

American Museum Novitates

PUBLISHED BY THE AMERICAN MUSEUM OF NATURAL HISTORY
CENTRAL PARK WEST AT 79TH STREET, NEW YORK 24, N.Y.

NUMBER 2170

MARCH 23, 1964

The Biology of *Svastra obliqua obliqua* (Say), with a Taxonomic Description of its Larvae (Apoidea, Anthophoridae)

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During the past 10 years a considerable amount of information regarding the biology and the larvae of the non-parasitic members of the Anthophoridae has been published. Many of the papers have been especially concerned with the interrelationships of the various subfamilies and the relationship of the parasitic anthophorids with the non-parasitic ones. It is obvious, however, that we must still learn much more about the biology and larvae of the members of the family before more than tentative conclusions can be drawn. The present paper treats the biology and first- and last-stage larvae of *Svastra* (*Epimelissodes*) *obliqua obliqua* (Say) (Eucerinae) with the hope that these data will eventually prove valuable in elucidating the phylogeny of the family.

One of the most widely distributed and abundant species of the genus, *Svastra obliqua*, ranges through the United States and parts of Mexico and Canada and is divisible into three subspecies. All available biological information refers to the nominate form. Custer (1928, 1929) has provided considerable information on the nesting habits and cocoon construction of this species, and LaBerge (1956), after reviewing Custer's 1928 paper, has discussed flower preference. Nothing is known about the biology of any other member of *Svastra*.

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The larvae, adults, cocoons, and cells involved in this study are deposited in the collection of the American Museum of Natural History.

I wish to thank Dr. William Robertson, Jr., biologist, Everglades National Park, and the other officials of the Park for permitting me to carry on the field observations there. The research was continued and partly written at the Archbold Biological Station, Florida.

BIOLOGY OF *SVASTRA OBLIQUA OBLIQUA* (SAY)

DESCRIPTION OF AREA AND OF NESTING SITE: I observed these bees nesting at Flamingo, Everglades National Park, Florida, during the afternoon of April 15, 1963, and the following morning. The nest areas occupied several continuous salt flats on the coastal prairie. The flats were barren, horizontal, unshaded patches occasionally dotted with bushes of *Dondia linearis* (Elliott) Millspaugh.¹ Irregular in shape, the largest flat was perhaps 50 yards long, and all were bordered with dense but low-growing, salt-resistant plants such as *Dondia linearis* and the pollen plant *Borrichia frutescens* (Linnaeus) DeCandolle.¹ The latter is a yellow-flowered composite locally termed blue weed. During rainy periods several inches of fresh water inundate the salt flats, and during storms salt water from Florida Bay only several hundred yards away probably covers them. The ground, permanently salty to the taste, consists of finely stratified, clay-like, and sandy marl devoid of stones and pebbles.

ADULT ACTIVITY: When the observations were made, I found only females about the nesting sites and on the flowers, so that no original observations were made concerning mating behavior. However, several males now in the collection of the American Museum of Natural History were collected at Flamingo, April 16, 40 years earlier. Custer (1928), in discussing the mating behavior, stated that "the males of the colony were darting back and forth" over the nesting site early in August at Boulder, Colorado.

I first saw females flying at 7.45 A.M., E.S.T., on a cool, clear morning, although they were not carrying pollen back to the nests until 8.15 A.M. Some were still active in the evening at 5.00 P.M.

NESTING ACTIVITY AND DESCRIPTION OF NESTS: Like the females of *Melissodes composita* Tucker (Hurd and Linsley, 1959), those of *Svastra obliqua obliqua* use a common nest entrance, a fact first noted by Custer in 1928. I collected nine females from one burrow opening, and several more

¹ Kindly identified by Dr. Leonard J. Brass, Archbold Biological Station, Lake Placid, Florida.

