

Nesting Biologies and Mature Larvae of Oxaeine Bees (Apoidea: Andrenidae)

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ABSTRACT

This study encompasses a number of field encounters by the author and others with nests of representatives of three of the four genera of the little-known New World andrenid subfamily Oxaeinae. Species treated include *Protoxaea gloriosa* Fox, *Oxaea flavescens* Klug, *O. austera* Gerstaecker, and *Mesoxaea nigerrima* (Friese), leaving the nesting biology of only the monotypic genus *Notoxaea* completely unknown. Nests, all subterranean, are described and diagrammed, and each is reported to consist of a moderately to very deep main burrow with vertical cells occurring at the lower end attached to the main burrow by subhorizontal lateral tunnels, each of which is closed immediately after egg deposition. To the extent known, eggs, mature larvae, and pupae are described. Two known cleptoparasites of the subfamily are reported: *Triepeolus kathrynae* Rozen, hosted by *P. gloriosa*, and *Thalestria spinosa* (Fabricius) (= *T. smaragdina* Smith), which attacks nests of both *O. flavescens* and *O. austera*. The mature larvae of these cleptoparasitic Nomadinae are described and illustrated as an appendix.

INTRODUCTION

This paper presents and analyzes the nesting biology of bees of the subfamily Oxaeinae of the Andrenidae. It is based both on (1) fieldwork carried out by the author and associates over the past 47 years when nesting sites of these ground-nesting bees were encountered and (2) accounts in the literature by others. In addition, the paper explores and describes the anatomy of oxaeine last larval instars and other immature stages available as a result of the fieldwork. After a section treating Methods and brief historical listing of biological studies of the subfam-

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FIGURE 1. Nesting site of *Protoxaea gloriosa* at 1 mile north of Rodeo, New Mexico, August 1970. View of area where numerous nests were discovered and excavated, demonstrating habitat, with K.C. Rozen standing to the left of excavation equipment and the Chiricahua Mountains of Arizona in the background at left.

ily, the comparative treatment of known nesting biologies of the subfamily is presented. At the end, an account of available last-stage larvae, eggs, and pupae of the subfamily is offered. Until now little had been reported on this small New World group of fast-flying bees. While this paper fills in a good many details about them, there is still more to learn. The generic classification of Hurd and Linsley (1976) is followed throughout.

METHODS

After a nest entrance is discovered, a hole is excavated a short distance from one side of it with shovel and trowel. The earth is then removed with trowel and penknife from the excavation toward the descending burrow to expose the path of the burrow in side view. Talcum powder or another dry, white powder can be blown down the burrow with a plastic squeeze bottle to better follow it (fig. 2). As the burrow descends farther, the excavation hole is deepened as needed, and the accumulation of excavated soil can be removed from the hole if necessary. Observations and diagrams of the shapes and sizes of nest elements are recorded as field notes. In chipping away the soil close to the burrow or cells with a penknife, a collecting aspirator with screen removed is used to provide a strong source of wind to blow away obscuring loose soil to reveal nest elements. When lateral tunnels and cells are encountered, records are made of orientation, depth, sizes of cells, cell contents, and ages. Thus a lateral diagram of the



FIGURES 2–7. Same area and date as figure 1. **2.** Main tunnel of partly excavated nest, approximate side view. White, dry plaster-of-Paris powder marking curved path of open descending tunnel. **3.** Excavated nodule containing cluster of four cells (arrows) adhering to one another because of thick walls. **4.** Single cell opened perpendicularly to show shape and characteristic shiny, waterproof lining. **5.** Cell with upper part removed to view curved egg at center of top surface of provisions, approximate lateral view. **6.** Cell with top part removed showing circular wall of cell at midlength with intermediate stage feeding larva on top surface of very moist, orange provisions. **7.** More mature larva than in figure 6 with one side of body now submerged while feeding on provisions that have further liquefied.



