the large series of specimens of all life stages of both that have been amassed in the American Museum of Natural History. On examining my old field notes, diagrams, and Kodachrome 35 mm transparencies, I recovered extensive information related to nesting biology associated with the specimens of *E. albofasciata* used in that investigation. I present this information here and also interpret it in light of recent studies regarding larval eclosion in solitary apids.

These notes were written on a fieldtrip to Trinidad in 1968 following three previous annual field trips there. During part of this trip I was accompanied by my late wife, Barbara L. Rozen, who assisted in the fieldwork. The locality was close to the Hollis Reservoir, near Valencia, Trinidad, and the site was studied first in early March just before the notes were written on March 3, 1968, with additional notes added on March 10, 1968. Adults were later identified by the late Roy Snelling

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(LACM). The mature larva of its cleptoparasite, *Mesoplia* (*Mesoplia*) *rufipes* (Perty), collected at the site was described and illustrated by Rozen (1969) as was its first instar (Rozen, 1991).

DESCRIPTION OF NESTING SITE: Most females of *E. albofasciata* nested in a mound of sand roughly 10–12 ft (3–3.6 m) long, 8–10 ft (2.4–3 m) in diameter, and a little more than 3 ft (0.91 m) in maximum height that had been dumped probably by a truck along the side of the Hollis Reservoir road just south of the entrance to the reservoir (figs. 1–3). As the sand supported no vegetation and was not eroded by rain, it had obviously been recently deposited, perhaps less than a month before. The loose, moist sand was easily excavated by bee and man. Although the greatest concentration of nest entrance holes occurred within the mound, some were also scattered in adjacent areas up to 2–3 m to the north where the soil was vegetated and compacted. The entire nesting area was near the bottom of a narrow valley and was still partly shaded at 9:30 A.M. when the bees were active. The vegetation immediately surrounding the area was low, and none shaded the nesting mound.

NESTING: Females preferred to nest in the sloping (45°) to vertical sides of the mound, especially on the west side, but not on the flat top. So many bees were present that their excavated sand formed a talus slope that tended to obscure some entrances in the lower half of the mound. Some females were provisioning while others were excavating, and still others (fig. 3) were actively searching out potential or actual nest entrances. No males were observed despite the large number of females.

An entrance of a fully excavated nest on the top surface was surrounded by a tumulus ring of excavated sand about 10 cm in diameter and 3.5 cm high. Tumuli on more sloping surfaces accumulated material on the lower side, but most entrances lacked tumuli because of the slope of the surface. Other bee species did not nest there, but a few wasps were observed. A few *Mesoplia rufipes* flew swiftly and erratically close to the surface while searching. No *Rhathymus* or other cleptoparasites were observed. Interestingly, female *E. albofasciata* flying over the surface of the mound seemed to chase one another, suggesting that this behavior might be a defense against nest usurpation.

Nest tunnels were generally 9.5–10 mm in diameter, open most of if not all the way to cells, did not anastomose, and apparently usually ended in more than a single cell. Each nest was occupied by a single female. Most cells seemed to occur at the level of the ground surrounding the mound indicating that nest tunnels leading to them had variable lengths (16–30 cm; 7 records) depending on the height of the entrance on the side of the mound. Tunnels descended at an angle of 60° from the horizontal earth surface.

