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Biology of the Cleptoparasitic Bee *Mesoplia sapphirina* (Ericrocidini) and its Host *Centris flavofasciata* (Centridini) (Apidae: Apinae)

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Appendix: A New Species of *Mesoplia* (Hymenoptera: Apidae) from Mesoamerica, by Gabriel A.R. Melo and Léo C. Rocha-Filho

ABSTRACT

This paper investigates the bionomics of the cleptoparasitic bee *Mesoplia sapphirina* Melo and Rocha-Filho, sp. nov. (described in the appendix), and of its ground-nesting host *Centris flavofasciata* Friese found along the Pacific coast of Guanacaste Province, Costa Rica. We explore the host-nest searching behavior, egg deposition, and hospicidal behavior of *M. sapphirina*. Anatomical accounts of its egg, first, second, and fifth larval instars are presented and compared with published descriptions of other ericrocidine taxa. Nests of the host bee as well as its egg and method of eclosion are also described.

INTRODUCTION

Here we explore the mode of parasitism and other aspects of the biology of the cleptoparasitic bee *Mesoplia* (*Mesoplia*) *sapphirina* Melo and Rocha-Filho, sp. nov. (fig. 1) (description appended), a representative of the totally cleptoparasitic New World tribe Ericrocidini, species

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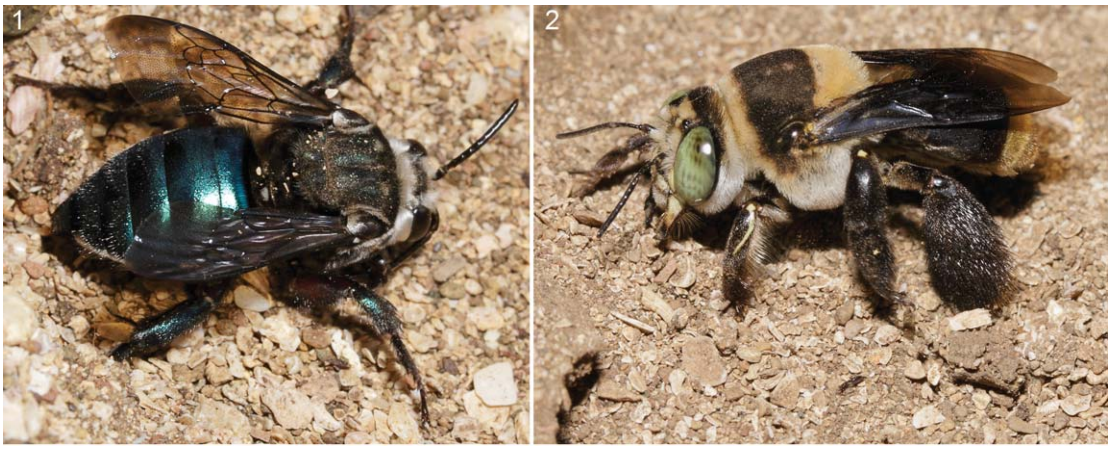


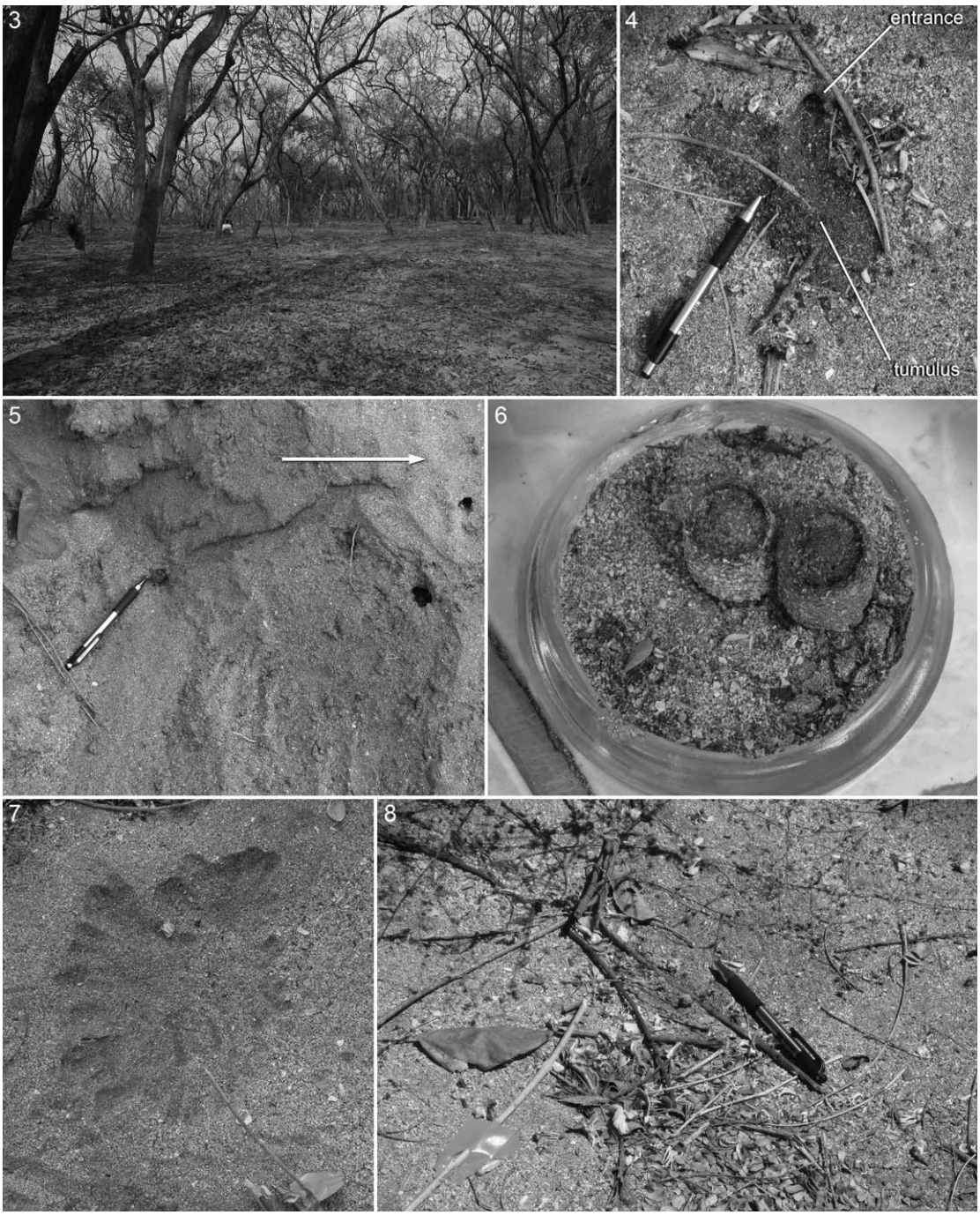
FIGURES 1, 2. Macrophotographs of *Mesoplia sapphirina* and its host, *Centris flavofasciata*, taken live by R.C. at nesting site at Playa Grande, respectively.

of which attack nests of Centridini (Apidae: Apinae) (Rocha-Filho et al., 2009). Because egg and larval anatomy (especially of the first instar) are functionally associated with cleptoparasitism, they are described in the final section of this paper, as is the second larval instar. The host of *M. sapphirina* at the study site was *Centris* (*Centris*) *flavofasciata* Friese (fig.. 2), although other large-bodied *Centris* may nest close by and host the same cleptoparasite. In the first section of this paper we present an overview of its nesting biology including new information stemming from the current investigation.

Gabriel A.R. Melo and Léo Rocha-Filho are currently revising the genus *Mesoplia*. After examining specimens from the study site, Melo recognized them as belonging to an undescribed species and kindly prepared the appended description validating the name.

Vinson et al. (1987) initially detailed the biology of *C. flavofasciata* and its parasite *Mesoplia sapphirina*. They recognized the peculiar habit of first-instar *Mesoplia* sp. (here assumed to be *M. sapphirina*) of carrying the vacated chorion on its abdominal apex (ibid.: fig. 7E). They reported that *M. "regalis"* i.e., *sapphirina*), *M.* (*Eumelissa*) *decorata* (Smith), and *M.* (*Mesoplia*) *rufipes* (Perty) were collected, and four specimens of *M. "regalis"* were reared and identified from the nests of *Centris flavofasciata.* Their study site was in the same general area as the current one. However, host and parasite then nested on the land edge of the open sandy beach under and among patches of the creeping vine *Ipomoea pes-caprae* (L.) R. Br. (Convolvulaceae), a pantropical beach morning glory that occurred just seaward of the row of wind-shaped bushes followed inland by the forest consisting of *Gliricidia sepium* (Jacq.) Kunth ex Walp. that was our site. Their site covered a much larger area than our current one.

Our study site was at Playa Grande, Guanacaste Province, Costa Rica, N10°19.63′ W85°50.59′, elevation 20 m, on the Pacific coast of Costa Rica. It was recognized in February 2009, but not studied until the following year, from February 13–28, 2010. Because of the paucity of data at the end of this trip, J.G.R. and S.B.V. returned the following year, February 8–21, 2011.



FIGURES 3–8. Nests of *Centris flavofasciata.* **3.** View of nesting area looking westward. **3.** Open nest; note track of tumulus. **5.** Partly excavated nest with pen pointed to cell and with pointer head on horizontal ground surface **6.** Two cells showing closure ends. **7.** Recently closed nest entrance. **8.** Nest entrance (in area upon which the front of the pen rests in the picture) closed a day earlier.

Playa Grande is a 3 km long, curved sandy beach that is bordered inland first by a narrow vegetated strip consisting of mostly grasses behind which is an open forested area with pedestrian footpaths. The study site (fig. 3) is in a segment of that forest. According to S.B.V., who has carried out bee investigations in Costa Rica for more than a quarter century, the study site had been cleared of low vegetation and hosted a youth camp previously. No longer used for that purpose, the site now consists mostly of moderate-sized trees with a partly open canopy, allowing considerable sunlight to reach the horizontal ground surface. Except for widely spaced trees, there is only spotty, low herbaceous vegetation (mostly dried by the time of the study periods); the ground is open and peppered with crab burrows. Although the prevailing breeze accumulates extensive, ground-obscuring masses of dried leaves in various places, most nesting activity of female *Centris flavofasciata* and *Mesoplia sapphirina* takes place where there is open sand spotted with small clumps of leaves and scattered loose dead twigs and branches. In these areas host bees establish nests and cleptoparasite females search for them. At the time of the study few other bee species were evident in the forest.

During the two-week field investigation in 2010 we noticed a daily decline of adult bee activity in terms of bees in flight and pace of nest establishment. Because of drought conditions in the province since 2007, this decline was probably influenced by a reduction of floral resources in combination with the end of the flight/breeding season. A similar decline was not evident the following season, possibly because of an increase in rainfall and associated temperature changes in the area starting in April 2010 that resulted in a longer or delayed flowering season (Frankie et al., 2005).

Previous studies on the biology and immatures of Ericrocidini are as follows. Rozen (1969) described the mature larva of *Acanthopus palmatus* (Olivier) (as *A. splendidus urichi* Cockerell) from Trinidad, recovered from brood cells of *Centris* (*Ptilotopus*) *derasa* Lepeletier, which nests in arboreal nest of *Microcerotermes arboreus* Emerson (Isoptera). In the same paper he compared the cast exoskeletons of the last larval instar of *Mesoplia rufipes* taken from the cells of both *C.* (*Trachina*) *carrikeri* Cockerell and *Epicharis* (*Epicharoides*) *albofasciata* Smith (Centridini) also from Trinidad. Vinson et al., (1987) published their account of *Mesoplia* sp. and illustrated the first instar with the chorion attached to its posterior end. Rozen and Buchmann (1990) described the mature larva and male and female pupa of *Ericrocis lata* (Cresson) from nests of *C.* (*Paracentris*) *caesalpiniae* Cockerell from Arizona, and Rozen (1991) gave an account of first instars of three species: *Aglaomelissa duckei* (Friese), *Mesoplia rufipes,* and *Ericrocis lata* (or *E. pintada* Snelling and Zavortink), the latter based on a cast skin. The first instar of *A. duckei* was from an egg found attached to the inner surface of a cell closure of *C. carrikeri* in Trinidad,[5] suggesting that it had been introduced through a hole in the closure. A first-instar skin of *M. rufipes* from a nest of *Epicharis albofasciata* in Trinidad was still attached to its chorion, and two parasitized cells of the host had small openings in the closures through which the eggs had been introduced.

Alexander and Rozen (1987) and Rozen (2003) presented descriptions of eggs/mature

5 Rocha-Filho et al. (2009) questioned this host association.

oocytes of Ericrocidini for the following: *Epiclopus gayi* Spinola, *Ericrocis lata*, *Mesoplia* probably *rufipes*, and *M. rufipes.* Pupal descriptions of only *M. rufipes* and an unknown species of *M.* (*Eumelissa*) were recorded (Rozen, 2000). Confirmed and suspected host associations of Ericrocidini, all with Centridini, were summarized and listed by Rocha-Filho et al. (2009).

Vinson and Frankie (1977) and Vinson et al. (2010) have described the nests of other species of *Centris* found in Guanacaste Province, Costa Rica.

METHODS

The most difficult part of this investigation was finding nests of *Centris flavofasciata*, which were widely scattered throughout the area. Initially this was accomplished by observing adults searching for nesting sites or while they were excavating, provisioning, or closing nests. Our recognition of a nest entrance, i.e., an open burrow obliquely entering the ground and a tumulus spread in the opposite direction, was a worthy landmark that we could flag on one day and excavate a day or two later, by which time the ground surface was altered due to nest closure, described below.