FIGURES 8–13. Nest components of Oxaeinae in the American Museum of Natural History, photographed at the time of preparation of this manuscript. **8.** Unit of cells of *Protoxaea gloriosa* collected in 1970 demonstrating hardness of cell and tunnel walls. **9.** Close-up of one opened cell with curved tunnel wall attached, showing smooth water-retardant cell inner surface with dried orange provisions on lower surface. **10.** Opened curved tunnel of *P. gloriosa*, approximate top view, showing series of septa resulting from cell closing and position of cell wall attached below. **11.** Plaster cast of open cell and connecting tunnel, demonstrating accurate shape of cell of *P. gloriosa*. **12, 13.** Inner surfaces of spiral closures of two cells of *P. gloriosa*. **14, 15.** From nests of *Mesoxaea nigerrima*, collected from Chamela, Jalisco, Mexico, 1986. **14.** Cell, side view, demonstrating smooth lining to inner surface and hard cell wall, lateral view. **15.** Cell closure, showing spiral closure.

nest is established. With more complicated nests where a top view is required, visualization of the cell distribution is made from above before measuring the distance and direction between the burrow and each cell. Samples of nest parts such as cells and entrance tunnels in addition to immature stages are retained for future detailed examination and comparison (fig. 8).

Illustrations of immature stages were prepared with a camera lucida attached to a Leitz Wetzlar stereomicroscope. In diagrams of immature stages, outlines indicated by dots are approximations of areas that were missing on the actual specimens. Photographs of anatomical structures were taken with a Cannon Power Shot A2300HD handheld to the ocular of a Leitz

Wetzlar stereomicroscope and a Carl Zeiss compound microscope. SEM micrographs were taken using a Hitachi S5700 in the Microscopy and Imaging Facility of the American Museum of Natural History.

PREVIOUS STUDIES

Bertoni (1911) reported finding in-ground nests of *Oxaea austera* Gerstaecker in Paraguay. The deepest had a vertical burrow that descended about one meter, and some burrows were “curved,” presumably meaning they descended at varying angles.

Cockerell (1933) briefly described a massive nesting site of *Mesoxaea texana* (Fries), as *Protoxaea texana*. Linsley and Michener (1962) provided an account of a nest of *Mesoxaea nigerrima* (Fries) (as *Protoxaea nigerrima*) from Mexico. Details are described below.

Truxal (1962) reported finding nests of *Oxaea* sp. in Peru. Rozen (1964) published the description of a mature (postdefecating) larva of *Protoxaea gloriosa* Fox based on specimens collected in southwestern New Mexico a year earlier by M.A. Cazier and M.A. Mortenson and given to Rozen for investigation. The paper also included the description of the presumed first instar collected by Cazier, Mortenson, and E.G. Linsley from the same locality. Based on data presented below, that specimen now is almost certainly a second instar. In that 1964 paper Rozen purposely did not provide information concerning nesting biology because he presumed it would be presented by others.

Roberts (1973) produced a detailed treatment of the immature stages and biology of two nests of *Oxaea flavescens* Klug.

Rozen and Ricardo Ayala in 1986 undertook a study of nests and immatures of *Mesoxaea nigerrima* (Fries) at Chamela, Jalisco, Mexico, that has remained unpublished until now. Sartzetti et al. (2014) provided a detailed account of the nesting biology of *Oxaea austera* Gerstaecker, reporting that nests were occupied by more than one female and were utilized by more than one generation. The current author (J.G.R.) had been unaware of this important study until he received a copy of *Ichnoentomology* (Genise, 2017) in which it was referenced. This paper supports some of the tentative conclusions on nesting biology of the subfamily that were deduced in the first draft of the current paper, in that *O. austera* also has nests containing more than one female and these may be used by successive generations.

Because of these studies, the following report encompasses representatives of three of the four genera assigned to the subfamily. Only the biology and last larval instar of the South American *Notoxaea ferruginea* (Fries), the sole known representative of its genus, remains unknown.