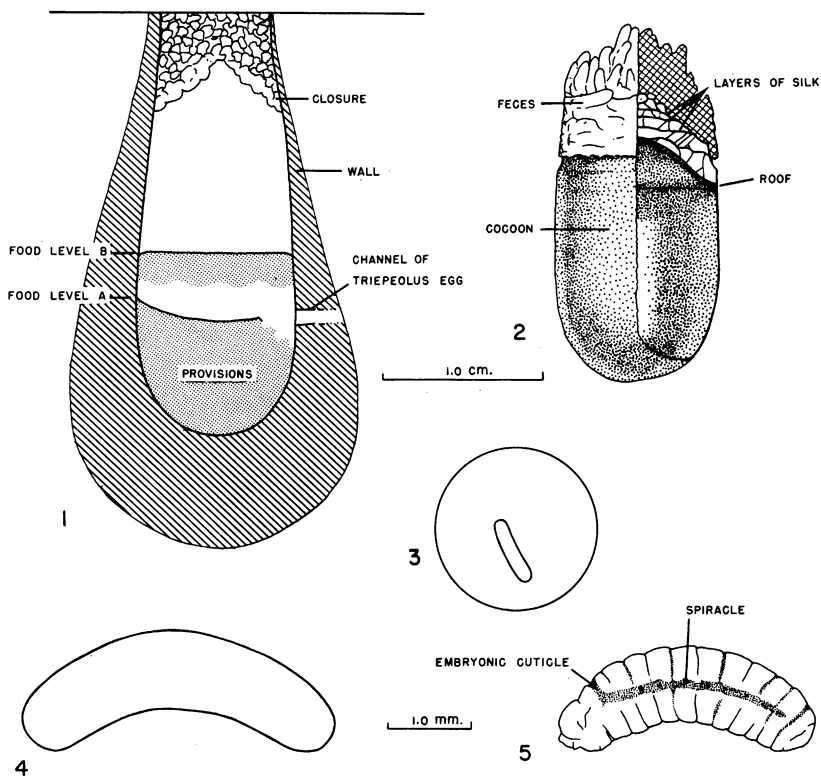
were still in the nest when the observations were abandoned. Further, because of the short duration of the observations, this count may represent only a fraction of the number that actually occupied the nest. In connection with the subject of communal nesting, Custer (*ibid.*) reported that a *Melissodes* (or perhaps another species of *Svastra*) half as large as *S. obliqua* used a nest currently occupied by eight females of *S. obliqua*. Two individuals of the smaller species "made their escape from a narrow tunnel which branched off from the wider tunnel" as he excavated the nest. The only other similar case known to me is that of *Exomalopsis solani* (Cockerell) which nested in old or possibly active burrows of several species of bees (Linsley, MacSwain, and Smith, 1954).

The burrows were scattered through the salt flats and often occurred in aggregations of 25 to 35 irregularly spaced entrances, with some being separated by only an inch or two. Though many holes occurred in the completely barren areas, others were located near and under an occasional *Dondia linearis* plant.

As with *Melissodes composita* (Hurd and Linsley, 1959), the entrances were open (that is, not plugged with soil), only roughly circular, without turrets, and usually without tumuli. Their diameters varied from 6.5 to 9.0 mm., and at times the large females seemed to experience difficulty in squeezing through them. Not infrequently orange smudges of pollen marked their periphery where pollen-laden females had entered. Approximately one entrance in 20 had a low tumulus, spanning at most 5 cm. Presumably the tumuli quickly blew away from new nests, and the excavated material from established nests was deposited in completed tunnels. These bees apparently do not employ water in their excavations, as I found no pellets of excavated material in the tumuli.

The nest structure is similar to that illustrated by Custer (1928). The entrance burrow descends at various angles, but even when descending vertically at first, they soon turn so that most of the burrow system is nearly horizontal. In some instances an antechamber like that described by Custer was definitely present near the opening, though at the time of excavation I thought it might represent the entrance to a completed and filled side tunnel. With other nests, the antechamber seemed to be missing. The horizontal portions of the burrows extend for considerable distances and rise, fall, turn, and branch. One such burrow had a depth of 10 to 12 cm., and this seemed about average for other burrows encountered. In view of the fact that many females occupy a nest, a single nest may extend for considerable distances under the surface.