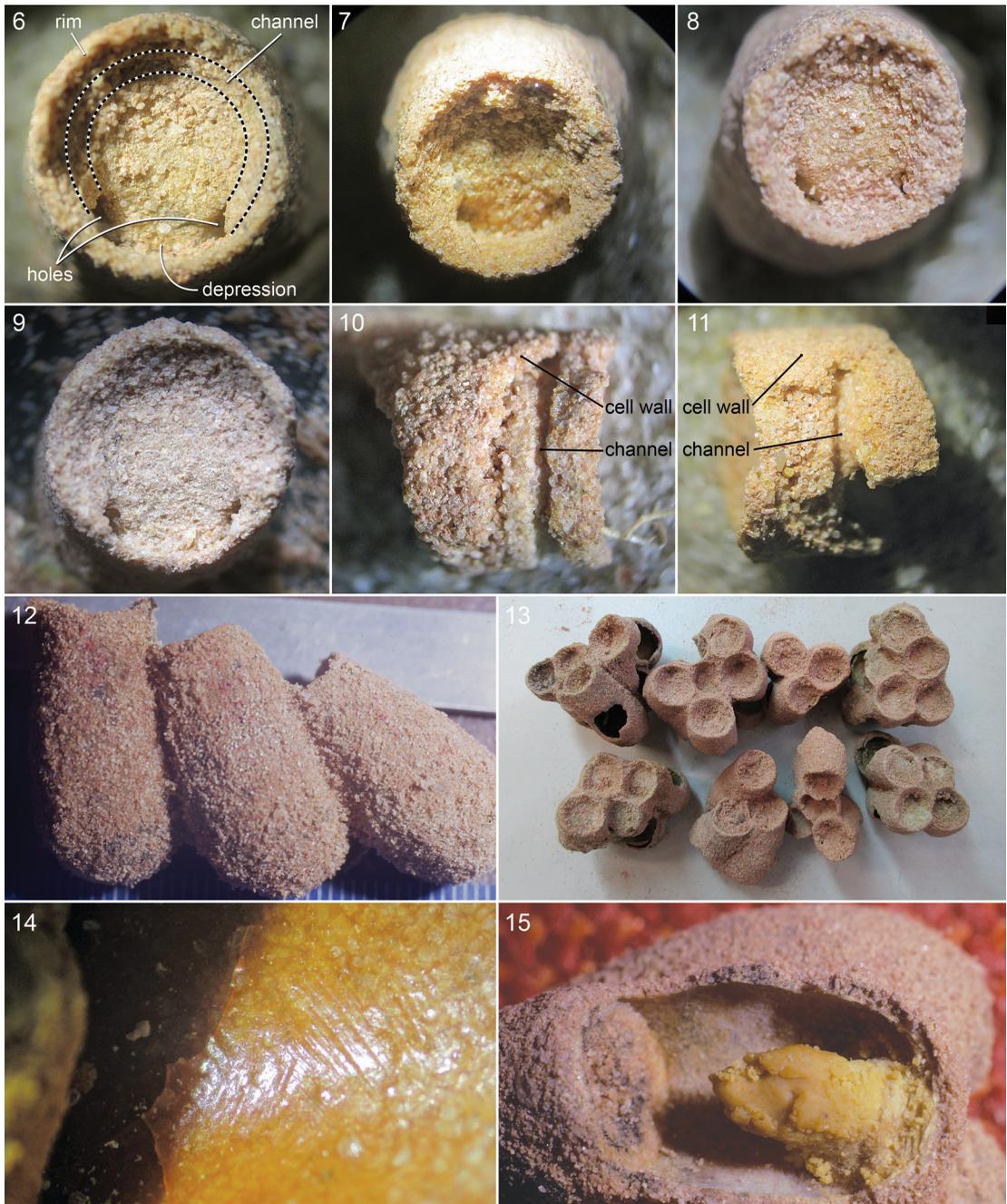
Cells (figs. 4, 5, 15) have slightly curved long axes that tilt 25° from horizontal in lateral view (fig. 5). Thus, the upper cell wall is more curved than the lower (figs. 4, 15). Cell walls are hard and somewhat shiny, contrasting with the surrounding soft sand, and are about 1.0 mm thick. They appear to be composed solely of sand held together by a transparent bonding agent, which is apparently waxlike, as explained below.

Cell inner dimensions are 9.5–10 mm in maximum diameter and 15 mm long. Cell closures are more or less recessed within the front end of the cell, which is about 9 mm in diameter, so that the cell wall provides a rim to the closure. Closures on newly completed cells have a characteristic crescentic depression about 5 mm long and roughly 1 mm wide. The depression is positioned along the low end of the outer surface immediately above the cell wall (figs. 6–11).

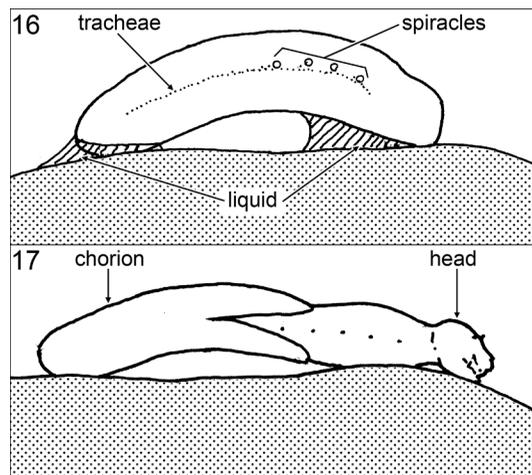


FIGURES 1–5. Nest elements of *Epicharis albofasciata* near Hollis Reservoir, Trinidad. 1. Nesting mound of sand. 2. Close-up of surface showing abundant nest entrances. 3. Flying female exploring surface presumably in search of nesting opportunities; note nest entrances. 4. Lateral external view of cell showing shape, oriented with closure end at left and with upper surface more strongly curved than lower surface. 5. Lateral view of partly opened cell, showing position of provisions and egg.