NESTING BIOLOGY OF THE OXAEINAE

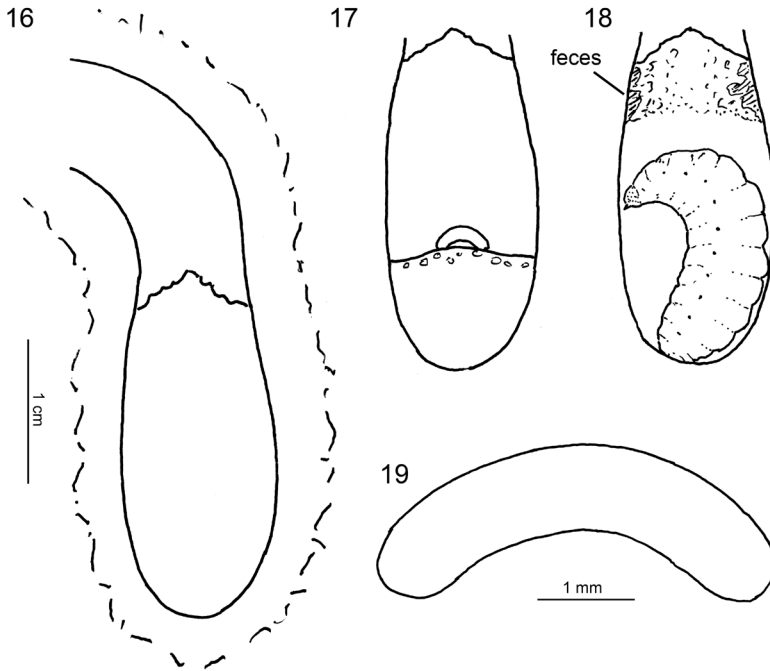
PROTOXAEA: Of the oxaeine nests that have been studied those of *Protoxaea gloriosa* have been examined most often (see table 1) and in greatest detail. The following account is based on the examination of nests made first by J.G.R. and the late Kenneth C. Rozen in 1970 at one mile east of Rodeo, Hidalgo Co., New Mexico. In 1989 nests were again discovered five miles

TABLE 1. Nest Statistics of Oxaeinae. Numbers in parentheses = number of data when known.

Taxon	Cell Depth (cm)	Burrow Diameter	Cell length; diameter	Source
<i>Oxaea flavescens</i>	195–245 cm		24 mm; 13 mm	Roberts, 1973
<i>Oxaea austera</i>	100 cm			Bertoni, 1911
	90–110 cm	9 mm	2.4 mm (15); 1.2 mm (15)	Sarzetti et al., 2014
<i>Oxaea</i> sp.		ca. ½ inch		Truxal, 1962
<i>Protoxaea gloriosa</i>	24–42 cm	8–10 mm	22–23 mm (6); 10 mm (7)	J.G. and K.C. Rozen, field notes, 1970
	44–50 cm	7–9 mm (6)	22–25 mm (8); 10–11.8 mm (19)	Rozen and Foster, field notes, 1989
	36–46 cm	10 mm		J.G. and B.L. Rozen, field notes, 1990
<i>Mesoxaea texana</i>	“several feet”	2 mm		Cockerell, 1933
<i>Mesoxaea nigerrima</i>	58 cm	0–12 mm	28–30 mm (2); 13–15 mm (2)	Linsley and Michener, 1962
	32–58 cm	0.5–11 mm	25–29 mm (7); 12.5–13 mm (9)	Rozen and Ayala, field notes, 1986

east of Sahuarita, Pima Co., Arizona, by Robert L. Foster and J.G.R., and in 1990 the late Barbara L. Rozen and J.G.R. studied them eight miles northeast of Portal, Cochise Co., Arizona. Diagrams of six nests (from a total field of about 17) have been selected from field notes and are reproduced here (figs. 20–24, 26) illustrating the diversity of nest structures. Following the treatment of nests of *P. gloriosa*, nests of other Oxaeinae are interpreted in light of our present understanding of *P. gloriosa*.