The main burrows are open and have a diameter of 10 mm., somewhat larger than the nest entrance. Their rather rough walls are not built-in,



FIGS. 1-5. *Svastra obliqua obliqua* (Say). 1. Diagrammatic representation of cell, showing level of newly supplied provisions (food level a), level after fermentation (food level b), and position of egg of *Triepeolus rufithorax* Graenicher. 2. Cocoon and feces, with right half partly cut away. 3. Egg on provisions, viewed from above. 4. Recently deposited egg, lateral view. 5. Egg at time of eclosion, lateral view. Figures 4 and 5 drawn with aid of camera lucida. Upper scale refers to figures 1-3; lower scale, to figures 4 and 5.

though spots of excavated marl adhere to them. Further, the walls are not lined with waterproof material as are those of the cells. The tunnels leading to the cells are similar, except that they may be somewhat narrower and are filled with loose soil after the cell is completed and provisioned. Near the cells they exhibit a built-in, smooth wall that reduces the passageway to a diameter of about 7.5 mm. This wall, a continuation of the cell wall, may be uneven in thickness.

As described by Custer (1928), the cells are arranged singly and are oriented essentially vertically, with the opening at the top. Shaped as

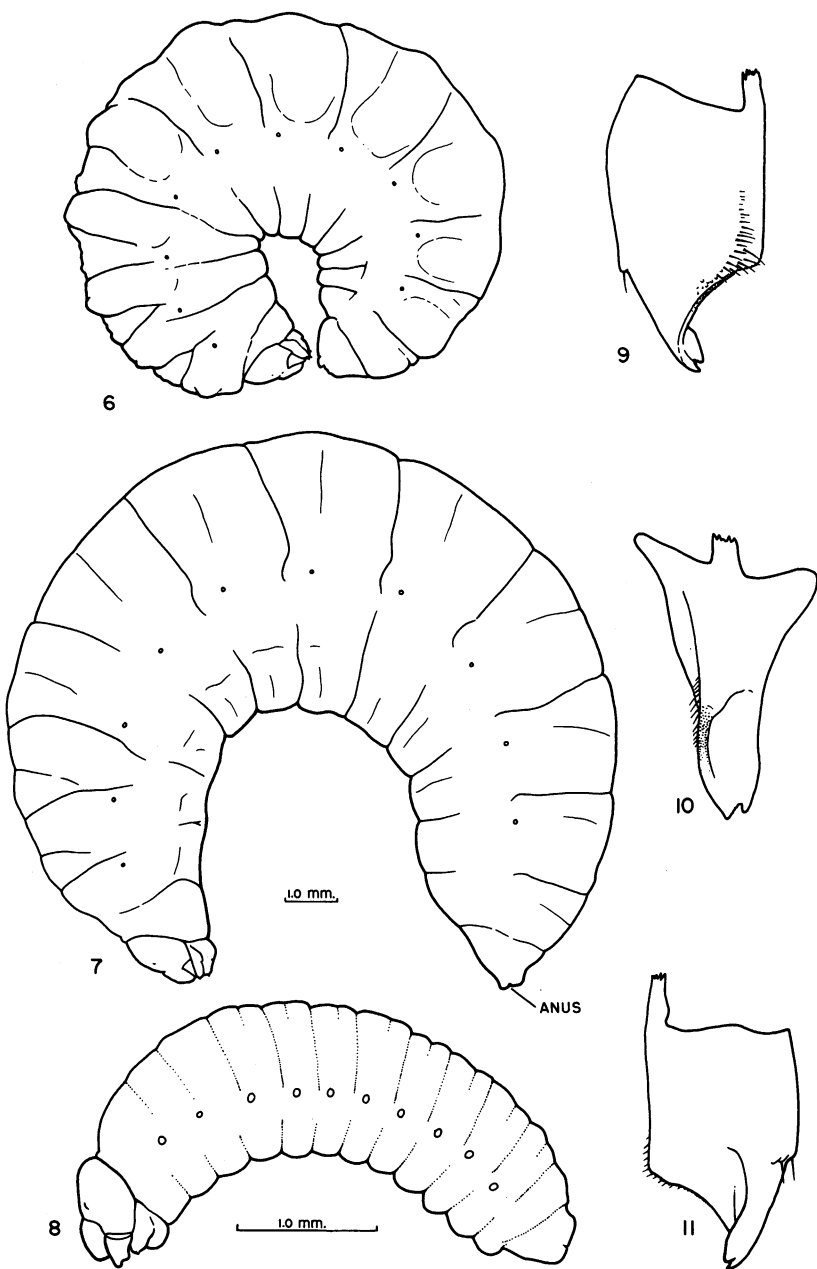
shown in figure 1, they have a maximum length of 20 mm. and a maximum diameter of 10 mm. During cell construction, the female excavates a larger chamber than the completed cell and then partly refills it on all sides. The resulting cell wall varies somewhat in thickness from cell to cell (fig. 1 represents one of the thicker walls). In contradiction to Custer, I found the walls much thicker toward the bottom of the cells. The construction material is harder than the surrounding soil, so that, after the larva spins the cocoon, the cocoon and attached wall often can be removed as a nodule. The female lines the extremely smooth inner surface of the wall with a thin, transparent, waterproof substance. More than 100 cells were excavated, all at a depth of from 10 to 25 cm.