At both ends of the depression there is an opening to a hidden channel somewhat less than 1 mm wide that circumscribes the inner surface of the cell rim, as indicated (fig. 6). As a consequence, the front surface of the closure above the crescentic depression is broadly concave because of the closure material covering the channel. Basically, the depression is an exposed continuation of the two ends of the channel.



FIGURES 6–11. Closures of cells of *Epicharis albofasciata*. 6–9. Frontal views. 10, 11. Side views, with cell walls partly chipped away to reveal channels that extend around the periphery of the closure plug, Cell fronts to the right. FIGURES 12, 13. Cells of *Epicharis albofasciata*. 12. Unopened cell cluster, side view. 13. Front ends of eight cell clusters preserved in the collections of the American Museum of Natural History. FIGURES 14, 15. 14. Surface of inner lining of cell of *Epicharis albofasciata* showing striations on surface of waxy surface presumably created by brushing. 15. Cell with partly consumed provisions that now have columnar shape.



FIGURES 16, 17. From field sketches, diagrams depicting larval eclosion from *Epicharis albofasciata* egg. **15.** Larva mostly covered by egg chorion although four spiracles visible. **16.** Larva now mostly free from chorion and actively eating provisions. For interpretation, see text.

This channel appears to be characteristic of cells of this species. How females construct it and what functions it serves is unknown. Might it accommodate the female's glossa as she distributes hardening secretions to the closure? An alternative explanation is that it serves as a passage for air exchange between the inside and outside of the cell, such as the central spout found on cell closures of *Centris* (Rozen and Buchmann, 1990). This seems less likely because there is no obvious passageway leading from the channel to the interior of the cell, although the inner part of the closure seems quite porous. Answers, it is hoped, will be forthcoming from future studies.

This channel has also been observed though not described by Camargo et al., 1975: figures 3, 4A, 4B, and 5A for *Epicharis* (*Epicharana*) *rustica* (Olivier). The channel was also noted in my unpublished field notes for that species and for *Epicharis* (*Hoplepicharis*) *fasciata* Lapeletier and Audinet-Serville, although with somewhat different openings on front surfaces of cells.

The inner surface of the closure of *E. albofasciata* is a poorly defined concave spiral seemingly composed of loosely compacted sand, although when probed with forceps, sand grains appear glued in place. Because the inner and outer surfaces of the closures are concave, closures are about 5 mm thick at their periphery and perhaps 2 mm thick at their center.

Cells are arranged singly (perhaps because the nest was just started) or in clusters of 3–6 cells or perhaps more. When in clusters they were roughly side by side and more or less parallel (figs. 12, 13). Cells in clusters can in some cases be easily split apart, but in other cases they are completely united. They may occur only at the end of main tunnels since no branching of tunnels was detected. Cell walls and closure are soft when first constructed but harden shortly thereafter.

Cell walls are thickly coated with a semitransparent, light-reflecting material that is almost certainly brushed onto the surface by fine but distinct brush marks (fig. 14) applied from various directions, suggesting that the female uses her legs when applying it to the surface. When a piece of the wall coated with the material was placed on a microscope slide and heated on a hot plate set at 110° C, the material melted, and on cooling it fused sand grains to one another and to the glass

slide, strongly suggesting that it is a wax, produced internally, or perhaps added by the female from external sources. This material has been tested by Maria Luiza Mello and Benedicto De Campos Vidal of the University of Campinas, Campinas, Brazil, and found to be a kind of wax “because it stains with Sudan Black and is miscible in a mixture of acetone/chloroform” (personal commun., Mello, August 20, 2016). It presumably controls cell humidity, provides strength and rigidity to the wall surrounded by soft sand, and excludes invasion by potential predators and parasites.

Since *Epicharis* females are known to visit flowers of Malpighiaceae (e.g., *Byrsonima*) to collect floral oils, it is likely that these oils may have been added to the pollen provisions of this bee, and may also be the origin of the mysterious transparent bonding agent comprising the cell walls (see Buchmann, 1987). As suggested by Buchmann (personal commun., October 17, 2016), *Epicharis* and *Centris* may be transforming their collected floral oils into hardened waxes used as cell linings by the addition of enzymes possibly originating from salivary gland secretions. Future work on Neotropical *Epicharis* and *Centris* will be required to determine what happens to floral oils that may be chemically modified by these bees into hardened cell linings.

PROVISIONING: Pollen first deposited in a cell is placed loosely at the rear floor and later shaped into a curved, firm, nearly dry mealy mass fully filling the rear floor of the cell and with its top surface forming a mound on which the female deposits its egg (fig. 5). By the time of egg hatching, the mass has become moist.