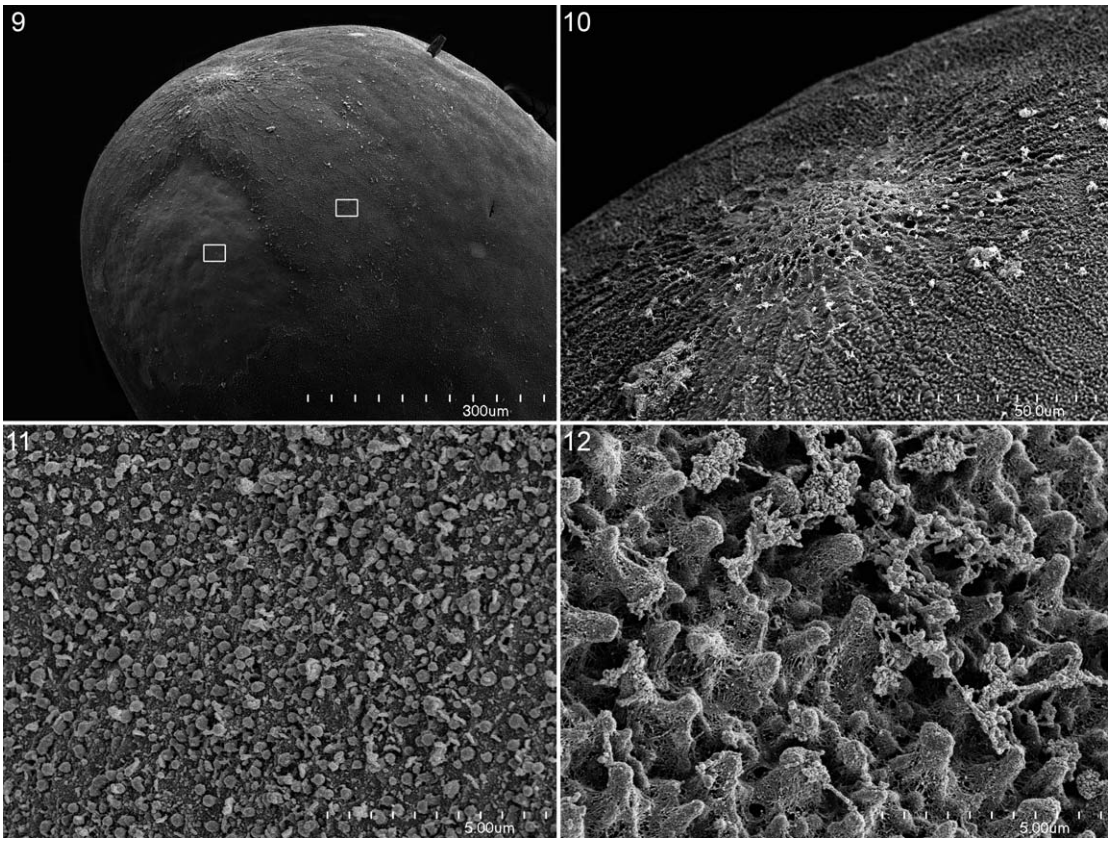
Our nest excavations were performed with trowels and penknives and with aspirators used to blow away loose sand that obscured descending tunnels and cells. Cells were retrieved intact and taken indoors to be opened under the microscope. There we examined and photographed them with a Canon PowerShot SD880 IS handheld to the ocular lens of a Leitz stereomicroscope, vintage 1960.

Preserved larvae were examined closely before being cleared in an aqueous solution of sodium hydroxide, after which they were stained with Chlorazol Black E and examined on glycerin-filled well slides. Specimens to be examined with an Hitachi S-5700 scanning electron microscope were critical-point dried and coated with gold/palladium. All specimens studied came from Playa Grande on the dates recorded in the Material Studied sections.

NESTING BIOLOGY OF *CENTRIS FLAVOFASCIATA*

As indicated above, *Centris flavofasciata* has been reported nesting along the northwestern shores of Costa Rica for many years (Vinson et al., 1987; Vinson and Frankie, 1999). In the current study we found nesting only in the adjacent forested area, partly shaded by overhead trees (fig. 3). Here the substrate is primarily sand with fine, shredded pieces of marine mollusk and crab shells, often loose and dry though with slight traces of moisture at the cell level below 12 cm. Richard K. Shaw conducted a textural analysis and determined, using USDA particle-size classification, that the soil is in the sand textural class, with 96.5% sand and 3.5% silt and clay. He commented that the sand was composed of a high percentage of shell fragments.

Nest entrances (best observed on nests under construction; figs. 4, 5) slant obliquely into the ground as described above. Tumuli consist of one or several excavation tracks leading away from the surface opening. A track is created as the female slowly backs out of the opening pushing excavated soil backward and sideways with her hind legs while the front legs rapidly

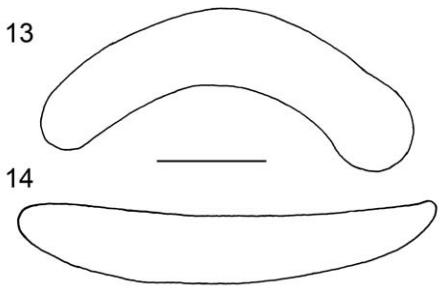


FIGURES 9–12. SEM micrographs of egg of *Centris flavofasciata*. **9.** Anterior end showing micropyle at anterior pole. **10.** Close-up of micropyle. **11, 12.** Chorion from left and right rectangles in figure 9, respectively, both to same high magnification showing differences in microtexture.

flip soil beneath her body toward her hind legs. Midlegs seem to stabilize her body and provide body motion forward and backward. In some cases the furrow created by the repetitive action of the female can become deeper than the surrounding surface.

Each nest (fig. 5) is an obliquely descending tunnel and a single vertical brood cell at the lower end. Tunnels tend to continue in the direction of the entrances. The tunnel descent rate varies from approximately 1 cm for every 2 cm horizontal distance from the burrow opening to nearly a 45° angle. Descent rates tend to increase just above brood cells. The extent to which the tunnel is filled by the female after cell closure is uncertain because during our study we used an insect aspirator to blow away the soft fill from the slightly more compact substrate. Tunnels are approximately 12–13 mm in diameter and uniformly wide except at cell entrances, where they widen presumably enabling females to construct cell walls and closures.

Brood cells of *C. flavofasciata* (figs. 5, 6) are oriented vertically and occur at depths of 12–17 cm. Each is large, approximately 22.5 mm long and 15 mm in maximum diameter measured on the outside of the wall and thus reflecting the thickness of the wall as well as its internal diameter.



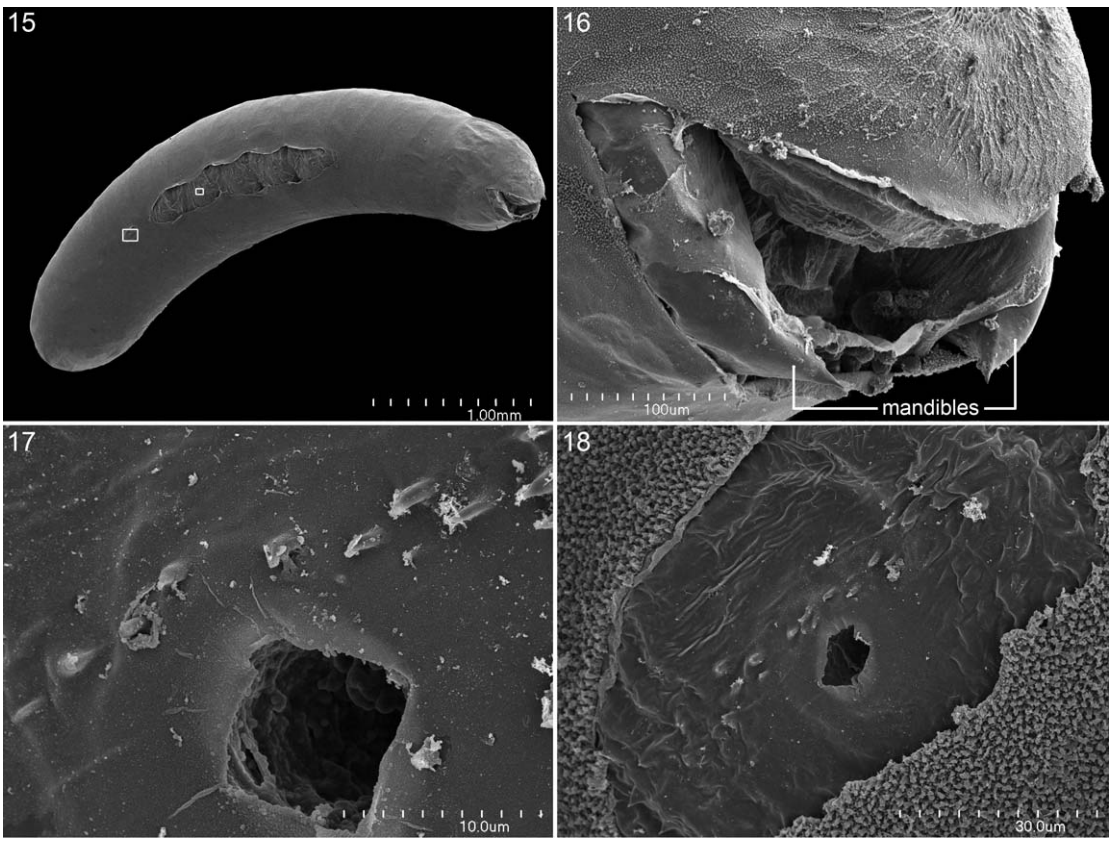
FIGURES 13, 14. Diagrams of mature oocytes of *Centris flavofasciata* and *Mesoplia sapphirina*, lateral view, with anterior ends at right, drawn to same scale, respectively.

Wall thickness varies with soil particle size and ranges from 1 mm to rarely as much as 4 mm thick. The cell's external shape is slightly constricted toward the upper end where the closure is attached, and the wall extends above the closure by as much as 4 mm, thus providing a rim to the closure. The wall is rough and dullish on the outside, composed of substrate material embedded in a dark matrix. On the inside the wall is smoother but uneven where the slightly darker surface reveals a reflective, transparent coating, which no doubt affords moisture-proof protection. The finished wall is hard and tough, so that a completed cell is in little danger of physical destruction. The closure externally is a slightly domed surface bearing a conspicuous central projection that on one side bears two small openings (occasionally interconnected by a narrow slit) allowing gas exchange between the cell chamber and exterior. The projection is variable in height, sometimes considerably higher than the rim of the closure, but other times distinctly lower, with the paired openings completely obscured. The inner surface of the projection is transparent and glistens like the visible cell wall, so that one can easily see the substrate particles within it. The coating is so clear that it gives the impression of having been thickly varnished. In general cell structure closely resembles that of *Centris caesalpiniae* Cockerell (Rozen and Buchmann, 1990: figs. 15–18) as well as that of *Centris aethyctera* Snelling (Vinson and Frankie, 1977: fig. 3). The central projection is a unique feature, found in brood cells of only *Centris,* though some species lack the projection.

Cells are obviously constructed in two phases. The first involves forming the bottom and vertical walls of the cell including the eventual rim of the closure. Then the female imports provisions and deposits her egg. The second phase is closure construction. Further details of cell construction were given by Vinson and Frankie (1999).

The initial step of nest closure appears to be filling or partly filling the tunnel with fine, dry substrate material. The final steps of nest closure are more obvious: the female backs surface sand (fig. 7) over the entrance thereby obscuring the characteristic shape of the tumulus and obliquely descending tunnel. While a former nest entrance can be obvious for a short period because of surface impressions created by the female's closure manipulations, these soon smooth through costal breeze action and through the female's grooming sand to remove ridges (fig. 8).

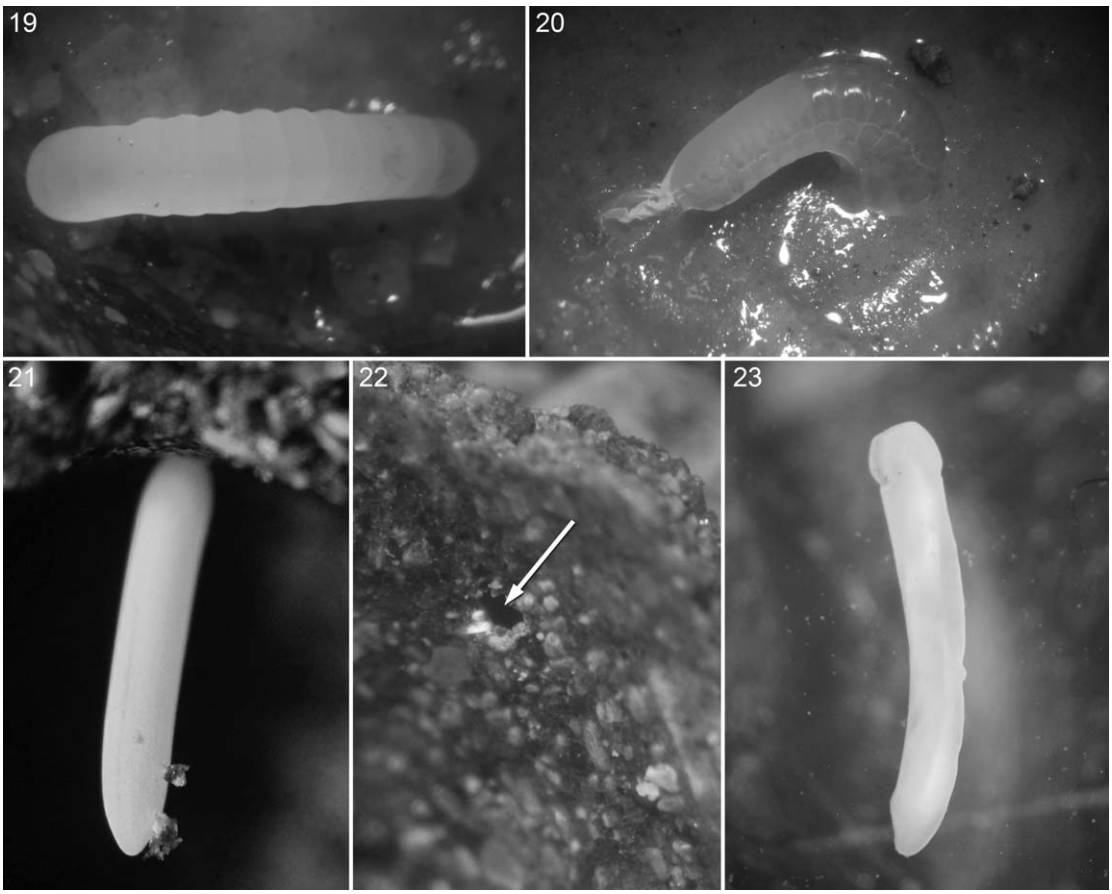
Two partly provisioned cells had masses of hard-packed pollen adhering to the curved lower surfaces of the cell wall. However, completed provisions were a soft, semiliquid orange mass (figs. 19, 20) filling about one-third of the lower end of the cell. At least four live, curved eggs of *C. flavofasciata* were discovered in different cells in 2010 mostly (one was considerably off center) toward the middle of the surface of the provisions, touching the provisions with only front and rear ends while the midsections of eggs arched upward. In 2011, the number of host eggs found in similar positions was 20.



FIGURES 15–18. SEM micrographs of eclosion of *Centris flavofasciata.* **15.** Entire first instar shedding its chorion, anterolateral view, anterior end to the right. **16.** Close-up of anterior end showing rent in chorion made by mandibles; note micropylar ornamentation dorsal to mandibles. **17.** Close-up of spiracle identified by right rectangle in figure 15, showing row of spicules above atrial opening. **18.** Close-up of spiracle identified by left rectangle in figure 15, showing continuation of row of spicules above spiracle.

All host eggs were faintly yellow with nonreflective chorions, and four were 4.0–4.8 mm long (a presumably mature oocyte[6] was 3.4 mm long), with the rounded rear end larger than the rounded front end and a maximum diameter of 0.8–1.0 mm at midbody. They were strongly curved; the outcurve was dorsal as determined by the orientation of the hatching larva (fig. 15). Under SEM examination the micropyle was a tight cluster of apertures at the anterior pole with low ridges radiating outward (figs. 9, 10). Elsewhere, the chorion appeared featureless except that under very high SEM magnification (10K) it consisted of massive, variable-sized projections (figs. 11, 12), no doubt accounting for its nonreflectiveness under stereomicroscopic examination. However, we were surprised to discover that in some regions the chorion (figs. 9, 11, 12) had a pattern consisting of smaller projections than in other regions, a matter that deserves future

6 As discussed by Iwata and Sakagami (1966), there are difficulties in determining when an oocyte is mature. The somewhat smaller size of this oocyte might suggest that it was not mature even though the nurse cell chambers were no longer evident.