The female transports the bright orange pollen unmoistened to the nest. She deposits the load in the bottom of the cell, apparently after moistening both the pollen and the cell floor with nectar. The surface of the partly supplied provisions is somewhat concave, as is the surface of the newly completed provisions. The latter are moist and mealy, though compact, and are without horizontal stratifications of moist and dry pollen. The female apparently does not float a distinct layer of nectar on the completed provisions as does that of *Xenoglossa fulva* Smith (Linsley, MacSwain, and Smith, 1955). Nor was there any indication of the "white cream-colored layer 2 mm. thick" on top of the provisions and egg as described by Custer (1928). This layer might actually have been a mold or yeast in the cell. The depth of the pollen-nectar mixture in a freshly completed cell in one case was 7 mm. (fig. 1, food level a).

DEVELOPMENT: The female deposits the cylindrical, curved egg near the middle of the cell on top of the provisions (fig. 3) and firmly attaches it at one end to the surface. Although the other end may also touch the surface, the middle arcs upward. In appearance the egg (fig. 4) is cream-colored, nearly opaque, and dull, with both ends identical and blunt. The dullness of the chorion is due to microscopic sculpturings. One egg measured 4.2 mm. in length and 0.95 mm. in maximum diameter (near the middle).

The female closes the cell with a rather fragile spiral plug (fig. 1). This plug is semiwaterproof in that it only slowly absorbs a droplet of water placed on its lower surface.

During the incubation of the egg, the pollen-nectar mixture apparently ferments, for the provisions in cells with larvae or eggs about to hatch are distinctly different from those described above. They are much more moist (almost a semiliquid) and are greater in volume (fig. 1, food level b), occupying at times as much as two-thirds of the cell. Further, they contain many gas bubbles, give off a distinctive though not unpleasant odor, and



FIGS. 6-11. *Soastra obliqua obliqua* (Say). 6. Live, postdefecating larva, lateral view. 7. Predefecating, mature larva, lateral view. 8. First instar, lateral view. 9-11. Right mandible of mature larva, dorsal, inner, ventral views. Upper scale refers to figures 6 and 7; lower scale, to figure 8.

are quite sweet to the taste. Linsley, MacSwain, and Smith (1956) report that the provisions of *Anthophora* but not those of known genera of other anthophorid subfamilies give off a fermenting odor.

Toward the end of the egg stage, the chorion adheres to the larviform embryo, which now exhibits pulsating movements of the head. These pulsations probably indicate ingestion of the amniotic fluid. A shiny stripe (fig. 5) appears laterally along the spiracular region on each side of the body, and then shiny lines develop along the intersegmental grooves. When a drop of water was placed on the anterior end of the egg, the dull patches of chorion floated away from the embryo. Thus it seems that the shiny areas are the embryonic cuticle and that the chorion is dissolved by some substance that first manifests itself just above the pleural region of the body and then works its way along the intersegmental grooves. With the first appearance of the shiny lateral stripe, the tracheae are filled with gas. Also at about this time, the embryo can ingest liquid from the outside, for after I placed a drop of red food coloring on the head region of an embryo, the dye appeared in the alimentary canal. However, these embryos and, later, the young larvae do not take in large quantities of liquid as do those of some Panurginae (Rozen, in manuscript), for the larva of *Svastra* several hours old will have a midintestine well packed with pollen and, furthermore, the larvae grow at a rate commensurate with the quantity of food taken in. In contrast, the newly emerged larvae of certain panurgines grow very rapidly, without consuming an appreciable quantity of food, the increase in size being caused by ingestion of liquid.

