The Bee *Svastra sabinensis*: Nesting Biology, Mature Oocyte, Postdefecating Larva, and Association with *Triepeolus penicilliferus* (Apidae: Apinae: Eucerini and Nomadinae: Epeolini)

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ABSTRACT

Information on the nesting biology of the large, ground-nesting, communal eucerine *Svastra* (*Epimelissodes*) *sabinensis sabinensis* (Cockerell) from Arizona is added to a previous account (Rozen, 1983). Details of nest size, location, depth, and structure are reported. Mature oocytes dissected from females are illustrated and described. Further information on its cocoon is presented and interpreted with respect to how it functions. The postdefecating larva is described and compared with that of *S. o. obliqua* (Say), the only other *Svastra* larva described to date. The association of this bee with *Triepeolus penicilliferus* (Brues) is further confirmed with the recovery of an immature larva of this cleptoparasite from one of the nest cells.

INTRODUCTION

While participating in a field trip on August 30 sponsored by Bee Course 2015, one of the students, Paige Muniz, discovered a number of large flying bees loudly buzzing as they circled around and entered a conspicuous hole in nearly level ground 4 miles east of Willcox, Cochise County, Arizona (figs. 1, 2). Shortly thereafter, she identified another similar open hole about a half meter away at the base of a low growing shrub where at least two more females of the same bee were emerging (fig. 3). A week later, Brice Lawley, volunteer at the Southwestern Research

FIGURES 1–7. Nesting site of *Svastra s. sabinensis* at 4 miles east of Willcox, Cochise Co., AZ. **1.** Habitat picture showing B. Lawley at the nest. 2. Nest entrance (arrow) above pen when first discovered. **3.** Students of Bee Course 2015 examining second nest entrance with first entrance identified by arrow. **4.** Females emerging from nest entrance (photo by P. Muniz). **5.** Partly exposed upper 15 cm of nest tunnel into which a slender straw had been inserted. **6.** The author excavating the nest on the third day. **7.** Inner surface of cell closure, showing spiral configuration.

Station, was assisting the author and discovered yet another nest entrance of the same species at the base of a bush several meters away from the original discovery. This locality is well known to many entomologists as a place of considerable biological diversity. The soil consists of very fine, consolidated sand deposited there after being blown from the Willcox Playa to the southwest. This soil supports and is stabilized by vegetation consisting of a variety of plants including *Prosopis*, *Psorothamnus*, *Euphorbia* (*Chamaesyce*), *Isocoma*, *Nama,* and *Verbasina.* Although the bees were recognized as a species of *Svastra*, their specific identity was determined only after specimens were compared with those in the collection at the American Museum of Natural History; it was recognized as *S.* (*Epimelissodes*) *sabinensis sabinensis* (Cockerell), a species whose nesting biology was briefly reported earlier (Rozen, 1983). The discovery of this new site now offers a more complete understanding of its nesting behavior and allows the descriptions of its mature larva, the mature oocyte, and a functional interpretation of its cocoon.

On the day of discovery at Willcox (August 30, 2015), numerous females were observed carrying pollen into the nest, and two female *Triepeolus penicilliferus* (Brues) were netted as they flew around the entrance. On the next visit a number of *S. sabinensis* females were observed emerging from the nest (fig. 4), and so on September 3 a plastic tumbler was inverted over the hole early in the day; later the same day 14 females of *S. s. sabinensis* were found captured in the tumbler when it was removed. Because no other females were encountered around the nest afterward, the captured females appeared to be the total nest population. They may have obtained their pollen from burro-weed (*Isocoma tenuisecta* Greene, Asteraceae, det. Marilyn D. Loveless), which grew abundantly at the site.

The nest entrance was open and lacked any indication of a tumulus. The open tunnel descending down from it was about 8 mm in diameter and completely unlined with any applied coating (fig. 5). It descended vertically for 30 cm, its lower part gently curving. Below that level, the tunnel began to divide dichotomously, in each case with both branches curving and continuing to meander obliquely downward in some cases as far as 70 cm in depth and 70 cm horizontally from the nest entrance (fig. 8). Although only one side of the nest was excavated, some branches were seen to start to descend in the opposite direction, suggesting that the nest might have had a horizontal spread of at least 140 cm.