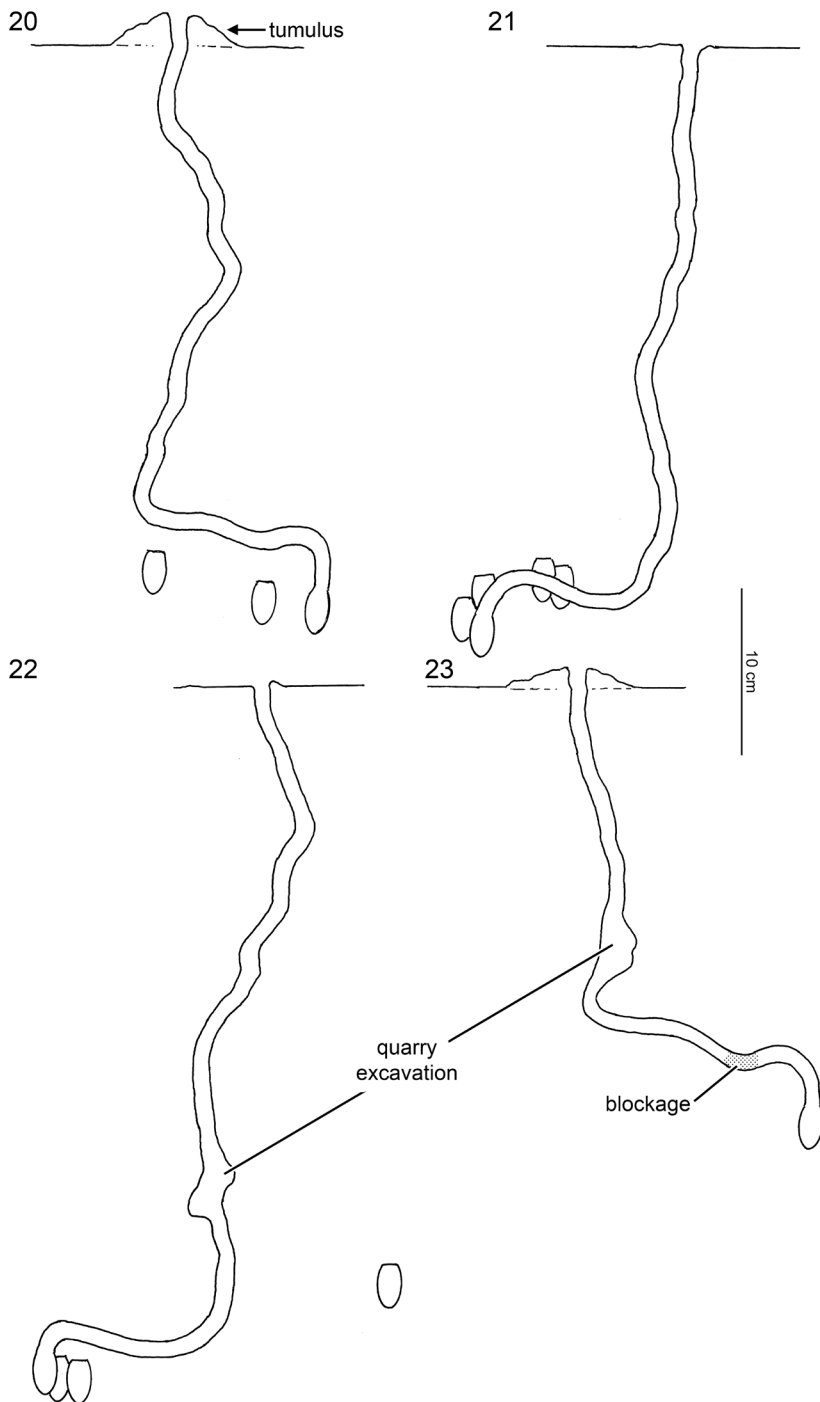
The overall nest pattern of this species in side view (figs. 20–24, 26) consists of a lengthy main tunnel that is mostly open. It descends following a somewhat crooked, irregular path to the cell level usually with an open vertical cell connecting to the end of the open main tunnel by a more or less horizontal open lateral tunnel 8–14 cm long. This cell was the one being provisioned at the time of nest discovery. Other nest cells, all vertical (or nearly so) and closed, occur at about the same level and are presumably connected to the main burrow by soil-filled and, therefore, often obscure laterals. All nest entrances observed were on nearly horizontal ground sometimes next to a rock or clumps of low vegetation. Main tunnels as well as laterals ranged 8–11 mm in diameter with most at 10 mm in diameter. Laterals (figs. 11, 16) narrowed several mm at cell entrances. After closing a cell, the female fills the lateral with soil before excavating the next lateral and cell. Main tunnels remain mostly open although some parts (figs. 23, 26) may be temporarily blocked with a short stretch of soil, presumably for a brief period during cell construction or closure. Some main burrows (figs. 22, 23) revealed a large, irregular enlargement partway down, here termed *quarry excavations*, almost certainly the result of a female removing soil to backfill a lateral after cell closure following egg deposition. At other times lateral fill is derived from new cell construction. Surface tumuli at burrow entrances are sometimes visible (figs. 20, 23). Although the irregular descending pattern of