FIGURES 19, 20. Microphotographs of hatching of egg of *Centris flavofasciata*, anterior end at right. **19.** First instar/embryo with dull chorion still intact. **20.** Shiny second instar of same individual next day partly emerged so that dull chorion and first instar skin sliding from posterior end. Figures 21–23. Close-up microphotographs of eggs and egg insertionsof *Mesoplia sapphirina.* **21.** Live egg with anterior end attached to cell closure while the rest of the egg dangles motionless. **22.** Inner surface of cell closure showing small hole (arrow) through which egg of *Mesoplia sapphirina* had been inserted into cell. **23.** Assassinated egg showing similar form to that of figure 29, anterior at top.

investigation. The strongly curved, yellowish host egg contrasted with the nearly straight, white egg of *M. sapphirina* (figs. 21, 23, 29), described below. Mature oocytes of the two (figs. 13, 14) differed not only in degree of curvature but also in the direction of curvature; the outcurved surface is dorsal in *C. flavofasciata* but ventral in *M. sapphirina,* and in shape and robustness.

Several observations provide insight into eclosion of first-instar *C. flavofasciata*. First, an SEM examination of a first instar preserved as it was beginning to eclose from the egg chorion (fig. 15) revealed the chorion starting to split along the spiracular line on each side of the body. A tear almost certainly caused by the mandibles had also occurred in the chorion at the head end (figs. 15, 16). Close-up SEM micrographs of the spiracular line show a row of sharp-pointed spicules that lead to the tearing of the chorion along the sides of the body (figs. 17, 18).

Second, a live egg had developed slight body constriction visible when observed through a microscope (fig. 19). The egg was allowed to develop and shortly before noon the next day liquid was seeping onto the surface of the chorion along the spiracular lines on each side of the first instar and invading intersegmental lines. By 2:20 PM, the first-instar exoskeleton with chorion attached had slipped backward, so the shiny integument of the anterior end of the second instar was free (fig. 20). The chorion and first-instar integument crumpled at the rear as it came loose from the larva, and faint highlights on a fine line of spicules above the spiracular lines were evident on parts of the first instar's crumpled exuviae. Where the chorion and first-instar integument were still taut along the rear of the live second instar, the tracheae of the first instar could be seen as they were pulled from those of the second instar. Subsequent SEM examination of the sides of the second instar revealed no sequence of sharp spicules immediately above the spiracular line, as found along this line of the first instar.

These two observations made in 2010 were repeated by others in 2011 and are consistent with the following scenario: hatching of the first instar results from the embryo/first instar initially ingesting amniotic fluid and afterward (or simultaneous with) tearing the chorion at the anterior end with its mandibles, ingesting fluid (presumably floral oils; see Vinson and Frankie, 1999) from the surface of the provisions. These actions cause the body to swell resulting in rupturing the chorion against the sharp spicules on each side just above the spiracular line. This interpretation explains the strong curvature of the egg: the lower part of the emerging head is positioned to ingest fluid from the provisions. This information has never been recorded before for any Centridini but is in agreement with observations on Eucerini (Rozen, 1964), Tapinotaspidini (Rozen et al., 2006), and on at least some Megachilidae (Baker, 1971; Torchio, 1989; Rozen and Özbek, 2004; Rozen and Kamel, 2007; Rozen and Hall, 2011).

We originally thought that nests of *C. flavofasciata* were initiated in the morning and completed late in the same day. We soon discovered that some nests were not completed so quickly, perhaps due to decreasing larval food supply. Also, many nests were abandoned after being started, in some cases because of underground obstructions such as roots or crab burrows.

BIOLOGY OF *MESOPLIA SAPPHIRINA*

In searching for nests of *C. flavofasciata*, female *M. sapphirina* fly swiftly over large areas, tightly circling a suspected spot of interest before dashing to the next one, making an unpredictable zigzag pattern across the landscape from one inspection point to the next. One suspects that they can quickly detect through sight or odor when a nest is present, because only rarely do they briefly land. We noted in 2010 when they found a nest where a female host bee was present, they showed great persistence in trying to scout the site and enter the nest. They repeatedly returned, each time either to be chased by the much larger host or to be blocked from the entrance where the host female stood guard. In 2011, we observed female *M. sapphirina* searching for nests as in the previous year, but they were fewer in number, and we were rarely present when they attempted to enter.

TABLE 1. Active cells of *Centris flavofasciata,* their contents including *Mesoplia sapphirina*, and other varying characteristics, February 2010.

Characteristic \ Cell	1	2	3	4	5	6	7	8	9	10
Total *M. sapphirina* present	3	6	3	1	1	1	1	5	4	0
Total live *M. sapphirina*	1	1	0	1	0	0	1	0	1	0
Holes in cell closure	1	3	3	?	Large	1	0	1	1	0
Live eggs of *C. flavofasciata*	0	0	1	0	0	1	1	0	0	1
Total cell contents dead	0	0	All but host	0	All	0	0	All	0	0
Ants detected	No	No	No	No	Yes	No	No	Yes	No	No

In 2010 female *M. sapphirina* entered nests that were still open as well as those that had been closed. Some visits were brief, perhaps less than 1 min, and almost certainly did not result in egg deposition, while others may have lasted for some minutes and thus were thought to result in parasitism. In one case a host female returned and entered while the cleptoparasite was still inside, resulting in the host rapidly chasing the cleptoparasite from the entrance. In 2011 we observed a female *M. sapphirina* take 8–10 min to enter a nest, the entrance to which we capped with a plastic tumbler. An hour later the female finally emerged. Thus it had taken her approximately 1 hr to penetrate the nest, successfully introduce her egg through the cell closure, seal the hole, and emerge. This observation casts doubts on the success of all presumed introductions of the previous year.

Our data on the number of nests (i.e., cells) containing recent instances of parasitism during six visits to the site over a 10-day period in February 2010 are limited because of the difficulty of finding nests. A total of 10 nests containing fresh inhabitants were discovered and studied. Cells from a number of older nests representing earlier generations were uncovered by chance. Some were cells from which adults had emerged, as shown by cocoon fragments, and others contained remnants of immatures that perished during development.

The 10 cells from the then current generation are listed in table 1 with features that varied among nests. As indicated (table 1: first row) nine cells had been parasitized by at least one female of *M. sapphirina* as evidenced by eggs or larvae found therein. Only one cell, discovered on the last day, had not (yet) been parasitized. This suggested an extremely high rate of parasitism, placing into jeopardy survival of the local population of *C. flavofasciata* if the rate was continuous through the entire adult breeding season (assuming that *C. flavofasciata* is univoltine). Not only were all but one cell attacked, but half of them (five of 10) had been visited by more than one cleptoparasite, and one was presumably visited by as many as six cleptoparasites (assuming that a cleptoparasite inserts only one egg per visit and visits a cell only once). The high rate of parasitism presented in these figures was supported by our casual observations of the rapid, thorough

searching behavior of female *M. sapphirina*. The study by Vinson et al. (1987) reported a parasitism rate of 59% based on a sample of 22 cells. Although somewhat lower than the rate suggested by the 2010 study, it still demonstrated a very successful cleptoparasite.

By returning to this study in 2011, J.G.R. and S.B.V hoped to ascertain what effect the heavy parasitism rate the previous year had on the host population. We also wanted to better understand how *Mesoplia sapphirina* attacks its host and how *C. flavofasciata* defends itself from such attacks.

On returning both authors were surprised to discover (1) the host population active and roughly as abundant as in the previous year and (2) the parasite population substantially reduced in numbers and seemingly far less aggressive, in that both authors only rarely observed female *Mesoplia* digging into closed host nests in nine visits to the site. During these visits, we uncovered 36 active host nests, which were excavated a recorded number of days after they were discovered for most trips. The most interesting statistics are as follows: 11 cells were parasitized by *Mesoplia* giving a parasitism rate of 30% (contrasting with 90% for 2010); no cell contained more than a single *Mesoplia* egg or early instar (contrasting with half of all nests of previous year parasitized by 3–6 cleptoparasites); 20 cells had live host eggs and 7 others contained early larval host instars (contrasting with 4 cells with live host eggs in 2010); no cells found where all bees had been killed (contrasting with 30% of all bee inhabitants had failed a year before); no ants were found to have invaded cells (whereas ants were associated with at least 2 nests in 2010).

Although we recognize that the small size of the 2010 sample is less than a reliable measure of the population for that year, the samples of both years show striking differences. We suspect that the activities of 2010 may have resulted from an overly large population of *Mesoplia* (for reasons unknown) relative to the host population resulting in multiple egg depositions in host cells and an extremely high rate of parasitism. Nests in which all bee inhabitants had died may have resulted from *Solenopsis* invasions. As table 1 indicates, most cells in 2010 exhibited small irregular holes (ca. 0.5–0.6 mm in diameter) in the cell closure through which *M. sapphirina* eggs are inserted (fig. 22), as also reported by Vinson et al. (1987). One cell also exhibited a small hole in the upper cell wall. As indicated in the 2011 study, most holes are probably egg insertion holes of *M. sapphirina*. However, in 2010 there was lack of congruence between the number of such holes and the number of cleptoparasites in a cell: generally fewer holes than parasites. Some evidence suggested that a female *M. sapphirina* sealed the oviposition hole afterward, as was affirmed in 2011. Some oviposition holes may have been reopened and even enlarged by ants (e.g., table 1, cell 5), as is suggested by the 2011 study, which revealed no ant infestations and, in general, showed a one-hole-to-one-cleptoparasite ratio.

The 2011 study helped resolve questions stemming from the previous year. Are *Mesoplia* eggs introduced into the brood cells only after cell closure? Some observations in 2010 indicated that *M. sapphirina* females enter host nests before nest closure, thereby suggesting that the brood cells may also be open and available to the parasite. Not only did we not observe any cleptoparasites entering open nests in 2011, but of nine parasitized cells only one did not reveal any parasite egg insertion holes, which are hard to detect because of their small size and sealing. We conclude that *M. sapphirina* probably attacks only closed host cells. Further, we reason that if parasite eggs were deposited before cell closure, any egg as large as that of *M. sapphirina*

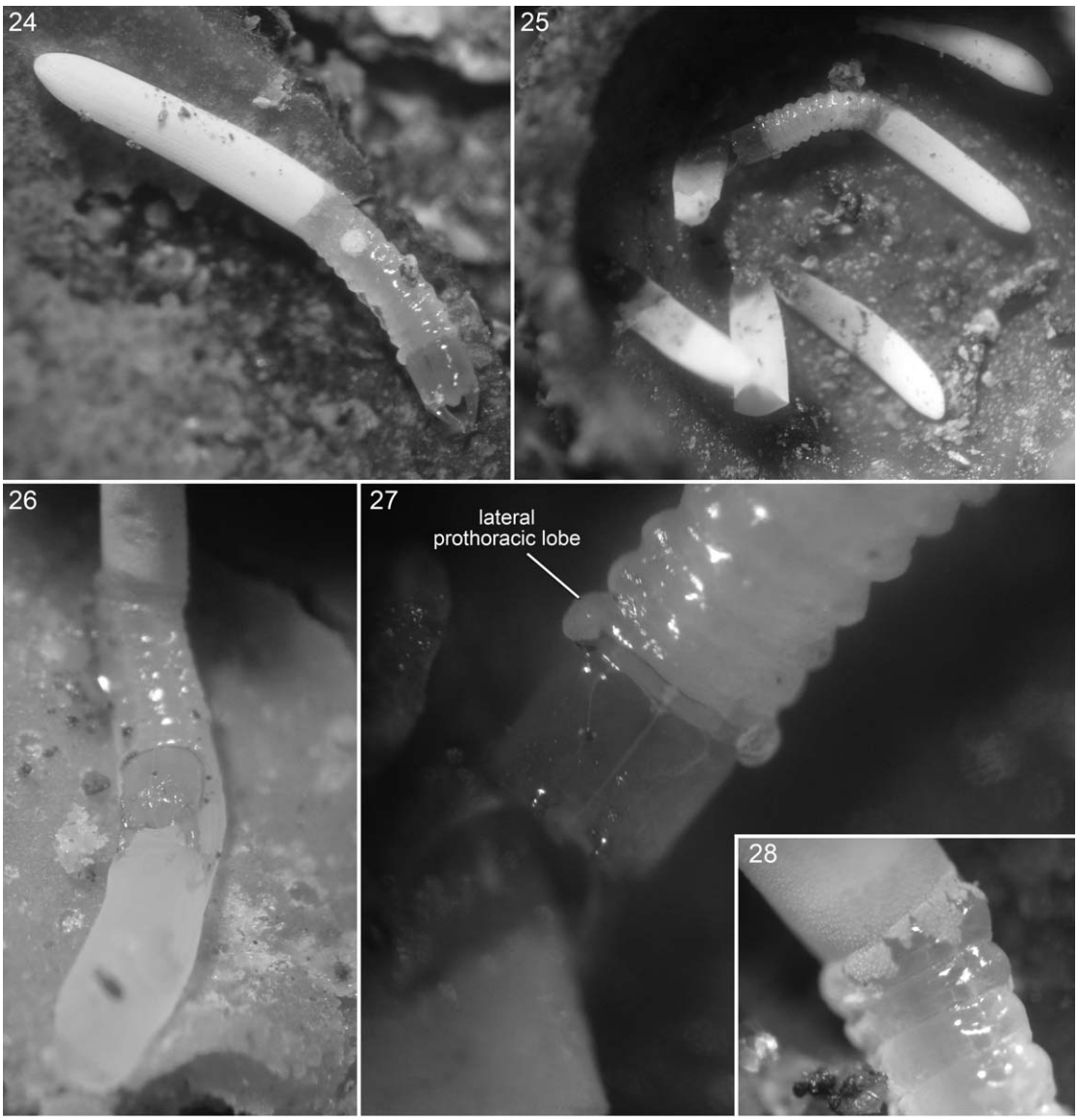
would be easily detected and eliminated by a returning female *C. flavofasciata*, as has been discussed for other cleptoparasitic bees (Rozen, et al., 2006: 24, 25).

In 2010, it was uncertain how many eggs a single female cleptoparasite deposits in a cell per visit. Limited data favored only one, but the high rate of parasitism in some cells, particularly when there was only a single hole in the closure, could indicate more. This matter was resolved from data gathered in 2011: 8 of 9 parasitized cells (10th cell destroyed in excavation) each exhibiting a hole, usually stoppered with sand grains, and each containing only a single *M. sapphirina.* The lack of numerous fully formed oocytes in dissected females also strongly points to only one egg being deposited per visit.