No recently provisioned cells were encountered during the first two days of excavation (September 3 and 7). Two cells close together, each containing a postdefecating larva, were encountered on September 7, permitting subsequent examination of cocoon structure and function (see Cocoon Description, below) and larval anatomy (see Postdefecating Larva Description, below). Although orientation of the cells could not be determined because the orientation of the clod of substrate in which they were recovered was uncertain, cocoon fragments from the soil elsewhere indicated the long axes of cells were vertical with front ends up, as also reported by Rozen (1983). These two larvae almost certainly belonged to the previous generation that had failed to develop further unlike other members of their generation. They were still in complete diapause and the cocoon surface was old and fragile, whereas adults flying about and provisioning were freshly emerged and without wing wear.
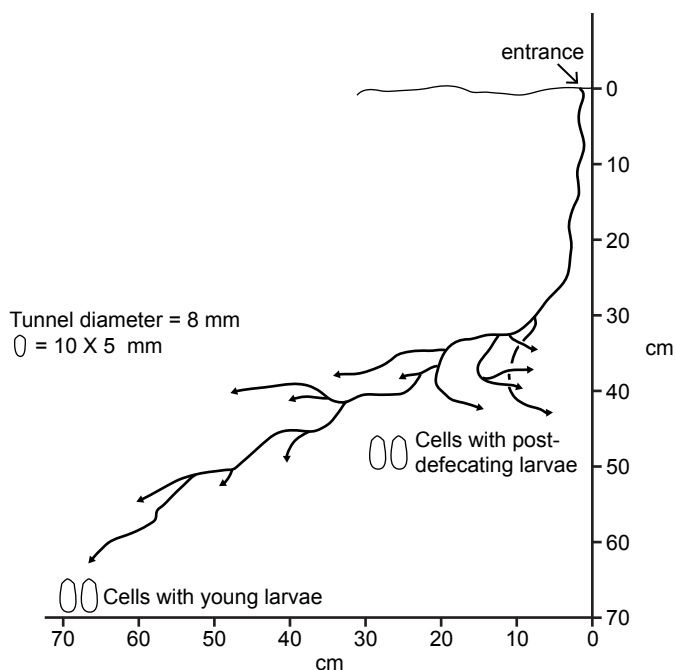
FIGURE 8. Schematic illustration of dissected part of nest showing gentle curvature of main tunnel above and proliferation of meandering burrow tunnels below as they repeatedly divided, and spread down- and sideward. Approximate position of new and older occupied cells indicated.

Although one cell from which a larva was recovered had been seriously damaged during excavation, the other cell was removed sufficiently intact to permit its description. It had an elongate oval shape 17.5 mm long and 8.5 mm in maximum diameter. The wall surface was remarkably smooth, and, although there was no visible lining, a water droplet placed on the surface beaded rather than being absorbed immediately. Thus, the surface had been rendered impervious to moisture. Some cell fragments from earlier generations displayed walls that were more consolidated than the surrounding soil, a further indication that the female had either mechanically consolidated (tamped) the soil or added some substance that did so. The entrance tunnel diameter at the closure was 7.0 mm. The closure plug itself (fig. 7) had a concave spiral inner surface consisting of about five coils, with an uncoated, rough texture. The entire closure plug was a soil cylinder about 10 mm long. Its outer end was smooth and evenly concave. The tunnel beyond was open.

Just prior to silk production the larva started defecating by placing feces at the closure end of the cell, given that all fecal material was found only immediately under the spiral closure surface and on the upper end of the cell wall. Because the fecal mass was impregnated with silk, production of silk commenced during defecation. Because lower cocoon walls contained no feces, it can be assumed that cocoon construction continues well beyond the end of defecation. The cocoon is described below under Cocoon Description. A strongly curled white larva in diapause with head partly hidden by the abdominal apex (fig. 15) was recovered from the bottom (posterior) end of each cocoon.