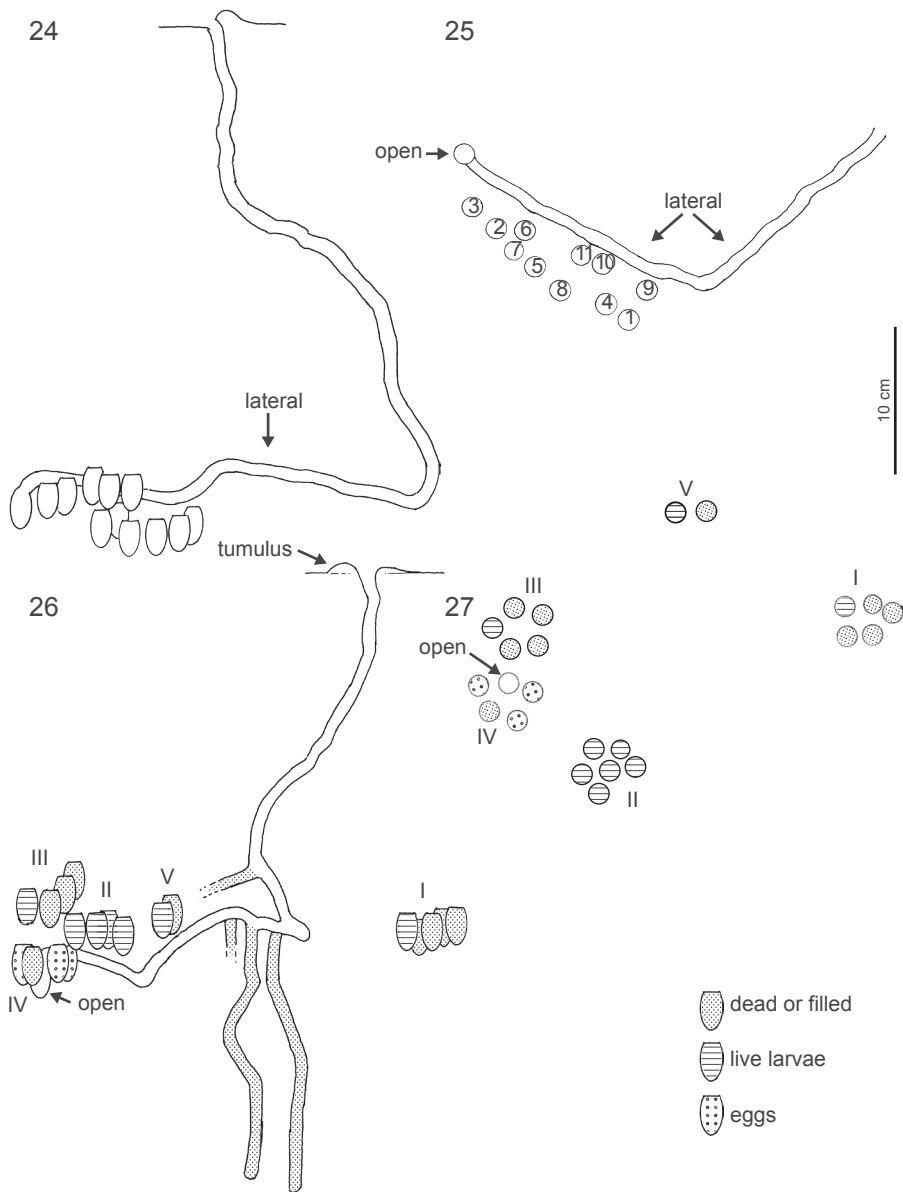
FIGURES 16–19. Diagrams of cells and egg of *Protoxaea gloriosa*. **16.** Demonstrating exact shape of lumen and entrance tunnel as well as approximation of cell and tunnel wall. **17.** Cell with provisions showing position of egg on provisions with subsurface bubbles presumably of gas. **18.** Cell with postdefecating larval of *P. gloriosa* with moldy fecal material applied to upper end. **19.** Egg, lateral view, anterior end to left.

main burrows may be due to rocks or roots that obstructed the constructing female as she descended, it may also be an adaptation to avoid rain water from reaching open cells since rainwater is likely to be absorbed through unlined burrow walls along the way. Vertical open cells with waterproof linings would be at risk if straight open main tunnels led directly to them. The long lateral tunnels of this species serve the same function as a crooked main tunnel since they too lack waterproof linings. Furthermore, although laterals tend to be subhorizontal, they almost invariably (figs. 20–23) curve upward a short distance in front of the cell and then curve strongly downward to join the top of the vertical cell, thus serving to protect the cell lumen from flooding with water. The curvature allows for further absorption of rainwater and also possibly may provide a “plumber’s trap.”