The transparent embryonic cuticle is quickly shed, apparently with the remnants of the partly dissolved chorion, and in one case was found in a single piece alongside the feeding larva. The mandibular lobes were quite evident on the cast skin, and the spiracles with associated tracheae could easily be discerned.

The first-stage larva is illustrated (fig. 8) and described taxonomically below. Young and intermediate-aged larvae lie on the surface of the provisions next to the cell wall, so that the full length of their curved body touches the wall. Like the known larvae of the Exomalopsinae and Emphorinae, they move while feeding, so that they form a channel with a width equal to the diameter of the body of the larva at the periphery of the provisions and thereby create a circular, elevated, central plateau. As the larva grows, the channel width increases, with the obvious result that the diameter of the plateau decreases. Toward the end of feeding, the nearly mature larva apparently reorients and consumes the provisions in a manner not understood as yet. The early-stage larvae are elongate,

though not so much so as those of emporhines such as *Diadasia*. Although they lack definite, posteriorly directed, dorsal elevations, the ventral surface of the ninth segment is nearly as large as the preceding segment, and the tenth segment is small and bears the anus dorsally (see taxonomic description of larva). Similar features are found in the Exomalopsinae and the Emphorinae.

Measurement of the head capsules of the larvae suggests that there are four larval instars after the embryonic cuticle is shed.

Cells uncovered after the larvae had consumed their food possess a distinct, even, brown coating on the walls. This lining becomes thinner above before it gradually disappears near the cell closure. Presumably it represents either the residue of the provisions (though it incorporates no pollen grains) or possibly some anal secretion. In any event, it is both darker than and lacks the texture of the salivary secretion that is applied later.

The rather active larva orients in the cells so that the anal segment reaches the closure and for the first time voids the feces. The elongate (1 to 2.5 mm. long, 0.6 mm. wide), orange, moist, fecal pellets consist of unruptured pollen grains and possess thin, tapering, transparent tails which are voided last. All the meconial mass is applied to the upper end of the cell near the closure. The larva then spins the cocoon (fig. 2). Although the cocoon has been thoroughly described by Custer (1929), certain clarifications are appropriate. He states that the wall of the cocoon is composed of three layers: a thin dullish brown one on the outside; a thick dull brown membrane; and a very thin, glistening, light amber-colored membrane sparsely supplied with interlacing fibrils. From my observations, I believe the first layer, which is light brown in color, is actually the cell lining supplied by the mother (the lining is sometimes left behind with the removal of the rest of the cocoon); the second is referable to the non-silken layer described above; and the innermost, nearly transparent layer with the fibrils is the only one composed of salivary silk. The three layers adhere closely to one another so that the wall of the complete cocoon appears as a single thickness of dark brown parchment closely applied to and with the same shape as the cell. Custer's description of the cocoon cap (fig. 2) is quite complete. When the adult bee emerges, it chews its way through the cap and associated fecal material, with the result that shredded particles of the cap and of the feces fill the vacated cocoon.

The predefecating and postdefecating mature larvae (figs. 6, 7) are described below; the latter is quiescent.

PARASITES: Although more than 100 cells of *Svastra* were excavated, few

parasites were encountered. A number of *Triepeolus rufithorax* Graenicher were collected at the nesting site and were observed flying from one burrow opening to another. One that descended into an opening for three minutes emerged with the tip of its abdomen clearly coated with pollen, which suggests that oviposition may have been in the cell wall beneath the surface of the provisions. A single dead egg of *Triepeolus* was discovered in a cell occupied by a postdefecating *Svastra* larva, and it projected at right angles into the wall 7 mm. from the bottom of the cell (fig. 1). Hence, it was presumably situated at about the same level as the surface of the newly provisioned pollen. With its anterior end flush with the cell lining, it occupied a channel 0.5 mm. in diameter. The cell contained no other *Triepeolus* eggs.

In addition to *Triepeolus*, two specimens of the mutillid *Timulla vagans rufinota* Mickel¹ were collected at the site, one having just emerged from a *Svastra* burrow.