EGG DEPOSITION: The elongate, curved, slightly yellowish egg with strongly reticulate chorion is deposited on the top surface of each mass with the long axis of the egg in line with that of the cell. The front end of the egg loosely touches the surface of the provisions, while the posterior end seems more strongly affixed to the surface. Because of its curvature, the mid part of the egg is elevated above the provisions. Eggs are fully described by Rozen (in prep.).

LARVAL ECLOSION: Detailed observations were recorded on an egg that was found hatching on March 3, 1968, at 4:30 P.M. These observations are presented here as noted then, but below they will be interpreted in light of more recent findings concerning larval eclosion of related bees. At the time of discovery, larval eclosion was diagramed in lateral view (fig. 16) with the larval head covered by chorion differentiated to the right and with four spiracles visible on one side behind the head and the air-filled tracheae visible through the chorion and body wall along the side for nearly the length of the body. The chorionic reticulation was absent in the vicinity of the four visible spiracles although the integument around the spiracles was slightly quivering. Where both ends of the egg touched the provisions liquid was clearly visible. By 5:15 P.M. that day little change had taken place except the ventral body segmentation was more evident than earlier.

On March 4, 1968, at 8:30 A.M. not much had changed from the previous evening, but by 1:10 P.M., the larva (fig. 17) now seemed to be hatching with its anterior half freed, and it was very avidly eating; the posterior half still was partly encased in chorion though all spiracles were fairly free.

From recent studies by Rozen et al. (2006, 2011), the following is an interpretation of these events:

March 3, 4:30 P.M., diagram (fig. 16) actually depicts the first instar after it ingested amniotic fluid and probably liquid from the front end of the egg presumably with a small

opening not visible near the mouth of the first instar. Because of the body swelling resulting from the fluid ingestion, the nearly invisible but reticulate chorion covering the spiracles on one side had partly split away, thus exposing four spiracles. Along the sides of the body the air-filled tracheae of the first instar were starting to be pulled out of the tracheal system of the newly forming second instar, thereby creating the visible streak along the sides of the body.

By March 4, 1:10 P.M., the second instar (fig. 17) has released itself from the combined remnants of the chorion and the nearly transparent integument of the first instar, both of which loosely surround the rear of the actively feeding second instar.

This explanation was based on confirmed observations recorded for eclosion in *Monoeca haemorrhoidalis* (Smith) (Rozen et al., 2006) and *Centris flavofasciata* Friese (Rozen et al., 2011). One test would have been the discovery of a small row of spicules above the line of spiracles on each side of the body; these rows presumably cause the rupturing of the chorion as the larva's body expands with ingestion of the fluid. Unfortunately, specimens of the briefly extant first instar of *E. albofasciata* could not be found among the collections of this species. Another test would have been a careful examination of the exuviae clinging to the actively feeding larva.

Nonetheless, notes and diagrams recorded in 1968 for *E. albofasciata* so exactly fit the observations dealing with eclosion in *Monoeca haemorrhoidalis* and *Centris flavofasciata* that it was unlikely that the interpretation presented here is not valid. Further support comes from the thesis of Werneck (2012), who reported (p. 45) and photographed the pharate first instar (fig. 23B) and the actively feeding second instar (fig. 23C) of *E. (Epicharoides) picta* (Smith). However, final convincing evidence came from a paper kindly sent to me by H.A. Werneck authored by Gaglianone et al. (2015: 406) in which it stated that both *E. picta* and *E. (Epicharis) nigrita* (Friese) had the same mode of development and behavior and that the analysis of the chorion and cuticle of "the first larval stage (evident due to the presence of spiracles and spicules) was attached to the chorion of the egg, indicating that the hatched larva represented the second larval stage."

LARVAL FEEDING: Although extensive observations were not recorded on larval feeding behavior, it was noted that young larvae tended to circle the perimeter of the exposed food mound as they fed. As a consequence of their continued feeding, the feeding channel around the perimeter deepens and the columnar central mass of uneaten provisions becomes more accentuated (compare figs. 5 and 15).

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Although these observations were made by me and my wife, they were carried out at the time I was pursuing a range of studies on bees in Trinidad in association with Fred D. Bennett and D. Bharath. Their enthusiastic interest in and knowledge of the bee fauna there was stimulating and infectious. This study should thus be acknowledged as an outgrowth of our past association. I express my thanks to Maria Luiza Mello and Benedicto De Campos Vidal for identifying as wax the material that coated the cell wall of *Epicharis albofasciata*.

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