Cells of a nest tend to occur at nearly the same depth rather than being distributed along a descending tunnel, as is the case with many bees. Cells in large nests seem to group into small clusters (fig. 26). When diagramed in lateral view they may seem to cluster into larger groups, but when viewed from above they are seen to be the result of long laterals radiating outward in various directions at one depth (figs. 24–27). While small clusters seem to represent the work of a single female because of the ages of the contained offspring, it is unlikely that larger nests represent the activities of a single female. Possibly several females are simultaneously using the same nest entrance or it may be evidence of successive generations. This information is sup-



FIGURES 20–23. Diagrammatic representations of patterns of simple nests of *Protoxaea gloriosa* with dimensions and shapes approximated, side view, identified by year of discovery. **20.** 1970. With three cells. **21.** 1990. With five cells. **22.** 1990. With four cells and quarry excavation. **23.** 1989. With one cell and quarry excavations; note short blockage of lateral!



FIGURES 24–27. Diagrammatic representations of more complex nests of *Protoxaea gloriosa*, side and top views of each nest, both discovered in 1970. **24, 25.** Demonstrating complex distribution of immature stages in cells, with sequence of egg deposition indicated by approximate age of immatures: cell 1, unknown; cell 2, one-half grown; cell 3, two-thirds grown; cell 4, unknown; cell 5, four-fifths grown; cell 6, three-fourths grown; cell 7, one-fifth grown; cell 8, full-grown predefecating larva; cell 9, full-grown predefecating larva; cell 10, egg on firm provisions; cell 11, egg on soft provisions (hence, older than egg in cell 10). **26.** Side view, demonstrating clusters of cells and varying contents of clusters I–V and contents of individual cells identified as follow: back-filled or containing dead immatures = grey; egg or live larvae = large stipples; live larvae = parallel bars. Upper back-filled lateral lost but possibly leading to back-filled cells (not shown); three descending back-filled tunnels at lowest part of nest presumably leading to unexplored old cells of previous generation(s). **27.** Top view of same nest showing approximate distribution of cell clusters from above.

ported by information presented in Sarzetti et al. (2014) concerning *O. austera* and is further discussed below concerning two of the larger nests of *P. gloriosa* that were studied.

Cells are positioned with their long axes vertical (figs. 16–19) though a few were tipped as much as 10° from vertical. Cell lumens are about twice as long as their maximum diameters. Shapes presented in most diagrams are approximations; for the exact shape of an open cell, see figures 11 or 16. Table 1 presents nest statistics. Cell walls from all three localities were noteworthy because of their thickness and hardness, and because walls extended beyond the cells to cover the curved connecting lateral for perhaps 4 cm in front of the cell closure (figs. 4, 9, 18), thus providing an antechamber. Walls were of the same soil composition as the surrounding soil and thus were not built with material from elsewhere. It was often possible when removing a cell from the ground to recover it as a hard nodule that was 5–6 cm long and 2 cm in width (figs. 3, 8, 14). Because of the irregular outer surface, the thickness of the wall varied from 2 to 3 mm or more, but gradually reduced in thickness toward the front end of the curved antechamber. This is clear evidence that the constructing female adds a hardening substance to the combined antechamber and cell wall that provides a strong barrier against predators or parasites. However, this substance does not control cell humidity during larval diapause since, when tested with a droplet of water on its inner surface, the antechamber wall immediately absorbed it, whereas the cell wall permits no absorption. Although the surface of the antechamber wall is smooth, it lacks the distinct but subdued luster of the cell wall, which is not only smooth but also moderately reflective. When the inner surface of the cell wall was tested with a drop of water, the droplet was still present 45 minutes later; even then the water had not penetrated the waterproof lining. That is, the female applies a hardening material to the cell wall as well as to the antechamber wall as well as a separate waterproofing coating only to the cell wall, both of unknown sources. The waterproofing material extends only to the cell entrance and not beyond, as was tested by applying a large water droplet to the area where the two surfaces met.