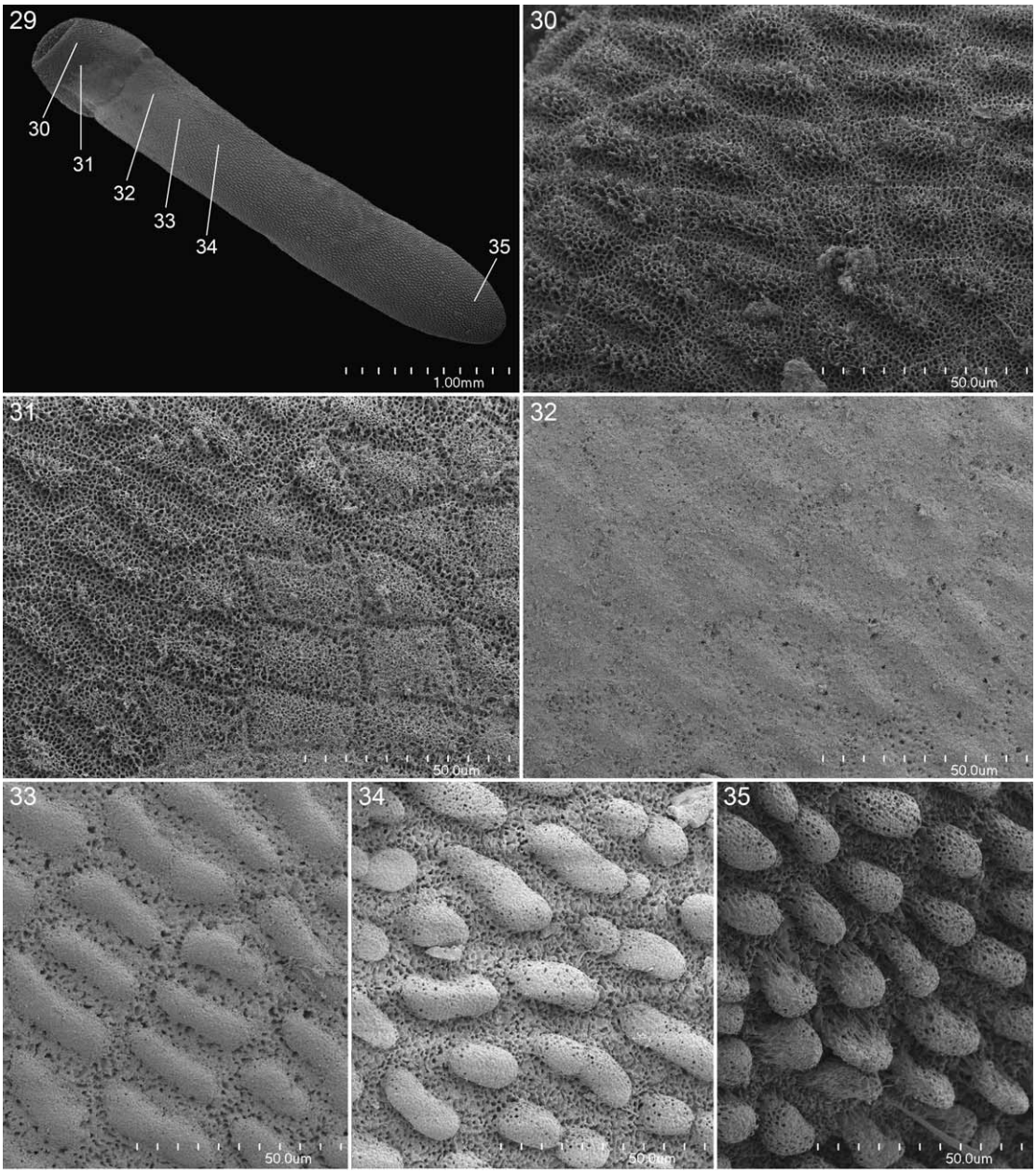
Partway through our examination of the collected cells in 2010, we examined provisions of cell 8 (table 1) submerged in water and discovered a large number of extremely small ants identified as *Solenopsis* sp. that had been totally overlooked in provisions not examined in water. Although it was impossible to review cells examined earlier, this discovery may well explain why in some cells, all *M. sapphirina* were dead, e.g., table 1, cell 3 (although why all parasite eggs were attacked, whereas the host egg was not, remains unexplained). Data from 2011 revealed that ants had not attacked a single cell among the 36 examined, possibly because most nests had been excavated by us within three days after closure.

In the 2010 study, evidence was unclear why cleptoparasite eggs in some cases hung by one end from the cell closure as was the situation in cell 3 where two eggs hung by one end next to the hole through which each had been deposited (before presumably being attacked by *Solenopsis*). An egg attached by one end to a closure had been reported for *Aglaomelissa duckei* (Friese) from Trinidad (Rozen, 1991: 32). In all other cases, eggs in the 2010 investigations were found on the provisions. With the 2011 study three eggs were attached by their anterior ends about 1–2 mm from the hole through which they were inserted. Since all five first instar *Mesoplia* were accompanied by holes through the cell closure, there is little doubt that *M. sapphirina* eggs are normally attached presumably always by their anterior ends to the cell closure. How the female attaches her egg to the inner surface of the closure 1–2 mm from the hole remains unknown, although possibly some *Mesoplia* egg detachments in 2010 resulted from numerous visitations by conspecific cleptoparasites that dislodged attached eggs while attempting to oviposit or by ants.

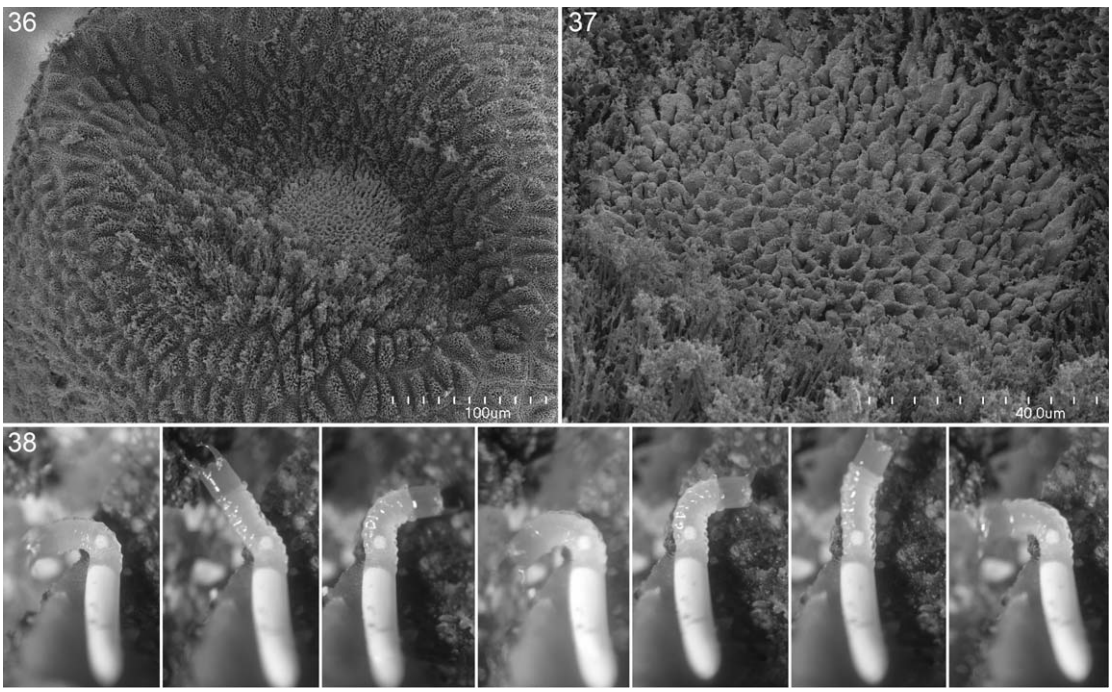
The egg incubation period for *M. sapphirina* clearly seemed brief, for an open nest was identified two days before a first instar was recovered from the cell in 2010, and in 2011, five first instars were removed from cells that had been closed within the last two or three days. Finally on February 19, 2011, an adult M. *sapphirina* descended into a host nest after flicking away sand at the surface for ca. 8 min. After it had disappeared from sight, we placed a plastic tumbler over the entrance and thereafter monitored the site while working the area. One hour later (10:45 AM) it had emerged and died in the heated tumbler. That day the brood cell was excavated, and a *Mesoplia* egg was found attached to the cell closure. The first instar hatched 29.5 hrs later. Unfortunately, we missed observing the hatching process, although the ragged connection of the chorion with the rear of the abdomen was well documented (fig. 28). We placed the larva on the surface of the provisions of another cell containing a host egg. It made no obvious efforts to locate the host egg, not surprising considering lack of sight, but reacted



FIGURES 24–28. Microphotographs of live first larval instar of *Mesoplia sapphirina.* **24.** Entire larva showing egg chorion attached to rear of abdomen. **25.** One live larva, with remnants of five conspecific eggs and first instars, all in one cell. **26.** First instar attacking host egg. **27.** Close-up of first instar with pronounced lateral prothoracic lobes biting egg chorion of another individual. **28.** Close-up showing junction of ragged anterior end of chorion attached to first instar.



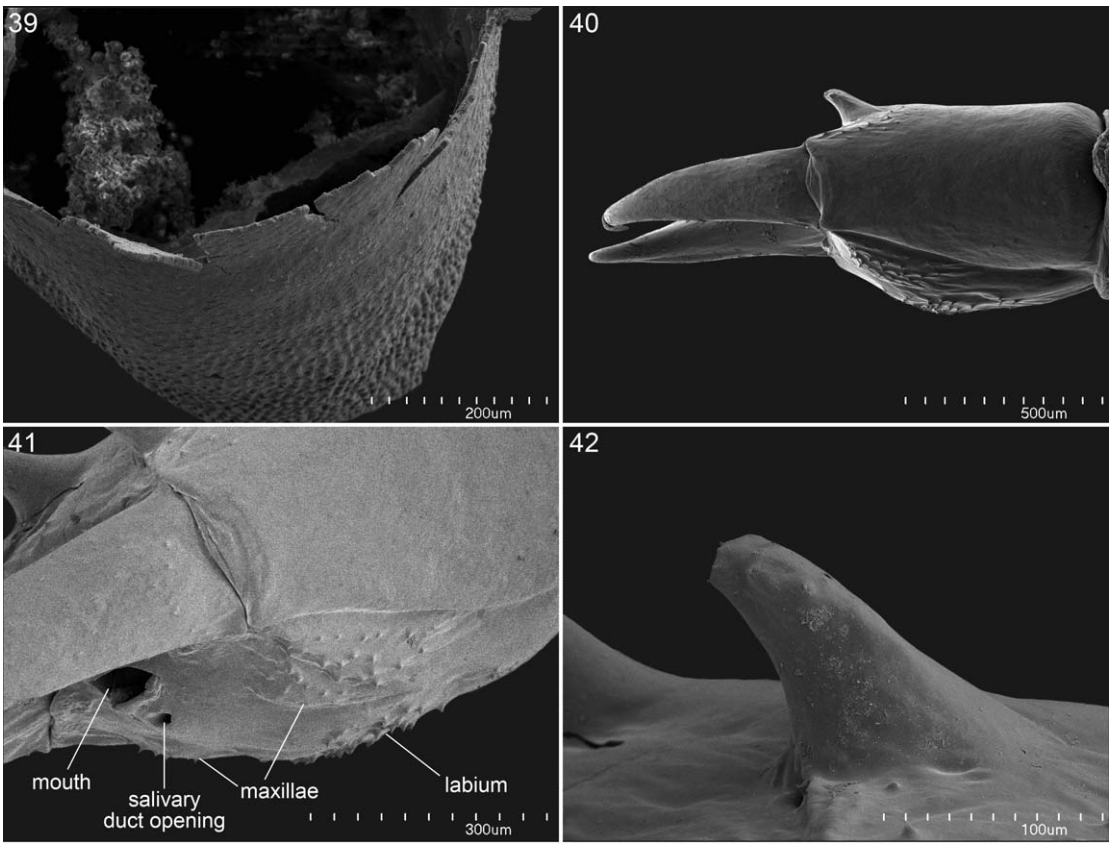
FIGURES. 29–35. SEM micrographs of egg of *Mesoplia sapphirina*, approximate ventral view. **29.** Entire egg. **30–35.** Close-ups of chorion from places identified in figure 29.



FIGURES 36, 37. SEM micrographs of anterior end of egg of *Mesoplia sapphirina*, and close-up of micropyle, respectively. Figure 38. Photographic sequence of first instar of *Mesoplia sapphirina*, showing range of rapid motion during a 2 min period.

with much body twisting and turning when touched with a forceps, perhaps suggesting a defense reaction to other cleptoparasites. When placed close to the host egg, it snagged the host chorion with one of its mandibles, but did not proceed to attack with both mandibles as if trying to eliminate the host. The larva seemed unable to crawl forward or backward but twisted rapidly and with agility, presumably defense tactics. However, when observed two hours later, the *Mesoplia* larva had completely destroyed the host egg. A subsequent observation of another first instar revealed that it could indeed slowly crawl forward and backward when not disturbed, e.g., by being touched with forceps.

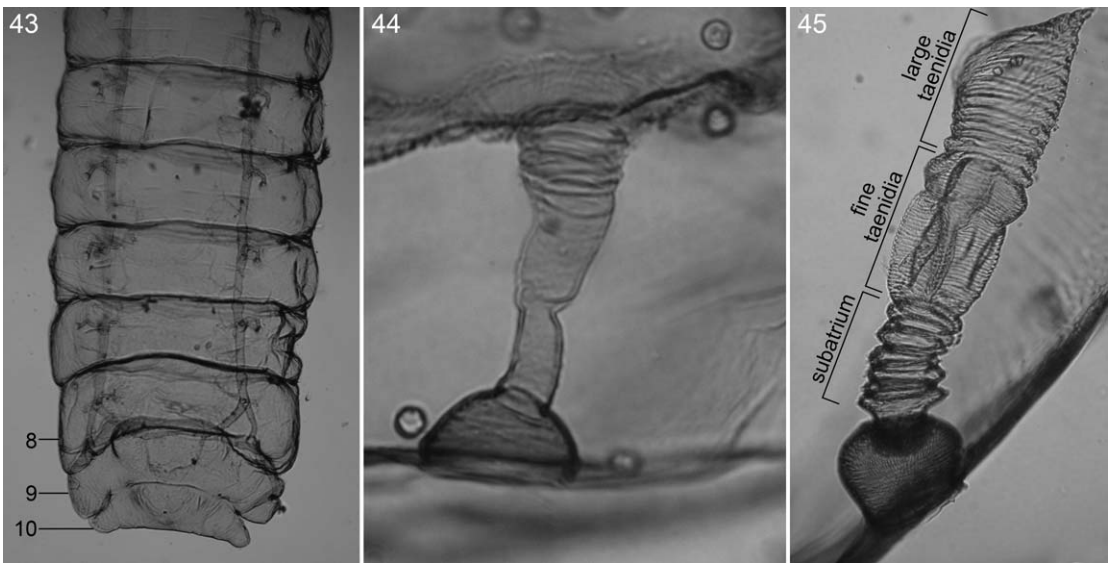
Some of the assassinated eggs in the 2010 study showed a swelling at the anterior end that is slightly wider than the diameter of the rest of the egg (figs. 23, 29). The ventral chorion immediately behind the front end was substantially smoother than elsewhere on the egg (compare fig. 32 with figs. 30, 31, 33–35). In one egg that had been killed we noticed that the length of this anterior part was approximately the same as the length of the mandible of the developing embryo within, whereas most of the head of the embryo was posterior to the swelling. Furthermore, on some other dead eggs the anterior pole containing the micropyle was invaginated (figs. 23, 29, 36). We wonder whether these apparent deformities are real: the swelling of the anterior end allows the mandible to open and close and the micropylar area invaginates (through some unknown mechanism), permitting the sharp apices of the mandibles (fig. 47) to reach and rupture the anterior end of the chorion. Verification of the



FIGURES 39– 42. SEM micrographs of first-instar *Mesoplia sapphirina.* **39.** Anterior edge of egg with first instar removed showing frayed chorion that had been attached to abdominal rear of larva. **40.** Head, near lateral view. **41.** Lower part of head showing mouthparts, anterolateral view. **42.** Left antenna, anterolateral view.

above speculation should be easily forthcoming by observing an egg that is hatching. The role played by the pronounced paired lateral lobes of the prothorax (fig. 27) of the first instar is unknown but might be involved with eclosion.