On the third (final) day of nest excavation (September 9) by which time the excavation had become large (fig. 6), two cells containing feeding larvae were encountered. They were found at depth of 70 cm and 70 cm measured horizontally from a perpendicular line descending from the nest entrance hole (fig. 8). One contained a feeding intermediate stage larva of *Triepeolus* (identified to genus by slender, apically elongate, sclerotized mandibles and a pair of erect, forward projecting labral tubercles). It almost certainly was *T. penicilliferus*, since in addition

to the two female specimens of this cleptoparasite collected at the time of nest discovery, two more females were collected near the nest on subsequent days. The occupant of the other cell was a third or fourth larval instar of *S. s. sabinensis*, recognized by its two curved, apically twisted teeth on each mandible. Both cells contained remains of moist, fresh provisions.

In overview, the nest appeared to be large in that the 14 females constructed tunnels that branched repeatedly, penetrating a considerable volume of ground. Since so few cells were encountered, we can probably assume that tunnels on just the one side of the nest extend farther than our excavation. The few other nests observed during this three-day excavation seemingly had fewer females, so that the excavated nest may be unusually large (i.e., well occupied). As suggested by the remoteness of cells, it is likely that each female, after entering the nest, seeks out its particular branch and alone attends to the construction and provisioning of its cells at the lower end. If this is true, then the only nest part used communally by the group is the entrance tunnel.

How each female when underground recognizes and finds its particular branch through the curving, meandering, and branching maze of the tunnel system will require further investigation. We can assume the presence of so many *Svastra* females would be a deterrent for adult cleptoparasites in light of observed receptions of cleptoparasites by other adult hosts. However, one cleptoparasite, *Triepeolus penicilliferus*, seems to have successfully overcome such intolerant encounters, but how? We have more to learn!

One approach in dealing with these challenges might involve selecting a study nest occupied by fewer cohabiting host females. Whatever size nest is selected, adequate nest-digging time should be allocated to explore the entire underground distribution of the nest tunnels. Although three working days were spent exploring the current nest, at most only one half of it was revealed and that included only a single series of current cells; considering the number of pollen-laden females, there must have been others extending farther out.

Other questions arise as a result of the current investigations: The nest was being used by two generations as evidenced by uncovering mature diapausing larvae in cocoons from the previous year and observing simultaneously pollen-carrying fresh females returning to their cells in the same nest. There was considerable evidence of pieces of old nest cells among the massive amount of debris removed during the current study. To what extent does a single nest persist through the years, and/or to what extent does the female progeny of one nest establish new nests rather than return to their natal nest?

In the final section of this paper (see Discussion), this study is compared with the early account of the biology of this species (Rozen, 1983) and with early biological investigations on other species of *Svastra* (Rau, 1922; Custer 1928, 1929; Rozen, 1964[2]).

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[2] In this paper, the egg of *Svastra o. obliqua* is depicted as it is undergoing eclosion (fig. 5). The interpretation presented was that at hatching, the shiny embryonic cuticle is first exposed on each side of the egg chorion along the spiracular line of the first. As the embryonic cuticle is sluffed off, it takes the remnants of the cuticle with it. There follows a total of four larval instars. However, a more recent interpretation documented in Rozen et al. (2011) with *Centris flavofasciata* Friese (Apinae: Centridini) is that the so-called embryonic cuticle is actually the cuticle of the first instar, and there is, therefore, a total of five larval instars, which likely will be found true for all bees. It follows that what is described as "first instar" of *S. o. obliqua* in Rozen (1964) is actually the second instar by this revised interpretation.
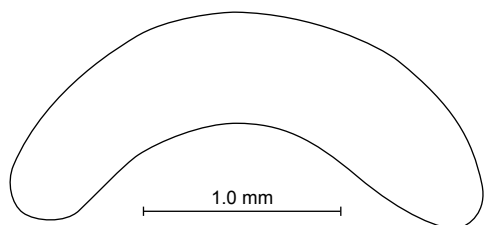
FIGURE 9. Diagram of mature oocyte, lateral view, showing curvature, rounded ends (anterior end to left).