TAXONOMIC DESCRIPTION OF MATURE LARVA OF *SVASTRA OBLIQUA OBLIQUA* (SAY)

Figures 6, 7, 9-13

As can be seen from the following description, the larva of this species is remarkably similar to that of *Melissodes* sp.? as described by Michener (1953).

HEAD (FIGS. 12, 13): Integument with a few scattered setae; apex of maxilla and apical margin and epipharyngeal surface of labrum with numerous small, hair-like spicules; area immediately mesiad of antenna, hypostomal ridge, and mandibular articulations somewhat pigmented; apices of mandibles darkly pigmented. Tentorium complete and moderately thick; posterior thickening of head capsule moderately well developed; hypostomal and pleurostomal thickening well developed; epistomal thickening and corresponding sulcus well developed laterad of anterior tentorial pits; mesiad of pits sulcus absent and thickening feebly defined; longitudinal thickening of head capsule pronounced but becoming weaker toward epistomal thickening with which it broadly joins; parietal bands very weak. Antennal prominences low; papilla about as high as basal diameter and bearing several sensilla. Labral tubercles low. Mandibles (figs. 9, 11), seen from above or below, broad basally, narrow apically; apex bidentate; cusp oblique; upper apical margin (fig. 10) a curved plane bearing numerous minute denticles; dorsal inner sur-

¹ Kindly identified by Mr. Karl V. Krombein, Insect Identification and Parasite Introduction Research Branch, United States Department of Agriculture.

face with numerous non-articulating, hair-like denticles probably corresponding to hair-like "teeth" on *Exomalopsis chionura* (Rozen, 1957). Maxillae with apices bent mesiad; palpi elongate. Labium strongly protuberant, divisible into prementum and postmentum by transverse fold, bearing salivary opening at apex; salivary opening elongate, bearing lips, and not armed with large teeth; labial palpi as long as but more slender than maxillary palpi.

BODY: Form (figs. 6, 7) moderately elongate though not so much as that of *Exomalopsis chionura* (Rozen, 1957) or that of the Emphorinae (Michener, 1953; Linsley, MacSwain, and Smith, 1956); in live postdefecating larva (fig. 6) body looped so that head actually or nearly comes in contact with tenth segment. Integument of quiescent postdefecating form soft and pliable and therefore unlike rigid body integument of hibernating larvae of the Panurginae and such parasitic anthophorids as *Oreopasites*, *Holcopasites*, and *Neolarra*. Body annulations and tubercles for both predefecating and postdefecating larva as illustrated, essentially same as in *Melissodes* sp.? (Michener, 1953). Integument without spicules and with only scattered, minute setae near the anus. Spiracles as described and illustrated for *Melissodes* sp.? (*ibid.*). Tenth abdominal segment small, with anus situated dorsally (fig. 7).

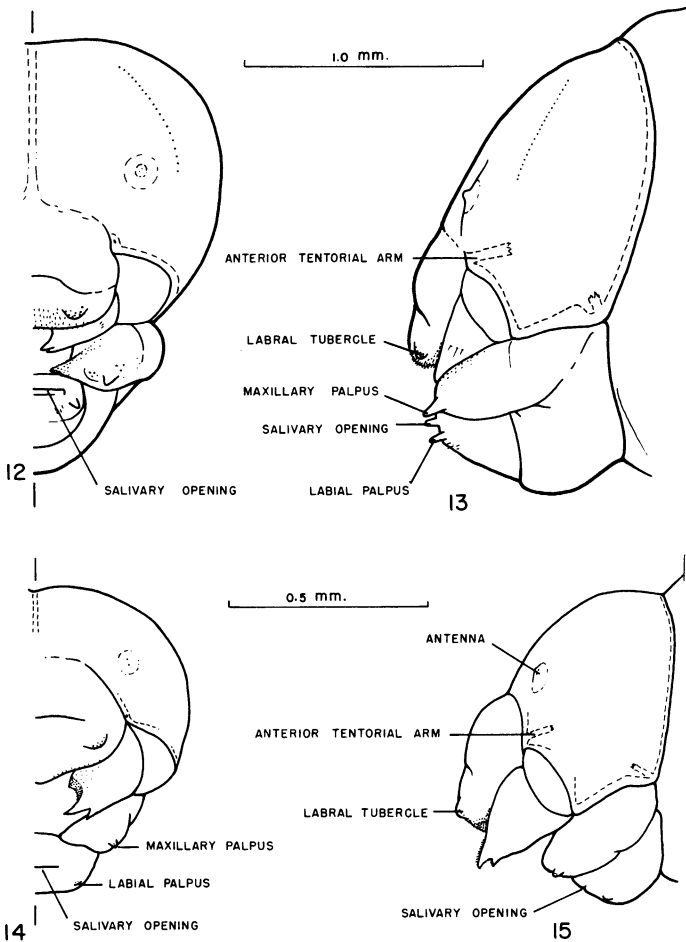
MATERIAL STUDIED: Numerous mature larvae, Flamingo, Everglades National Park, Florida, April 16, 1963 (J. G. and B. L. Rozen).