During both years virtually all live first instars of *M. sapphirina* and most dead ones had their seemingly still-inflated egg chorions (figs. 24–26) attached to the terminal abdominal segments, indicating that this is a normal behavior pattern for the species, the possible adaptive function of which is discussed below. Although the entire head, thorax, and first seven abdominal segments extend freely from the chorion, chorion covers abdominal segments 8–10, and the front end of the chorion is shredded (figs. 28, 39). As mentioned in the description of the egg, the chorionic surface texture a short distance behind the anterior pole is highly modified on the ventral and lateral surfaces. This region of the egg appears to adhere to abdominal segments 8–10 of the first instar. It is unclear how this attachment is maintained through the entire first stadium. Might the somewhat expanded form of abdominal segments 9 and 10 when viewed dorsally (fig. 43) and the declivity between 8 and 9 when viewed from the side (as in Rozen, 1991: fig. 55) play some



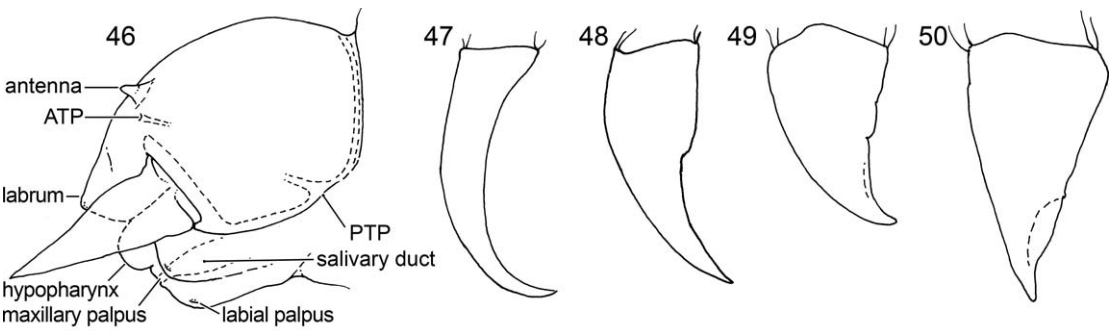
FIGURES 43–45. Microphotographs of *Mesoplia sapphirina.* **43.** Abdomen of cleared first instar, dorsal view. **44.** Spiracle of second larval instar, side view. **45.** Spiracle of fifth larval instar, side view.

role? Two of three first instars that were kept alive in 2011 lost their chorion several hours before molting to the second stage; the third kept the attachment until molting.

It is obvious that laterally expanded abdominal segment 10 in this species (and probably in all other Ericrocidini) has nothing to do with a pygopodlike function as suggested by Rozen (1991), since we now know that that segment 10 is encased in the chorion and cannot assist larval crawling.

First instars of *M. sapphirina* are extremely agile and feisty. They are capable of bending their entire body from where it is attached to the egg chorion sideways or overhead, so that the head is pointed completely backward in the same direction of the tail of the body. By reaching backward it can quickly defend itself against any adversary that might be attacking its attached empty chorion. This agility is demonstrated in figure 38, a sequence taken in a 2 min period. Second instars, though no longer carrying chorions, also display considerable agility and combativeness, features that fade in successive instars.

Data suggest that all larval stadia are brief, for one larva collected in 2010 as a second instar had reached the fifth instar within a period of four to five days, and started defecating two days later. Soon thereafter it started spinning a cocoon, but when preserved, it was removed from its cocoon while still feeding on a large mass of food and with its digestive tract still containing food, perhaps a developmental artifact resulting from being reared under artificial conditions. In 2011, an egg of *M. sapphirina* that hatched at 10:45 AM on February 20 was preserved as a third instar at 4:49 AM on February 25. The same year a first instar collected on February 21 was observed as a second instar at 4:30 PM on February 22, and as a third instar at 6:45 AM on February 24. Clearly, developmental behavior and timing need further detailed investigation.



FIGURES 46–50. Diagrams of *Mesoplia sapphirina*. **46.** Head of second larval instar, lateral view. **47–50.** Diagrams of right mandible, all to same scale, dorsal views, of following larval instars: first, second, third or fourth, and fifth, respectively; mandible of third or fourth instar from single cast skin in cell from which fifth instar retrieved. ATP = anterior tentorial pit; PTP = posterior tentorial pit.

DISCUSSION OF BIOLOGIES

One compelling reason to investigate *M. sapphirina* was to try to understand the adaptive function involved with its first instar carrying the eclosed chorion attached to the rear of its abdomen. In advance, three hypotheses occurred to us: (1) chorion serving as a flotation device allowing *M. sapphirina* to search for a host egg under a layer of nectar (holdover hypothesis suggested by a previous study of a *Centris* that floods larval food with nectar; Rozen et al., 2010); (2) chorion serving as air reservoir, allowing larva to submerge in search of host egg (hypothesis supported by enlarged spiracles of abdominal segment 8); and (3) chorion attached to cell closure giving larva at opposite end long reach to attack host egg from above. Since our current studies show that the provisions of the host are not protected by a layer of nectar, hypotheses (1) and (2) fail, though enlarged spiracles of abdominal segment 8 remain unexplained. Since the length of first instar plus chorion is roughly 8 mm and the distance from closure to provisions is probably 10 mm, hypothesis (3) fails because the host egg is out of reach, and in any event the parasite egg is attached by its anterior end, not its posterior end, to the closure.

Our current hypothesis formulated from all information on hand is that the chorion attached to the rear of the first instar is a shielding device that protects a larva from first-instar sibs that may be in the cell. This is suggested by the numerous instances where we found more than one first-instar *M. sapphirina* in a cell in 2010 and our observing the extreme agility of a larva to reach around and aggressively attack other first instars, or forceps, pinching its egg chorion. The larva first attacked from behind by a conspecific sibling has a greater chance of leaving the battle uninjured since the attacker is likely to continue biting an empty chorion while its adversary reaches around and clamps its mandibles on the unprotected anterior party of the attacker.

It is instructive to evaluate evolved strategies that allow success of a cleptoparasite to parasitize a host and conversely those that allow a host to successfully defend itself from a cleptoparasite. In the case of *M. sapphirina*, the rapid, aggressive behavior of the female looking for host nests and its first instar's mandibular shape, heavily sclerotized, prognathous head capsule with strong muscular development, and crawling ability are obvious features required for

attacking host immatures. The short egg-incubation period of the parasite contrasting with the longer one of the host (as evidenced by host egg deposited before cell closure whereas parasite egg introduced after cell closure) seems to assure the parasite has to deal only with the totally inactive egg of the host. Obvious if not fully understood, is the ability of the *Mesoplia* female to identify a nest that is appropriate to attack (there would be no point in inserting a cleptoparasite egg into a closed cell if a host larva had already consumed the food), and a mechanism to insert her egg into a cell that has already been closed.

It is more difficult to identify defense strategies of *C. flavofasciata*, although the single-celled nest is a good defense against cleptoparasitic trap-liners whose females travel from one multicelled nest to another waiting for the next cell in each nest to reach the appropriate condition to be attacked. There is a strong tendency for *C. flavofasciata* to initiate nests under dried leaves on the ground or next to dead branches, thus partly hiding the nests from searching parasites. Other possible defenses, such a closing the brood cell with a hard cover did not work in the case of *M. sapphirina* since we know it is able somehow to penetrate the cell closure. Piling sand over nest entrances obviously helps to obscure detection by *Mesoplia,* but fails frequently. Defenses, such as removal of parasite eggs from the cell by a returning host female is not likely since, after she closes the cell, she does not return to it. However, if a host female detects a *Mesoplia* female attempting to enter the nest, the much larger host will chase or block the parasite from entering. Finally, after working a restricted area for several weeks we were left with the impression that an adult *C. flavofasciata* may continue to nest in the same restricted area, and thus guard the area by chasing large bodied bees (*Centris* or *Mesoplia*) that attempt to explore the same area.

The differences in early developmental biologies of host and cleptoparasite are remarkable. The first instar of the host remains pharate, i.e., covered by its chorion, essentially inactive while the anatomically highly specialized first-instar cleptoparasite squeezes out of the front end of its chorion that then remains attached to the end of its abdomen, and the larva itself actively moves around and battles everything that might compete for provisions.

OVARIAN STATISTICS OF *MESOPLIA SAPPHIRINA*

Of the three females of *M. sapphirina* examined, each had four oocytes per ovary (ovarian formula 4:4), the typical number for Apidae and consistent with reports on other *Mesoplia* (Rozen, 2003). Although they had on average only 0.25 oocytes per ovariole, many other oocytes had almost completely lost all nurse-cell material and thus seemed close to being mature. Average egg index 0.75 ($N = 3$) indicates they were well within the *median* category of Iwata and Sakagami (1966: table 2), an unusually high value for many cleptoparasitic bees (Rozen, 2003) but entirely in keeping with indices of other Ericrocidini (ibid.).

IMMATURE STAGES OF *MESOPLIA SAPPHIRINA*

Descriptions of the egg/mature oocyte and of the first and last larval instars are presented with brief accounts of the second and third instars. We assume that there are five larval stages,

TABLE 2. Active cells of *Centris flavofasciata,* their contents including *Mesoplia sapphirina*, and other varying characteristics, February 2011.

Of the 36 cells recovered, 11 cells had been attacked by *Mesoplia sapphirina* and are shown here; others containing 17 host eggs, 9 host larvae, and no *M. sapphirina* have been removed to fit table to page.

Characteristic \ Cell	1	2	4	5	6	7	8	22	30	31	36
February day nest excavated	09	10	12	15	15	15	15	19	21	21	21
February day nest found	09	09	12	13	13	13	13	19	?	?	?
Stage of *M. sapphirina*	Egg	Egg	1st	1st	1st	1st	1st	Egg	1st	1st	2nd
Total live *M. sapphirina*	1	1	1	1	1	1	1	1	?	1	1
Total *M. sapphirina* present	1	1	1	1	1	1	1	1	1	1	1
Holes in cell	1	1	1	?	1	1	1	1	?	1	?
Stage of *C. flavofasciata*	Egg	Egg	0*	0*	0*	0*	Dead egg	Egg	0*	0*	?
Total cell contents dead	0	0	0	0	0	0	0	0	0	0	0
Ants detected	No	No	No	No	No	No	No	No	No	No	?

*Host remains not found, presumably deteriorated.

as has been demonstrated for other bees, and accordingly refer to the final instar as the fifth. However, because the number of larval instars of no ericrocidine has been demonstrated, this information needs confirmation. The pupa of *M. sapphirina* is unknown.

Egg/Mature Oocyte

Figures 20, 23, 29–35

Diagnosis: Color, comparative lack of curvature, shape, and difference in chorionic ornamentation distinguish egg of *M. sapphirina* from that of its host, as indicated below.

Description: Length approximately 4.01–4.65 mm ($N = 9$) (about same length as that of host); maximum diameter 0.70–0.83 mm; in mature oocytes, diameter uniform for entire length except wider at rounded anterior end and abruptly narrowing to narrowly rounded posterior end; in at least some eggs, anterior end slightly swollen compared with rest of midsection. Shape (figs. 21, 23, 29) elongate, parallel sided (aside from some deposited eggs in which front end somewhat swollen, figs. 23, 29), circular in cross section, only slightly curved with outcurved surface ventral as determined by developing first instar (contrasting with strongly curved host with outcurved surface dorsal, fig. 15). Egg color white (not yellowish like host egg); chorion seemingly smooth under low magnification, nonreflective but under high stereoscopic examination with distinct pattern; micropylar area not evident under stereomicroscope. Under SEM examination micropyle (figs. 36, 37) clearly evident as tight cluster of pores (not unlike that of host) at anterior pole; area around it fibrous, without radiating ridges but with patterning as in figure 34; elsewhere chorion with polygonal patterning (figs. 30–35); each polygon at anterior end of egg with fibrous elongate

elevations, which becomes almost tuberclelike toward rear of egg (fig. 35), except about 2.8 mm from anterior end, polygons losing elevations and becoming nearly smooth on ventral surface but not on dorsal and lateral surface of egg; posteriad of smooth polygons, elevations again appearing and extending to posterior end of egg.

Material Studied: Three eggs, collected II-09, 19-2011; various, more or less damaged eggs (fig. 25), various dates; various mature oocytes from 3 females, collected II-14, 17-2010.

Remarks: The smoothing of the chorionic polygons (fig. 32) appears to coincide with the attachment of the chorion to the posterior end of the first instar, thus implying that it might functionally pertain to the attachment and that the anterior end of the chorion is lost on hatching, as discussed in Biology of *Mesoplia sapphirina*, above.

First Instar

Figures 27, 40–44

Diagnosis: The reader is referred to the tribal description of first instar Ericrocidini (Rozen, 1991). Because the head capsule of *M. sapphirina* is almost identical to that of *M. rufipes*, the diagnosis of first-instar *Aglaomelissa duckei* (Friese) (ibid.: 30) distinguishes known first instars of *Aglaomelissa*, *Ericrocis*, and *Mesoplia*, with the exception of a character on the prothorax. Both *Ericrocis* (ibid.: figs. 64, 67) and *M. sapphirina* (fig. 27) have a pair of pronounced lateral prothoracic tubercles, whereas such tubercles appear to be missing in the other taxa. The most pronounced difference between *M. sapphirina* and *M. rufipes* is the presence of lateral prothoracic tubercles in the former.