MATURE OOCYTE DESCRIPTION

Figures 9–11

Although no freshly deposited eggs were recovered from the nest, examination of the mature oocytes dissected from ovaries of females preserved in Kahle's solution is informative. Three females had an ovarian formula of 4:4, as expected for most nonparasitic, solitary Apidae. The largest mature oocyte dissected from each of three pollen-carrying females was strongly curved with both front and rear ends rounded (fig. 9). Although somewhat misshapen after being preserved in situ in the females' body for about a month, each oocyte had a length of 3.0, 2.6, and 2.7 mm respectively and a maximum width of 0.65 mm toward the rear in all cases. The front end maximum widths were slightly less in all three. The chorion of each oocyte examined was poorly developed and thin, so that its sculpturing could not be determined. The micropyle on one (figs. 10, 11) was partly formed and seemed to be on a slight protuberance exhibiting a developing cluster of pores (fig.11) on the front end. On another oocyte a single hole at the front end was interpreted as the start of micropylar development.

COCOON DESCRIPTION

Figures 12–14

Cocoons containing fecal material at the upper end completely filled their cells, i.e., their shape is the shape of the cell lumen. The upper end of the cocoon is opaque viewed from the outside due to the incorporated fecal material. The lower end, however, is transparent dark brown, although this is hard to see without light being transmitted through. The cocoon wall consists of several layers of transparent smooth silk, which is highly reflective when viewed from the inside. However, the top of the cocoon on the inside is a nearly flat, thick circular disc of fine silk fibers, in one case with a diameter of 8.2 mm, which is opaque but reflects a soft sheen. Several thin, loosely attached sheet of transparent brown silk are found above the disc. They enclosed air spaces between the inner and outer surfaces of the cocoon top, as was diagrammed for the related *Svastra o. obliqua* (Say)[3] by Rozen (1964: fig. 2).

SEM examination of the cocoon confirmed the shiny cocoon wall is a sheet of silk. Even though it has a coating of fibers, it is without openings, an indication that it is airtight. The nearly flat circular disc of the top of the inside is indeed a thick mat of fine fibers, through which air can flow. SEM examination of the brown sheet silk above the disc was inconclusive

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[3] The surface of the inner layer of the cocoon top of *Svastra o. obliqua* is depicted as somewhat domelike in Rozen (1964: fig. 2, termed "roof" therein), rather than as a nearly flat disc as in the case of *S. s. sabinensis*. This distortion in the early study may have been caused by body pressure from the larva or pupa within the cocoon lumen below.
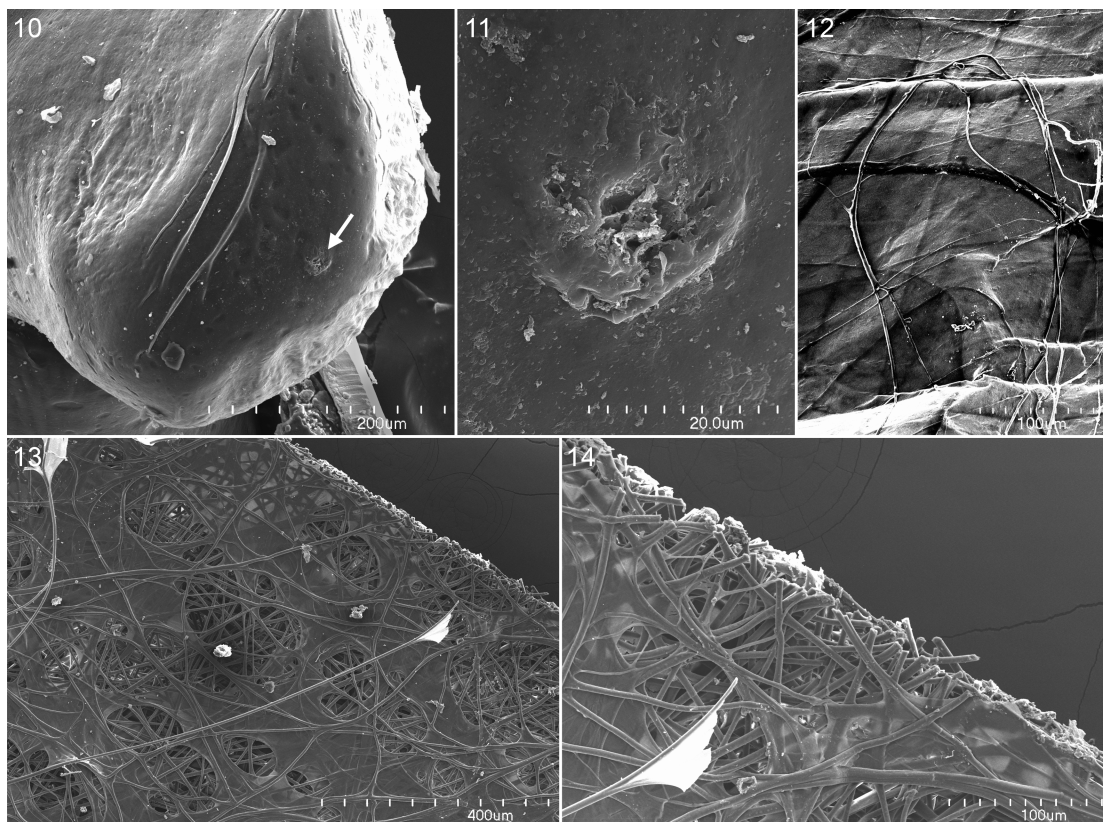
FIGURES 10–14. **10.** SEM image of front end of oocyte of *Svastra s. sabinensis* showing position of micropyle (arrow). **11.** Same, close-up of developing micropyle. 12–14. SEM images of cocoon fabric. **12.** Cocoon wall, showing lack of fenestration in fabric. **13.** Cocoon disc, inner view, showing ample passageways through dense fibers. **14.** Same, close-up of cut edge.