TAXONOMIC DESCRIPTION OF THE FIRST-STAGE LARVA OF *SVASTRA OBLIQUA OBLIQUA* (SAY)

Figures 8, 14, 15

The following description is intended to be comparative with that of the first instar of *Exomalopsis chionura* (Rozen, 1957).

HEAD (FIGS. 14, 15): Capsule and mouth parts with a few widely scattered short setae; tentorium complete but weaker than that of mature larva. Posterior thickening of head capsule weak; hypostomal thickening well developed; pleurostomal thickening weak, being evident only near mandibular articulations; epistomal thickening moderately developed laterally but fading medially; longitudinal median thickening of head capsule distinct dorsally but fading below. Parietal bands apparently absent. Antennae scarcely noticeable, unlike those of *Exomalopsis chionura*, but bearing several sensilla. Labrum and clypeus large and protuberant; labral tubercles present; labrum bearing elongate fine spicules laterally, apically, and on epipharyngeal surface. Mandibular corium non-spiculate; mandibles stout, sharp pointed apically, with upper and lower



FIGS. 12-15. *Svastra obliqua obliqua* (Say). 12. Head capsule of mature larva, frontal view. 13. Same, lateral view. 14. Head capsule of first instar, frontal view. 15. Same, lateral view.

apical edges sharply serrate; lower edge bearing large, sharp-pointed, subapical tooth (corresponding to lower apical tooth of mature form); this tooth larger than that found in *Exomalopsis chionura*; upper apical edge with broad band of denticles; dorsal inner surface with smaller, more widely scattered denticles (spicules). Maxillae with tips non-spiculate, bent mesiad and with palpus subapical in position; palpi moderately developed though much shorter than in mature larva. Labium not pro-

tuberant and not divided into prementum and postmentum; palpi shorter than those of maxilla; salivary opening an elongate transverse slit without lips.

BODY: Form elongate-cylindrical (fig. 8), without tubercles but with intrasegmental annulations dorsally. Integument non-setose but minutely spiculate; anal area without spines. Spiracles large and unlike those of adults; second pair of spiracles smaller than others. Ninth abdominal segment approximately same diameter as preceding ones; tenth segment somewhat smaller.

MATERIAL STUDIED: Two first-stage larvae, Flamingo, Everglades National Park, Florida, April 16, 1963 (J. G. and B. L. Rozen).

CONCLUSIONS

The information presented above on the biology and larvae of *Svastra obliqua obliqua* obviously emphasizes the close relationships of the Exomalopsinae, Emphorinae, Eucerinae, and Anthophorinae (see Linsley, MacSwain, and Smith, 1955, 1956; Rozen, 1957; and Rozen and MacNeill, 1957; data not yet available for the Centrinae). It does not, however, elucidate the relationships of the numerous, distinct, *Nomada*-like groups of parasitic anthophorid bees (the Nomadini, Ammobatini, Holcopositini, Neolarrini, and others, of Michener, 1944) with the pollen-collecting anthophorids. Although Linsley, MacSwain, and Smith (1956) and Michener (1944, 1953) have suggested that the Exomalopsinae and the parasitic groups may be closely related, Rozen and MacNeill (1957) concluded that the only biological information that supported this hypothesis was nest appropriation in *Exomalopsis* and its ambulatory larva. As the same features are found in the Eucerinae, one can only conclude that the nomadine taxa could just as easily have arisen from the eucerines, if indeed they arose from any anthophorid group.

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