Description: The first instar of *M. sapphirina* is so similar to that of *M. rufipes* (Rozen: 1991) that a formal description and diagrams are unnecessary, although figures 40–44 show numerous features of interest. Slight differences in mandibular length and elevation of antennae could be individual variation or species differences. The following details should be noted: antenna bearing numerous sensilla (probably 10 or more, fig. 42), as characteristic of all described first-instar ericrocidines; sclerotization of head extending short distance behind posterior tentorial pit ventrally; dorsally sclerotization ending at posterior constriction of head capsule that lacks defined postoccipital ridge; mandible (figs. 40, 41) with numerous sensilla over entire length; hypopharynx membranous, bilobed, surface spiculate (not detected previously on described ericrocidine first instars); venters of all body segments with median transverse patch of fine spicules; abdominal segments 9 and 10 separated dorsally by distinct but faint intersegmental line (fig. 43), contrasting with situation in *Aglaomelissa duckei* (ibid.); anus not detected (fig. 43).

Material Studied: Nine first instars and cast skins of first instars, II-17, 19, 20–22-2010; 4 first instars, II-14-2011.

Remarks: The body form of *M. sapphirina* is nearly identical to that of *Aglaomelissa duckei* and no doubt *M. rufipes,* although the former was more fully described than the latter (Rozen, 1991: fig. 54).

By examining numerous specimens of the first instar of *Mesoplia sapphirina* one is impressed with its hospicidal adaptations. Not only is the head heavily sclerotized (and thus darkly pigmented), but its entire ventral surface is fused to the cranium above and the maxillae

and labium are fused with one another and with the rest of the ventral surface. Palpi, as articulating appendages, are missing although the numerous sensilla are grouped, so their homologies with the approximate positions of the palpi are easily recognized. However, many of the sensilla are from areas surrounding the palpi of the next instar (see below). The labrum is small and completely fused with the front of the head. The mandibles are long, massive, and heavily sclerotized, and of course articulate with the front of the highly prognathous head capsule. The sclerotization of the elongate head capsule extends behind the posterior tentorial pits. With such a strongly constructed head, it is not surprising that the tentorium, while complete, is extremely thin and delicate and internal head ridges found on most bee head capsules are essentially missing (except for the hypostomal ridges, which are faintly represented). These features are all interpreted to reflect the great strength of the overall exterior surface of the head, required to support powerful mandibular muscles. The numerous mandibular and antennal sensilla may be evidence of the ability of the first instar to quickly detect and attack the host egg or conspecific competitors. The opening to the salivary duct is conspicuous as is the internal duct itself, but the function (if any) of these structures is unknown. The heavy head sclerotization might also suggest that it is protection (armor) against mandibles of competing cleptoparasites. Although this might be true to a degree, the lack of any protection immediately behind the head suggests the main function is to support musculature.

As already pointed out by Rozen (1991), there exists a notable similarity between the first instars of Ericrocidini and Isepeolini that needs additional consideration. He (ibid.: tables 1–3) found the similarity between these two tribes to be greater than between any other two tribes of the nonnomadine apine cleptoparasitic tribes. Furthermore, two more similarities need reinterpretation: (1) The labrum of each is fused to the front of the head, although that of *Isepeolus viperinus* (Holmberg), *Melectoides tristis* (Friese) (unpublished data, from cast skin collected by J.G.R. from Chile: Limari Prov.: 5 mi SE Las Breas, XI-6-2000) comes to a single pointed apex while that of *Mesoplia sapphirina* is shallowly bituberculate. (2) The sclerotization of the head invades the area behind the posterior tentorial pit, admittedly far more so in *Isepeolus* and *Melectoides* than in ericrocidines. Although the similarities between heads of the two tribes could be convergences driven by both developing extremely sclerotized heads, the similarities of enlarged spiracles on abdominal segment 8 that are positioned toward the rear margin of the segment would appear to have nothing to do with the head modifications.[7] Other similarities of first instars not itemized by Rozen (ibid.) should not be overlooked in future investigations into phylogenetic relationships of these two tribes, such as the truncate appearance of the body from above, the tendency of abdominal segments 9 and 10 to fuse, the similarity (except for size) both of labra and of antennae, and the overall fusion of the head into a single elongate, thickly sclerotized basically single sclerite. There are far fewer structural similarities shared by the last larval instars of ericrocidines and isepeolines than those of first instars (see Remarks

7 In Rozen (1991: table 1) several features of the Isepeolini were then unknown but have now been determined: Character 0. The egg is introduced into the cell that is still open (Rozen, 2003). Character 1. The egg adheres to the cell lining (Rozen, 2003). These features are not concordant with those of Ericrocidini.

under Fifth Instar, below), nor are adults notably similar (Michener, 2007) or closely related in a morphological analyses by Roig-Alsina and Michener (1993), although the molecular analysis by Cardinal et al. (2010) places the two tribes somewhat apart in a single large parasitic clade. This matter deserves further study.

Second Instar

Figures 44, 46, 48

The second instar (fig. 46) begins to assume many features of the last instar: head capsule more globose, with sclerotization reduced so that internal ridges more evident, antennal papilla reduced and less flattened, and labrum apparently differentiated from clypeus. The tentorium is more robust than that of the first instar, as might be expected with the decrease in cranial sclerotization. The mandibles (figs. 46, 48), however, are still large, apically curved, sharply pointed but not as thin basally relative to length. Because of this anatomy and observations of this instar's agility, there is every reason to suppose this larva capable of battling other inhabitants of the brood cells, although none were found alive in cells containing second instar *Mesoplia.*

The sclerotization of the ventral head surface between the hypostomal ridges is now nearly absent. The mouthpart components are clearly differentiated lobes. The maxillary and labial palpi are clearly recognizable as small sensilla-bearing protrusions shorter than their basal diameters. Each maxilla is apically lobelike, as is the labial apex, but the largest, most forward-directed protrusion is the weakly bilobed, spiculate hypopharynx. Maxillary and labial sclerites are weakly defined and faintly pigmented. A thin articulating stipital arm is evident branching from the anterior end of the almost nonexistent stipital rod. A dominant feature of the prelabium is the large transverse salivary opening (wider than the distance between labial palpi) to which is connected a large, noncollapsed salivary duct (fig. 46).

The postcephalic region is broadened, becoming slightly physogastric posteriorly, but the lateral pronotal tubercles are still evident. Body segmentation is featureless (except for spiracles), and abdominal segment 10 is much narrower compared with that of first instar, with the anus identified by a dorsally positioned integumental scar with attached tissue but no intima to indicate a proctodaeum. The last pair of spiracles are still enlarged compared with the others that are subequal in size. All have a wide, shallow atrium with concentric faint ridges, to which is connected a chamberless, straight subatrium (fig. 44).

Material Studied: One first instar collected II-19-2010, preserved as second instar II-22-2010 (because head capsule larger than that of following, this specimen possibly third instar); one second instar II-21-2011.

Other Larval Instars

We had insufficient material to develop an understanding of all larval instars or even to determine whether there are five larval stages. However, from a cast skin, we recognize an intermediate stage between the second instar and the fifth instar. This instar obviously represented either the third or fourth instar. It has a darkly pigmented mandible (fig. 49) that is shorter compared with its basal width than that of the second instar described above. The inner apical surface is now slightly concave and curved apically with sharp upper and lower apical

edges. Thus, it is approaching the scoop-shaped apical concavity of the last larval instar. However, viewed dorsally or ventrally the mandibular apex was strongly curved and ended in an acute point. Viewed from above or below, the mandible tapered gradually toward the apex, giving little hint of an incipient oblique apical truncation as in the fifth-instar mandible.

Material Studied: One cast skin, II-17-2010.

Fifth Instar

Figures 45, 50–54

The shed skin of a last larval instar of *Mesoplia rufipes* was previously compared with that of *Acanthopus palmatus* (as *A. splendidus urichi*) (Rozen, 1969), but the following is the first account of a complete last larval instar of any species in the genus.

Diagnosis: In general, known last larval instars of this tribe show close agreement in features pertaining to head capsules and mouthparts. However, the large, darkly pigmented articulating arms of the stipes immediately distinguishes this species from *Acanthopus palmatus* (Rozen, 1969) and *Ericrocis lata* (Rozen and Buchmann, 1990), neither of which reveals evidence of such arms. A reexamination of the cast exoskeleton of *Mesoplia rufipes* from Trinidad clearly shows darkly pigmented articulating stipital arms.

Although the oldest of the three specimens described here is clearly the fifth instar, it is not postdefecating. As discussed in the biology of this species, the larva was preserved before reaching postdefecating status, making anatomical comparisons with postcephalic bodies of postdefecating larvae of related taxa difficult.

Head: Scattered sensilla nonsetiform; integument mostly nonspiculate, except dorsal surface of maxilla weakly spiculate and most of hypopharynx heavily spiculate with large, regularly spaced spicules. Sclerotized integument faintly pigmented except following areas moderately to darkly pigmented: postoccipital, hypostomal, and pleurostomal ridges, anterior and posterior tentorial pits, mandible, particularly at apex, articulating arm of stipes.

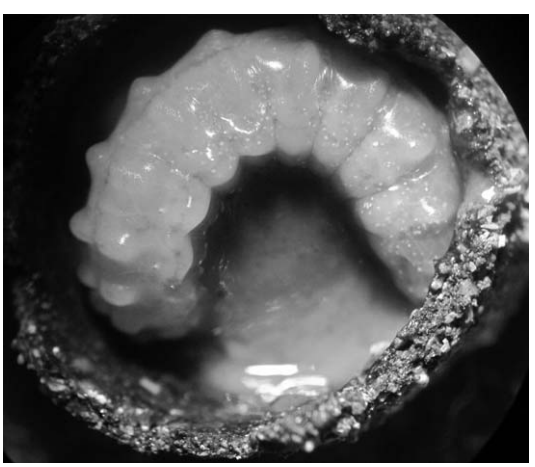
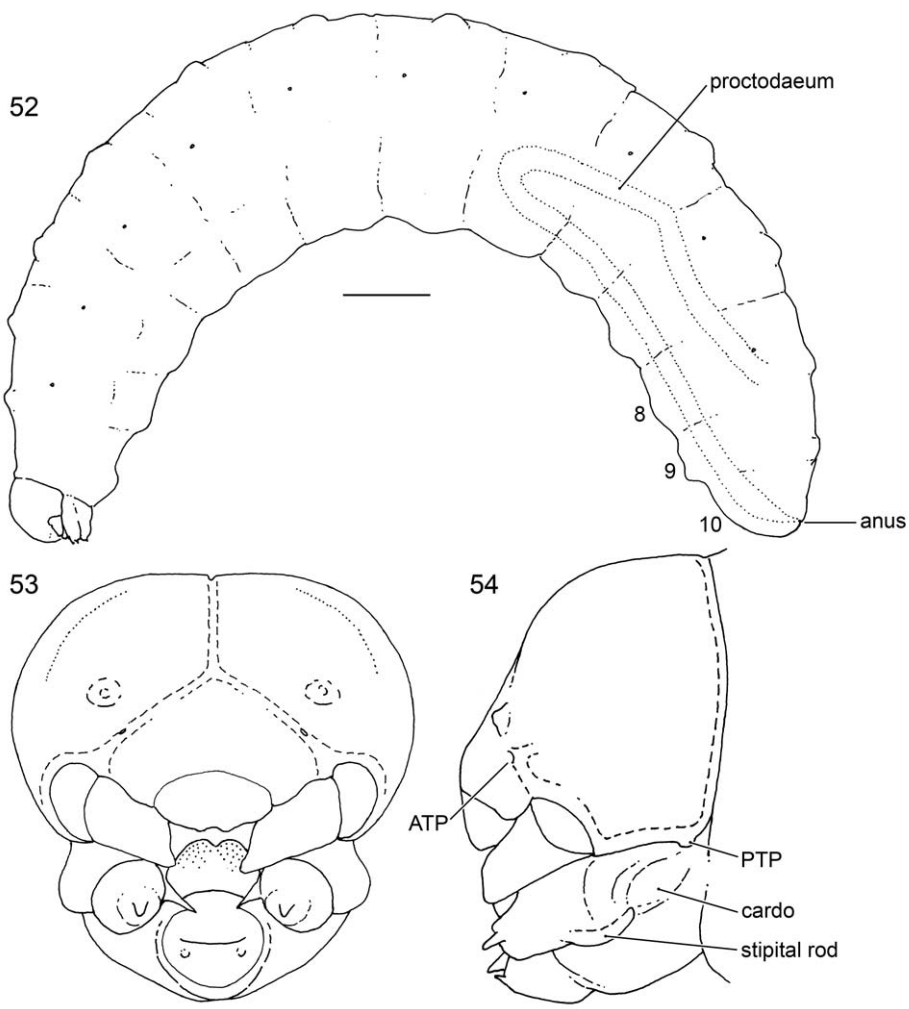


FIGURE 51. Feeding live fifth instar of *Mesoplia sapphirina*, showing paired dorsal tubercles.

Head size small compared with large, elongate body. Head capsule at least 1.5× wider than length from top of vertex to lower clypeal margin. Tentorium complete, robust, with dorsal tentorial arm; distance between anterior mandibular articulation and anterior tentorial pit about equal to distance between pit and antennal papilla; posterior tentorial pit in normal position; postoccipital ridge not bending forward at midline as seen in dorsal view; coronal ridge well developed above, fading slightly before meeting epistomal ridge; postoccipital, hypostomal, and pleurostomal ridges well developed; epistomal ridge between anterior mandibular articulation and anterior tentorial



FIGURES 52–54. Diagrams of fifth larval instar of *Mesoplia sapphirina.* **52.** Entire larva with proctodaeum illustrated, lateral view. Scale = 2.0 mm. **53, 54.** Head front and lateral views, respectively. ATP = anterior tentorial pit; PTP = posterior tentorial pit.

pit well developed; hypostomal ridge without dorsal ramus; median section of epistomal ridge slightly weaker, straight, directed dorsomedially, so that each half forming right angle with one another at juncture with coronal ridge seen in maximum profile; that junction point somewhat above level of antennae. Parietal bands evident. Antennal prominences not developed; basal ring of antenna projecting; papilla distinctly shorter than basal diameter, bearing numerous sensilla. Vertex evenly rounded in lateral view; frontoclypeal area not projecting beyond labrum in lateral view (fig. 54); clypeus not as strongly projecting as that of *Acanthopus palmatus* (Rozen, 1969: fig. 47). Labrum short, its lower margin not projecting forward; apical margin weakly, narrowly bituberculate; each tubercle pigmented apically, bearing small cluster of sensilla.

Mandible (fig. 50) (similar to that of *Mesoplia rufipes*, Rozen, 1969: figs. 54–56) massive,

short, obliquely truncate apically with most apical angle rounded, with large, scoop-shaped apical concavity; outer surface with numerous, scattered, nonsetiform sensilla; mandible without projecting cusp, teeth, or denticles. Labiomaxillary region strongly projecting. Maxillary apex not bent mesad but inner apical angle with slight bulge probably homologue of apex; palpus thus apical; cardo and stipes well defined; maxillary rod nonpigmented except articulating arm of stipes large, darkly pigmented (see Remarks); palpus large, darkly pigmented, tapering from broad base, thus conical, about twice as long as basal diameter. Labium divided into pre- and postmentum, bearing transverse, projecting salivary lips; premental sclerite present but weakly pigmented; palpus tapering, about one-half size of maxillary palpus. Hypopharynx exceedingly large, dorsally projecting, bilobed, spiculate.