as to whether air exchange was in spaces around these sheets through the fecal layer above or through spaces along the upper sides of the cocoon.

POSTDEFECATING LARVA DESCRIPTION

Figures 15–21

Although alive, the two tightly curled postdefecating larvae retrieved were flaccid and badly misshapen, presumably because of loss of fat tissue and water, and therefore were difficult to illustrate. The distortion of body mass is further evidence that the specimens represented the previous generation.

The descriptive anatomy of the mandible of a eucerine bee larva used here follows Rozen (1965, 1991) and Michelette et al. (2000).

DIAGNOSIS: The strong dorsolateral swellings of most caudal annulets on both sides of the larva give it a strong robust appearance. These swellings, however, are not pronounced when

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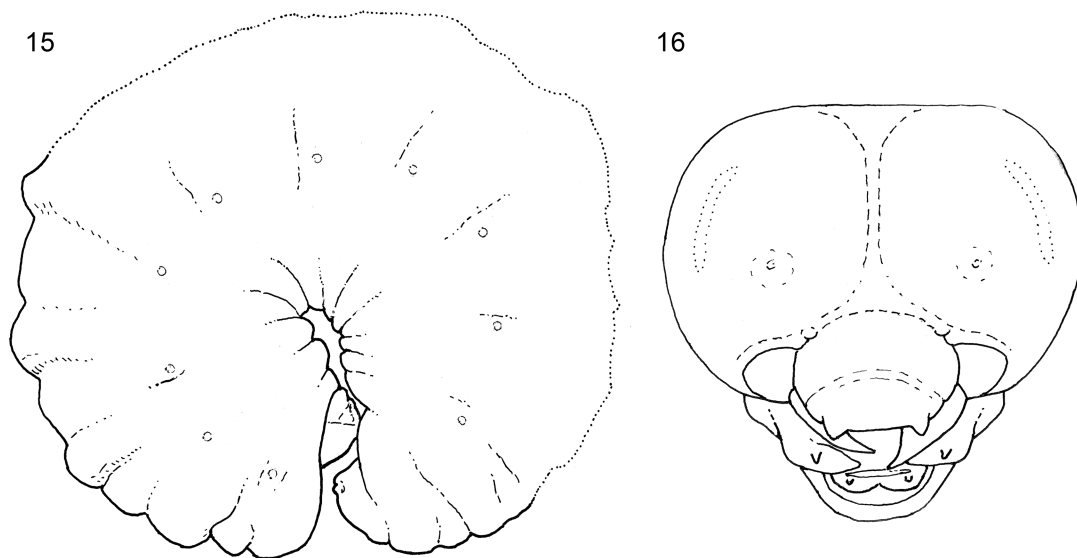
FIGURES 15, 16. Diagrams of postdefecating larva of *Svastra s. sabinensis*. **15.** Entire larva in diapausing posture, lateral view. **16.** Head, frontal view.

the larva is viewed in lateral profile (fig. 15). Although the larva of *Svastra s. sabinensis* described here appears to be somewhat more sclerotized than specimens of *S. o. obliqua* preserved from collections described by Rozen (1964), no other differences could be detected.

DESCRIPTION: **Head** (fig. 16): Integument with a few scattered fine setae. Except for darkly pigmented mandibular apex, natural pigmentation at most faint. Fine, dense spiculation restricted to apex of labrum and epipharyngeal surface. Coronal ridge well developed, extending from postoccipital ridge to epistomal ridge; postoccipital ridge well developed, extending nearly directly across cranium as seen from above, scarcely curving forward at median line; hypostomal ridge well developed; dorsal ramus not developed: epistomal ridge present laterad of (below) anterior tentorial pits and between pits, its ventral edge between pits well defined, its dorsal edge grading into more heavily sclerotized frontal area; tentorium moderately robust including dorsal arms. Parietal bands evident but not pronounced. Antennal prominence weakly developed and cranium above prominence evenly curved in lateral profile; antennal papilla small, shorter than basal diameter, and bearing about three sensilla. Clypeus, labrum, and labial apex broad in frontal view (fig. 16). Labral apex bearing pair of tubercles widely separated along lower edge (fig. 16).

Mandible (figs. 17–19) robust in dorsal and ventral views; mandibular apex becoming slender in inner view with extreme apex with two flattened, apically pointed and twisted teeth, dorsal one of which is distinctly longer. Apical concavity directed ventrally because dorsal edge of concavity directed much farther adorally than ventral edge; dorsal inner edge of concavity closely paralleled by inner ridge (fig. 18, ridge); narrow surface between this edge and inner edge, termed dorsal plane, denticulate; these denticles[4] (fig 19, denticles) becoming long, seta-