Body: Much of integument very finely spiculate, without setae; body without sclerotized spines; integument of paired dorsal tubercles nonsclerotized although thoracic ones perhaps faintly so. Form (as probably characteristic of predefecating larva) (fig. 52) extremely elongate; intersegment lines weakly incised; intrasegmental lines not evident; thoracic segments and abdominal segment 1–9 with low, paired dorsal tubercles on caudal annulets (fig. 52), though demarcation of annulets sometimes vague; venter of abdominal segment 9 with median swelling; segment 10 attached to segment 9 centrally in lateral view (fig. 52); anus positioned dorsally on segment 10. Spiracles (fig. 45) small, subequal in size, not surrounded by sclerites; peritreme flat; atrium projecting slightly beyond body wall, with pronounced rim; atrium globose, with outside diameter distinctly greater than outside depth; atrial wall with concentric rows of evenly spaced small denticles; primary tracheal opening guarded by long projections all directed toward single point near center of atrium; each projection covered by mass of fine barbs; hence tracheal opening similar to but denser (darker in value) than that of *Ericrocis lata*; subatrium consisting of 4–6 chambers of approximately equal outside diameter, to which is attached a section of trachea somewhat wider in diameter with fine taenidia obviously corresponding to optically dense area of *Ericrocis lata* (Rozen and Buchmann, 1990: fig. 56) (see Remarks, below); this section connected to trachea with larger taenidia. Male sex character a transverse integumental scar on apex of median ventral swelling of abdominal segment 9; female characters unknown.

Material Studied: One second instar collected II-17-2010, preserved as fifth instar II-26-2010; one first instar collected II-19-2010 preserved as early fifth instar II-26-2010; one first instar collected II-21-2011, preserved as fifth instar II-25-2011.

Remarks: Paired dorsal body tubercles of late stage fifth instar (fig. 52) were less exaggerated than those of the early fifth instar (fig. 51).

The articulating arm of the stipes in cocoon-spinning bee larvae is a cuticular process that branches from the anterior end of the stipital rod at the point where the inner surface of the maxilla branches from the hypopharyngeal/labial column, and its apex articulates with the premental sclerites (Rozen and Michener, 1988). Because the stipital rod of *M. sapphirina* is nearly pigmentless and very thin just before branching and the articulating arm is darkly pigmented, we were able to clearly see the connection only after removing the mandible.

The section with fine taenidia (fig. 45) that connects the trachea to the spiracular subatrium is wider in diameter than the subatrium but clearly is homologous to the much nar-

rower, denser section found in the same relative position in *Ericrocis lata* (Rozen and Buchmann, 1990: fig. 56), as evidenced not only by its position but also by the fine taenidia in both taxa. This connection between the tracheal system and body wall presumably allows flexibility, so that the body wall can bend and twist without straining or collapsing parts of the tracheal system. Thus, the different appearance of this feature in these two taxa is an indication that when preserved the larva of *Mesoplia sapphirina* was still active and prediapausing, whereas that of *E. lata* was in diapause.

A seemingly unusual feature of this larva is the great length of its proctodaeum (fig. 52) easily identified in the cleared specimen because its cuticular lining persisted and retained the undigested pollen exines. If straight, the proctodaeum would have extended 18 mm, roughly three-quarters of the length of the entire body.

Because we comment above on the many similarities of first-instar Ericrocidini and Isepeolini, we consider here similarities of last larval instars, those of the latter described by Rozen (1966) and Michelette et al. (2000). However, most of the shared features are plesiomorphic, found in unrelated taxa that have cocoon-spinning larvae. Mature larvae of these two taxa differ in many ways, including mandibular shape, spiracular features, and body form. Only two features might hint at a relationship: (1) numerous antennal sensilla on each antenna and (2) the close approximation of the two apical labral tubercles of *Mesoplia* could be considered a step toward the single projecting apical tubercle of *Isepeolus viperinus* and *Melectoides bellus* (Jörgensen).

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Gabriel A.R. Melo and L.C. Rocha-Filho kindly prepared the appendix published herewith so that we had a valid name for *Mesoplia sapphirina*. Melo also confirmed the identity of the adult specimens of *Mesoplia rufipes* from Trinidad, whose mature oocyte, larva, and pupa are mentioned in this paper. In addition, we acknowledge with sincere appreciation the assistance of the late Roy R. Snelling in identifying Costa Rican *Centris* referred to here as well as in earlier studies by the authors.

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APPENDIX

A New Species of *Mesoplia* (Hymenoptera: Apidae) from Mesoamerica

by Gabriel A.R. Melo,[8] and Léo C. Rocha-Filho[9]

INTRODUCTION

The genus *Mesoplia* contains medium to large bees and is the most diverse within the obligatory cleptoparasitic tribe Ericrocidini. Its species attack nests of *Centris*, except for *M. rufipes* (Perty, 1833) which also attacks *Epicharis* (Rocha-Filho et al., 2009). Currently a total of 20 available names are attributed to *Mesoplia*, with 16 of them considered to represent valid species (Moure and Melo, 2007).

In an ongoing revision (Melo and Rocha-Filho, unpubl.), 22 species are recognized, one of them here described as new. This new species has been cited under the name *M. regalis* (Smith, 1854) in Cheesman (1929: 144; as *Mesonychium*), Michener (1954: 146, 147), Ayala et al. (1996:

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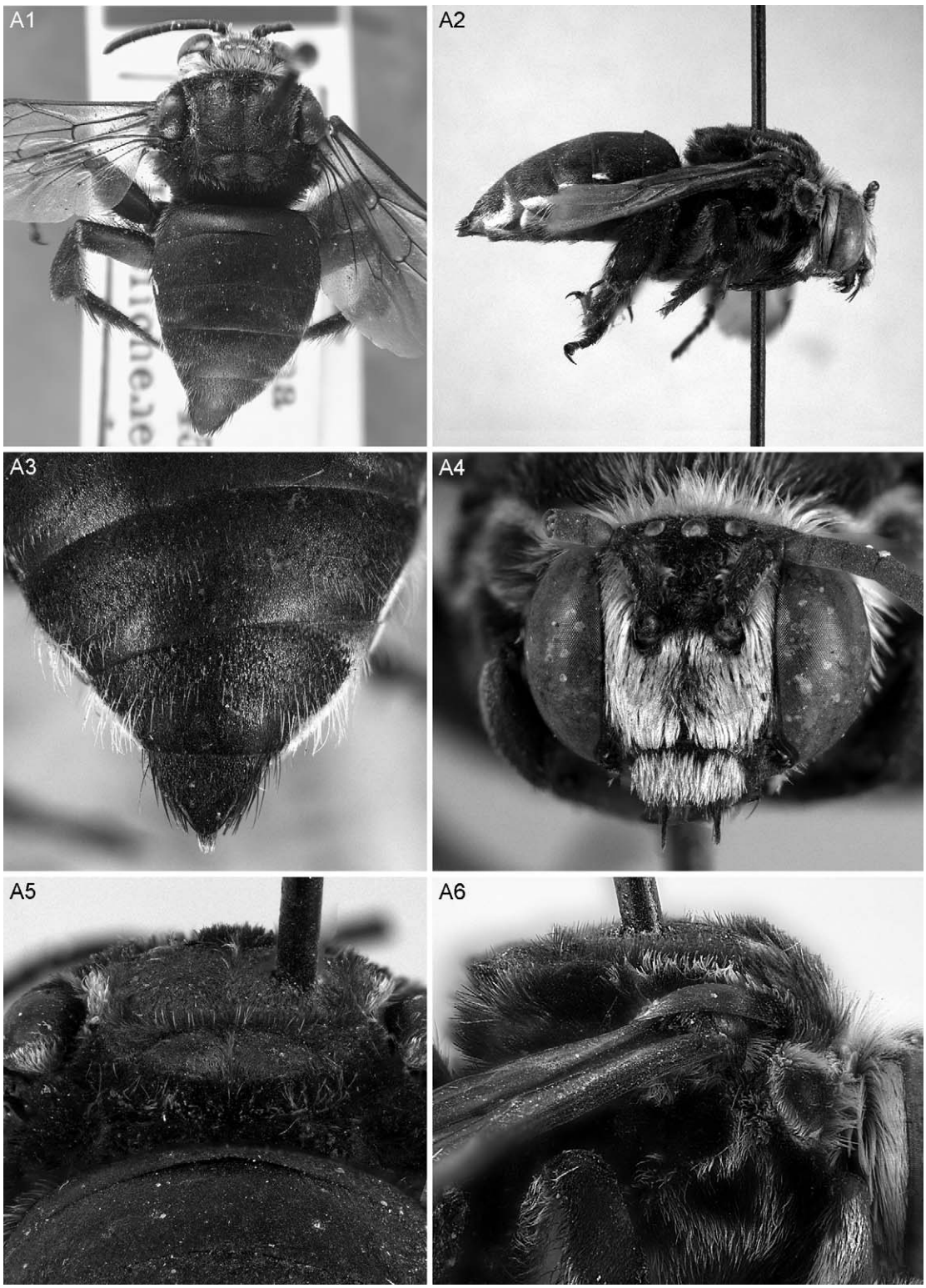
458), Vinson et al. (1987: 258), and Rocha-Filho et al. (2009: 302) and also as *M. bifrons* (Fabricius, 1804) by Ayala et al. (1996: 458). The studied material belongs to the American Museum of Natural History, New York (AMNH); Departamento de Zoologia, Universidade Federal do Paraná, Curitiba, Brazil (DZUP); Illinois Natural History Survey, Urbana, Illinois (INHS); Los Angeles County Museum, Los Angeles, California (LACM); Snow Entomological Collection, Division of Entomology, Natural History Museum, University of Kansas, Lawrence, Kansas (SEMK); Instituto de Biología, Universidad Nacional Autónoma de México, México (UNAM).

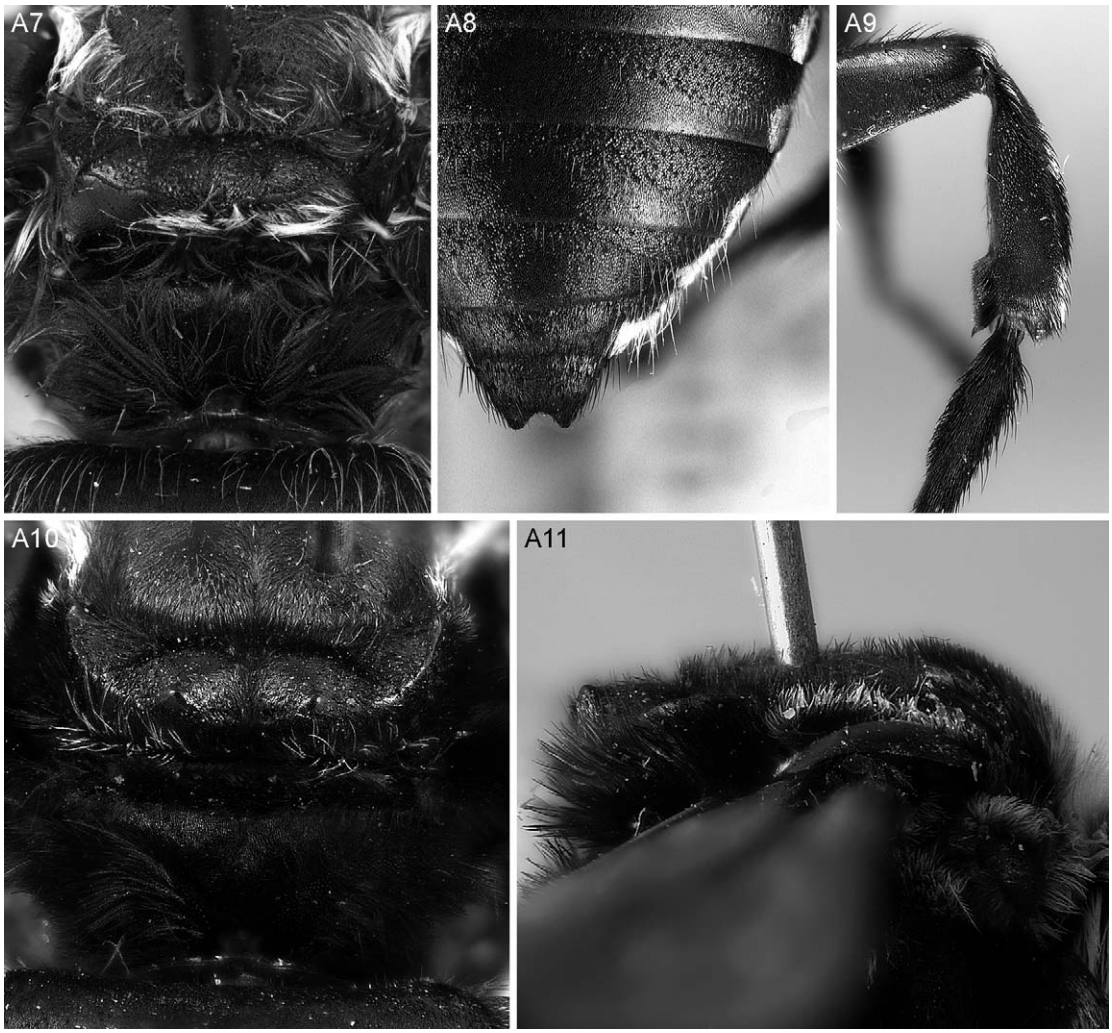
Mesoplia sapphirina, sp. nov.

Figures A1–A9

Diagnosis: *Mesoplia sapphirina,* sp. nov., is very similar to *M. regalis*, both species belonging to a large group whose males have a hind tibia with a conspicuous and dense apical tuft of short black setae on its inner surface and a hind femur lacking a basal ventral projection. Besides these two species, the group contains *M. bifrons*, *M. insignis* (Smith, 1879), *M. pilicrus* (Friese, 1902) plus eight undescribed species (Melo and Rocha-Filho, unpubl.) *Mesoplia sapphirina,* sp. nov., differs from *M. regalis* mainly in the shape of the mammilliform protuberances of the scutellum. In *M. sapphirina,* sp. nov., the protuberances are weakly developed, their surface only slightly convex and their tubercles low and broadly rounded. Also, in this species, the carina delimiting the protuberances posteriorly is well developed and runs continuously from one side of the scutellum to the other. In *M. regalis*, the protuberances are stronger, with a deep trough between them and with conspicuously pointed tubercles (figs. A10, A11); the delimiting carina is most developed only along the tubercles, fading gradually toward the sides.