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[4] Although elongate and curved, the denticles are not setae as seen in close-up view for they do not rise from alveoli.
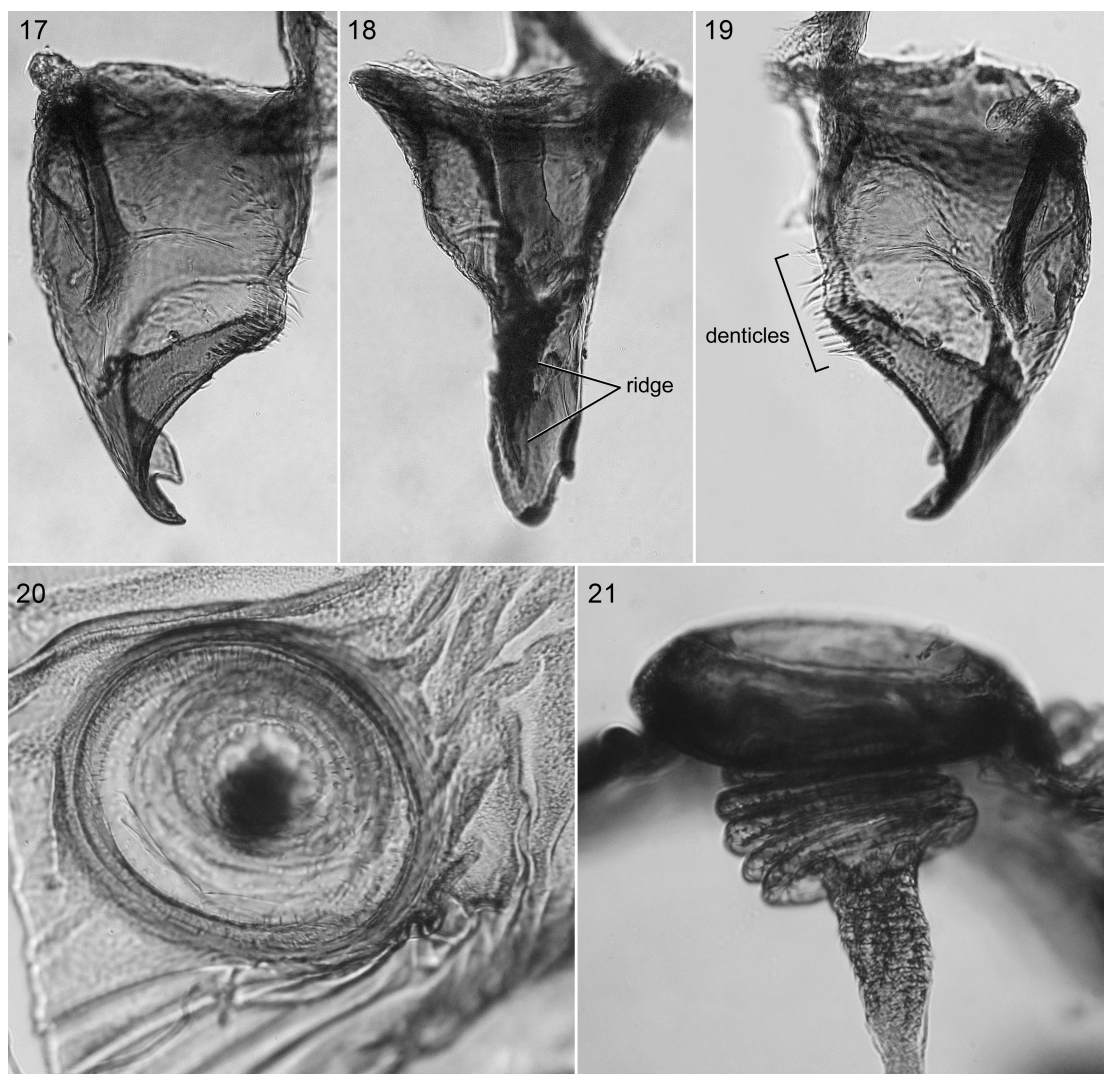
FIGURES 17–21. Macrophotographs of right mandible (with setae on outer edge accidentally removed), in **17.** dorsal, **18.** inner, **19.** ventral views, respectively, **20, 21.** Macrophotographs of spiracle of cleared specimen, showing fine spicules, pigmentation, and shallow atrium, in **20.** outer and **21.** side views, respectively.

like in vicinity of the‑cusp where they form distinct brush and where inner ridge becomes lamelliform; mandible apically bidentate with dorsal tooth longer than ventral tooth; outer surface of mandible with three conspicuous setae arising near base (accidentally destroyed during dissection). Cardo and stipital rod sclerotized but not extensively pigmented; articulating arm of stipes evident; maxilla narrowing to moderately pointed apex directed mesad beyond insertion of maxillary palpus, so the palpus is subapical in position; galea distinct mound, bearing sensilla; maxillary palpus cone shaped, length about twice basal diameter. Labium clearly divided into prementum and postmentum, wide (fig. 16); premental sclerite weakly sclerotized, labial palpus moderately slender, length about three times basal diameter,

shorter than maxillary palpus. Salivary lips projecting, widely transverse because of breadth of prelabium, width about equal to distance between bases of widely separated labial palpi. Hypopharynx with flat surface.

Body (figs.15, 20, 21): Body entirely lacking vestiture of setae and spicules (though with nonsetose sensilla on abdominal segment 10); body surface of postdefecating form strongly wrinkled. Body form of postdefecating larva robust (fig. 15); caudal annulets of thoracic segments and of abdominal segments 1 and 2 with dorsolateral swellings on each side of midline; these swellings on subsequent abdominal segments not developed. Abdominal segment 10 attached to approximate middle of segment 9; anus presumably positioned toward top of segment 10.[5] Spiracles (figs. 20, 21) well sclerotized, large, distinctly pigmented, subequal in diameter; atrium extremely shallow, with diameter more than twice depth, not projecting much beyond body wall, presumably with rim expressed; subatrium short, consisting of about four chambers; both atrium and subatrium very finely spiculate. Sex-specific characters unknown.

Material studied: Two postdefecating larvae: **USA:** AZ: Cochise Co.: 4 mi E. of Willcox, 7 Sept. 2015 (J.G. Rozen, B. Lawley).

DISCUSSION

The only previous account of the biology of *Svastra s. sabinensis* (Rozen, 1983) described and pictured a similar nest from near Tucson, AZ, which was also occupied by more than one female. The one significant difference from the current nest was the occurrence of pebbles (see figs. 2, 3, therein) clustered in the main shaft and side tunnels, then a puzzling observation, which can now be explained. Oddly the explanation is derived at least in part from a recent study of a wood nesting bee, *Lithurgus chrysurus* Fonscolombe (Rozen, 2013), in which it was suggested that blind tunnels, chambers, and antechambers found in many nests may often be a source of materials to block tunnels leading to recently closed cells, securing them from parasites and predators. This suggests that the pebbles in figure 3 from the 1983 study were cumbersome residue left behind by the female when she quarried soil to fill the tunnel to her recently constructed, provisioned, and closed cell, after egg deposition. Figure 2 therein demonstrates the heavy load of pebbles in the soil at the site near Tucson. In contrast, fine soil at the current site lacked pebbles, as did nest tunnels.

The only other investigations on the biology and immatures of the genus *Svastra* are those of Custer (1928, 1929) and Rozen (1964) of *S. o. obliqua*. Custer (1928), who assigned the species to *Melissodes,* recognized that many nests were occupied by more than one female, identified *Triepeolus concavus* Cresson as its possible cleptoparasite, and presented diagrams of a nest (showing antechamber) and a close-up of the cell containing provisions and a small larva.

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[5] Because of the close overall agreement between the mature larvae of *Svastra s. sabinensis* and *S. o. obliqua,* the predefecating larva can be relied upon to interpret certain features of larval anatomy of *S. s. sabinensis.* Postdefecating larvae of both species recovered strongly curled so that heads deformed the abdominal apices. As demonstrated for *S. o. obliqua* (Rozen, 1964: fig. 7), abdominal segment 10 has the anus positioned on a terminal projection toward the top of abdominal segment 10. Thus, the prediction for *S. s. sabinensis.*

Interestingly, in one case he found a nest entrance that was being used simultaneously by a smaller species of "*Melissodes.*"

In his subsequent paper, Custer (1929) concluded that the *Triepeolus* was "carnivorous." Although 29 of the total 30 cleptoparasites died before maturing, all were in cocoons identical to those spun by *S. o. obliqua.* He concluded, therefore, that the *Triepeolus* larva feeds on the cocoon-covered host larva. We now know that no larva of any Epeolini has been found to feed on the mature host larva. His statement that "the parasitic larvae possess two rows of dorsal tubercles which are more highly developed than in the case of the host" does not correspond to current descriptions of *Triepeolus* larvae (Michener, 1953; Rozen, 1966). None possess paired dorsal tubercles, and all are cleptoparasites whose larvae feed on the provisions stored by the adult host, the egg or young larva of which is killed by the first larval instar of the cleptoparasite. First instars of *Triepeolus* have hospicidal anatomies (slender body, heavily sclerotized and pigmented head capsules, extremely elongate mandibles, elongate and forward-projecting labral tubercles; Rozen, 1989).The source of Custer's misunderstanding is not understood.

Rozen's (1964) account of the larva and nesting biology of *Svastra o. obliqua* demonstrates a close agreement with the feature described above for *S. s. sabinensis.* The only difference detected between the two was that the nest of *S. o. obliqua* as measured by cell depth was 10–25 cm, contrasting with 70 cm (current study) and 80+ cm (Rozen, 1983) for *S. s. sabinensis.*

It is interesting to note that the circular shape of the postdefecating larva (with head embedded in abdominal segment 10) that seems characteristic of both *Svastra sabinensis* and *S. obliqua* is not unique to them. Postdefecating larvae of the eucerines *Xenoglossa angustior* Cockerell (Rozen, 1965: fig. 1) and *Canephorula apiformis* (Friese) (Michelette et al., 2000: fig. 22) are also circular, a posture probably dictated by a long diapause at the bottom of a vertical cocoon.

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