Description: **Holotype female**: Approximate body length, 20.5 mm; maximum head width, 6.1 mm; length of fore wing, 15.3 mm. *Integument color:* Predominantly dark brown to black; first flagellomere light reddish brown; remainder of flagellum, subapical one-third of mandible, pronotal lobe, tegula, most of legs and of sterna, dark reddish brown. Wing veins dark brown; membrane lightly brown infumated, except for dark brown infumation on anterior half of marginal cell and wing apex along anterior margin. *Pilosity:* Most of head with dense cover of relatively long, white plumose hairs (figs. A1, A2, A4); midportion of frons and hypostomal area with abundant brown plumose hairs intermingled; strip in front of ocelli with bluish metallic hairs; frontal and dorsal surfaces of scape covered with brown short, decumbent pubescence; lower margin of mandible with long, simple brown setae; apex of labrum with a pair of tufts of long dark brown simple setae (fig. A4). Dorsal portion of pronotum mostly with white plumose hairs; disc of pronotal lobe covered by brown hairs (fig. A6) and a few bluish metallic hairs. Remainder of thorax, including legs, mostly with dark brown to black hairs (figs. A1–A2). Posterior two-thirds of mesoscutum, dorsal surface of axilla, most of scutellum, narrow band along outer surface of mid tibia and most of outer surface of hind tibia and basitarsus with bluish metallic decumbent hairs. Anterior and lateral margins of mesoscutum, as well as two sublateral spots on posterior margin of pilose band on anterior one-third of mesoscutum, with white hairs (figs. A1, A5, A6); scattered white hairs along mesoscutum-scutellum suture and abundant white pilosity on posterior margin of scutellum (fig. A5). Lateral portion of mesepisternum with one transverse





FIGURES A7–A11. A7–A9. *Mesoplia sapphirina* sp. nov., male paratype (Panama). **A7.** Mesosoma, dorsal posterior view. **A8.** Apex of metasoma, dorsal view. **A9.** Hind leg, view of inner surface. A10–A11. *Mesoplia regalis*, female specimen (Trinidad). **A10.** Mesosoma, dorsal posterior view. **A11.** Upper portion of mesosoma, lateral view.

and three longitudinal thin stripes of white hairs (fig. A6). Large band along outer surface of foretibia and small patches of white hairs on basal one-third of midfemur, apex of midtibia, apex of hind femur and of hind tibia. Dorsal surface of terga covered mostly with bluish metallic scaly hairs. Anterior margin of dorsal surface of T1 also with a few scattered simple erect setae, most of them dark brown; lateral portion of T1 with a narrow dorsal stripe of erect plumose pubescence, composed mainly of dark brown hairs with a few white hairs intermingled; remainder of

FIGURES A1–A6. *Mesoplia sapphirina* sp. nov., female holotype. **A1.** Habitus, dorsal view. **A2.** Habitus, lateral view. **A3.** Apex of metasoma, dorsal view. **A4.** Head, frontal view. **A5.** Mesosoma, dorsal posterior view. **A6.** Upper portion of mesosoma, lateral view.

lateral surface of T1 with dense dark brown decumbent pubescence. Lateral portions of T2–T5 with mostly decumbent pubescence, composed of a white band dorsally and a brown band ventrally, the length and breadth of the bands varying among the terga (fig. A2). Erect simple setae on T2–T5 mostly white (fig. A3), except for lateral portion of T2 entirely with brown setae and a few brown setae laterally on T3. Lateral portion of T6 with simple dark brown setae; pygidial plate covered with decumbent bluish metallic scaly hairs, except for bare apex (fig. A3). Sterna covered mostly with decumbent dark brown pubescence; erect simple setae mostly brown, except for a few white setae laterally; lateral posterior margins of S2–S5 with white decumbent pubescence. *Structure*: First flagellomere shorter than second (fig. A4). Vein 3rs-m angled; width of submarginal cell 3, along Rs, slightly more than two-thirds length of submarginal cell 2. Midbasitarsus with row of teeth on posterior margin; midtibial spur relatively broad, both apical branches with robust teeth, outer branch with two small teeth. Mammilliform protuberances of scutellum relatively weak, their surface only weakly convex (figs. A5–A6), protuberances delimited posteriorly by continuous carina, trough between protuberances relatively shallow. Pygidial plate well developed, broad, apex broadly rounded (fig. A3).

Male paratype: Approximate body length, 18.9 mm; maximum head width, 5.8 mm; length of forewing, 15.5 mm. Similar to female in integumental color, pilosity, and structure. Base of mandible yellowish brown. Clypeus, labrum, gena, frons, and parocular area with yellowish white pilosity; erect simple setae on basal portion of dorsal surface of T1 mostly white; lateral portion of T1 with a strip of white plumose hairs, white plumosity on lateral portion of T2–T6 forming oblique rectangular strips; lateral posterior margins of S2–S4 with white decumbent pubescence, apical fimbria of S4 and S5 dark brown. Mammilliform protuberances of scutellum less developed, posterior carina well developed, conspicuous (fig. A7). Hind tibial spurs relatively short, apex of tibia with conspicuous tuft of dense erect setae (fig. A9). Dorsal surface of T7 intumesced, its ventral projecting portion conspicuously excavated; pair of apical projections of T7 with rounded apices, emargination between projections relatively deep (fig. A8).

Type Material: Holotype female (DZUP). **PANAMA**. "Old Panama, Panama, XII-12-45, C.D. Michener," "*Mesoplia regalis* (Sm.), Det. C.D. Michener, '51." **Paratypes**: **COSTA RICA.** 1 female (AMNH), "Culebra Bay, CR. I-26-38," "Zaca Exped., Acc. 37483"; 1 female (LACM), "Playa Grande & vicin., Guanacaste Prov., G. W. Franckie Coll., 27 February 1982," "G. W. Frankie Collector," "LACM ENT 235220"; 1 female (LACM), same data except "LACM ENT 237763"; 1 female (LACM), "Tamarindo Beach, Guanacaste Prov., Costa Rica IV-2 1984, G. W. Frankie coll.," "LACM ENT 237599"; 1 male (LACM), "Costa Rica, PU Puntarenas, III 1 76, R M Bohart," "LACM ENT 240120"; 1 male (INHS), "INHS Insect Collection 314,814," "COSTA RICA, Parque Manuel Antonio, Quepo, sea level, 8-III-1986, M. E. Irwin, Coastal dunes." **EL SALVADOR.** 1 female (INHS), "INHS Insect Collection 314,816," "EL SALVADOR: La Libertad, Majagual 10 October 1976, ME Irwin, JR Quezada, beach vegetation on sand *Ipomea* [sic]," "INTSOY." **MEXICO. Jalisco.** 1 female (AMNH), "MEXICO, Jalisco: Playa Teopa, 8 km. S. Careyes, Oct. 4, 1985, J. G. Rozen"; 1 female (LACM), "MEXICO, Jalisco: Chamela, 9.10 1981, S. Bullock, coll., SB #736," "LACM ENT 235744"; 1 female (LACM), "MEX., Jal.: Chamela, Est. Biologia UNAM, 1071 13.9.1982, coll. S. H. Bullock," "LACM ENT 235995"; 1 female (SEMK),

"MEXICO: Jalisco, Playa Careyes (near Chamela) 30 Sept 1985, Charles D. Michener"; 1 female (SEMK), "MEXICO, Jalisco: Chamela, 19.10 1985, S. H. Bullock 1949," "Mesoplia regalis [plus female symbol], det. Ayala '87"; 1 female (SEMK), "MEXICO, Jalisco, Chamela, Fecha 27-IX-1985, Col. R. Ayala RA220," "Mesoplia regalis [plus female symbol], det. Ayala '87"; 1 female (UNAM), "MEXICO, Jalisco, Chamela, Fecha 27-IX-1985, Col. R. Ayala RA220"; 1 female (UNAM), same data except "Mesoplia grupo bifrons, R. Ayala det."; 1 female (UNAM), "MEXICO, Jalisco, Chamela, Playa Careyitos, Fecha 27-X-1985, Col. R. Ayala RA218"; 2 females (UNAM), "MEXICO, Jalisco, Playa Careyitos, 6 km S. Chamela, 27 Sept., 1985, (R. B. Roberts)"; 1 female (UNAM), "MEX, Jalisco, Est. Biol. Chamela, La Huerta. 18 XII 89, Rodriguez G."; 1 male (UNAM), "MEX., Jal.: Chamela, Est. Biologia UNAM, 1435 20.2.1983, coll. S. H. Bullock," "Mesoplia regalis (F. Sm.) [plus male symbol], det. Snelling '83," "Mesoplia group bifrons"; 1 female (UNAM), "MEXICO: Jalisco, Careyes, 18-IX-1995, Col. R. Ayala." 1 female (INHS), "INHS Insect Collection 314,809," "MEXICO, Jalisco, Biol. Sta. nr Chamela, 27-IX-1985, W.E. LaBerge, on Acacia sp."; 1 female (INHS), same data except "INHS Insect Collection 314,810"; 1 female (INHS), "INHS Insect Collection 314,812," "MEXICO, Jalisco, Playa de Careyes, nr. Chamela, 27-IX-1985, W.E. LaBerge, Canabalia [sic] brasiliense [sic]"; 1 female (INHS), same data except "INHS Insect Collection 314,813." **Michoacán.** 1 female (LACM), "56 mi S Tecoman, Mich., MEX., 23 Dec. 1982, Coll. D. Cornejo," "LACM ENT 240118." **Nayarit.** 1 female (LACM), "San Blas, Nayarit, Mexico, VI-25-29-1956, W.A. McDonald," "U.C.L.A. COLL., Accessioned L.A.C.M. 1965," "LACM ENT 238951." **Oaxaca.** 1 male (AMNH), "Tehuantepec, Oaxaca, Mex., Dec. 13, 47–Jan.23, 48, T. MacDougal." **Sinaloa.** 1 female (SEMK), "MEXICO: Sinaloa, Rio Piaxtla, nr. SIN. Hwy. #04, III-18-1990, Gelhaus, Minckley & Calhoun #461"; 1 male (DZUP), "Presidio, Mexico. Forrer.," "Br. M. N. Hist., *Mesoplia* B, Det. J.S. Moure 1957." **Sonora.** 1 female (LACM), "MEXICO, Sonora: Rio Cuchuhaqui, 8 mi S Alamos, 1–13 Apr. 1975, coll. A. Brewster," "On flrs. of *Parkinsonia* sp.," "LACM ENT 240220." **Tamaulipas.** 1 female and 1 male (DZUP), "Tampico, Tamps. Mex., VI-10-51," "H. E. Evans Collector"; 4 females and 1 male (SEMK), same data; 1 female (SEMK), same data except "Mesoplia spp. bifrons group [plus female symbol], det. Snelling '82"; 1 female (SEMK), same data except "*Mesoplia* A, Det. J. S. Moure 19"; 1 female (LACM), "Playa Altamira, Tamaulipas, Mex, VI 3 1968" "M S Wasbauer, J E Slansky, Colrs," "LACM ENT 235604"; 1 female (LACM), "Cd. Madero, Tamps., MEXICO, July 1 1964, E. Fisher, D. Verity," "LACM ENT 235634"; 6 females (SEMK), "MEXICO: Tamps., La Pesca, 1-VII-1981, B. Miller, C. Porter, L. Stange, Dune Vegetation"; 1 male (SEMK), "Llera, Tamps. Mex., VII-19-54," "Univ. Kans. Mex. Expedition," "*Mesoplia* A, Det. J. S. Moure 19." **Veracruz.** 1 female (DZUP), "Tecolutla, V.C., Mex. VI-19-51," "H. E. Evans Collector," "*regalis* (Sm), Det. J. S. Moure 1957"; 1 female (SEMK), "Tecolutla, V.C., Mex., VI-19-51," "P. D. Hurd Collector"; 1 female (LACM), same data except "LACM ENT 237752"; 1 female (LACM), same data except "LACM ENT 235632"; 1 male (SEMK), "MEXICO Veracruz, 1.5 mi. N. Tecolutla, 12 June 1961 15 ft., U. Kans. Mex. Exped."; 1 female (DZUP). "Vera Cruz, V.C. Mex., VI-20-51," "H.E. Evans Collector," "*Mesoplia* A, Det. J. S. Moure 19"; 1 female (LACM), "MEXICO, Veracruz, 16 km. ne. Cardel, 2-IX-1975, E.M. Fisher, collr.," "LACM ENT 235218"; 1 male (LACM), "MEX: Ver., Mocambo, 2 mi. S. VI-29-

62," "D.H. Hanson Collector," "LACM ENT 240241"; 1 male (SEMK), "MEXICO: Veracruz, 8km SE. Bocal Del Rio, 21–22 July 1990, W. Bell, D. Conlon, and R. L. Minckley." **NICARAGUA.** 1 female (INHS), "INHS Insect Collection 314,817," "NICARAGUA, Montelimar, 50 km W Manágua, 2-X-1998, M. E. Irwin, coastal vegetation." **PANAMA**. 1 male (DZUP), "Mojinga Swamp, Ft Sherman CZ, 28-VI-1951," "FS Blanton Collector," "*Mesoplia* A, Det. J.S. Moure 19"; 1 female (AMNH), "Patilla Pt., Canal Zone, Jun 15 1929," "Collector C. H. Curran," "*Mesoplia regalis* (Smith), Det. H.F. Schwarz [plus female symbol], see Ckll., 1912, Annals and Mag. 9, 567"; 1 male (AMNH), "Bruja Pt., Canal Zone, Jun 26 1929," "Collector C. H. Curran," "*Mesoplia regalis* (Smith) [plus male symbol], Det. H.F. Schwarz, see Ckll., 1912, Annals & Mag., IX, p. 567"; 1 male (AMNH), "T. Halliman, Balboa, C.Z., Panama, March. 14–15," "*Mesoplia regalis* (Smith), det. H.F. Schwarz, see Ckll., 1912, Ann. & Mag., IX, p. 567." 1 male (LACM), "PANAMÁ Canal Zone, Fort Kobbe, 11 January 1960, (W. J. Hanson)," "LACM ENT 240212"; 1 male (SEMK), "Bruja Pt., Canal Zone, Jun 25, 1929," "Collector C. H. Curran," "*Mesoplia regalis* (Smith) [plus male symbol], Det. H.F. Schwarz, see Ckll., 1912, Annals & Mag., IX, p. 567"; 1 female and 2 males (SEMK), "PANAMÁ Canal Zone, Fort Kobbe, 11 January 1960, (W.J. Hanson)"; 1 male (SEMK), same data except "Mesoplia spp. bifrons group [plus male symbol], det. Snelling '82"; 1 male (SEMK), "Old Panama, Pan., IV-19-45, C. D. Michener," "*Mesoplia regalis* Sm., Det: C.D. Michener."

Distribution: This species occurs from central Panama and the western coast of Costa Rica, in the south, to the Mexican states of Sonora and Tamaulipas, in the north.

Etymology: From the Greek *sappheiros,* "sapphire," in reference to the bluish metallic coloration of the scaly hairs covering the metasomal terga.

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