The cell closure provided by the female after egg deposition is a circular disc with a distinctly spiraled lower surface composed of four to five rows to the radius (fig. 12–15). The center of the disc is recessed about 2 mm compared with its periphery, and the entire disc tilts noticeably from a right angle with the long axis of cell. When the surface was tested with a water droplet, the droplet was immediately absorbed, thus suggesting that air exchange takes place through the closure, permitting the diapausing larva to survive months on end. However, another possible consequence of the permeability of the cell closure is that it may also permit water vapor to enter the cell, which might account for the rapid liquification of the stored provisions, as noted below, suggested by J. Cane (personal commun., 6/26/2017) with respect to another group of bees.

An interesting discovery detected in cells from two of the localities was a series of transverse septa extending along the entrance tunnel from the cell closure toward the main burrow for at least 4 cm. Figure 10 shows six of the 11 septa that were revealed in one sample. The septa are composed of consolidated sandy material with the intervening spaces filled with loose sandy material. This suggests that, as the female backfills a tunnel, she repeatedly applies some

material to consolidate the sand, thereby creating the series of septa. Whether this tends to make the egress of the emerging offspring easier or to ward off predator/parasites is unknown.

On reviewing the literature dealing with the Andrenidae, the author remembered that he had reported similar septa occurring in entrance tunnels to cells of communal nesting *Ancylandrena larreae* Timberlake (Andrenini) (Rozen, 1994). On checking the collection of stored cells and other nest fragments of several collections of this species housed in the American Museum of Natural History, he noted another similarity in nesting material: the cells walls and antechamber walls, though far thinner than those of oxaeines, were still harder than the substrate and were completely continuous with one another. Such observations invite further investigation, particularly since similar septa have been identified in present day nests of Stenotritidae (e.g., Houston, 1984: fig. 6; Houston and Thorp, 1984: figs. 6–8) and Emphorini (Apidae), as well as in trace fossils (Genise, 2017).

While most nests of *P. gloriosa* seemed to consist of a small number of cells, two seemed more complicated (figs. 24, 26). The substantial number of cells in the case of figure 24 suggests the possible presence of more than one female in the nest. The complexity of the old as well as current cells in figure 26 might indicate the nest was used by more than one generation; such a multigenerational nest has been described for *Svastra* (Rozen, 2016), some of whose female offspring return to reuse their natal nest, which has already been proven safe, and thereby avoid the effort and time in constructing a long main burrow. With the information on *O. austera* provided by Sarzetti et al. (2014) added, it seems likely that communal nest occupancy and multigenerational nests would seem to be common features in the subfamily.

Provisions in nests of *P. gloriosa* were bright orange (figs. 5, 6), and, when fresh, the pollen-nectar mass was moderately soft because of high liquid content. It easily supported the egg that was invariably placed on its surface (figs. 5, 17). Because of its soft nature, the mass, in one case 9 mm in depth, occupied the bottom of the cell, leaving the open space above approximately 13 mm high. Small bubbles just beneath the surface of the provisions supporting the egg suggest that the mixture undergoes fermentation. When tasted, provisions from a cell containing an egg were sweet with a hint of sour, but were noticeably sour from a cell containing a feeding larva. Provisions become softer and more liquid over time. Thus, while young larvae resting with their venters on the surface of the mass fed on its surface (fig. 6), intermediate-stage larvae at some point in their development submerged partway and continued feeding now on their side with only the other side of their bodies exposed above the nearly liquid food mass (fig. 7). At this time, the spiracular openings on the exposed side rose above the food along the summit of a long ridge extending along the side of the body. Such a feeding larva is active in moving its head and mandibles and in curling and uncurling its body, thereby presumably ingesting large quantities of provisions as well as dueling with tips of forceps or surface debris, suggesting that the elongate mandibles might serve in defense.

The curved elongate eggs of *P. gloriosa* (figs. 6, 19) are described in the treatment of immature stages of the subfamily, below. Females deposit them centrally on the upper surface of the provisions. The front and rear ends (fig. 17) are attached to the provisions and the middle part loops freely upward.

Several preserved specimens provided some insight into egg eclosion. Two eggs of *P. gloriosa* had been preserved while they were hatching. With each the vacated head capsule of the first instar clung to the undersurface of the body about halfway to the rear while the chorion still covered the entire surface of the rear part of the body. The head and forepart of the body of the second instar projected from the remainder. This confirmed that both specimens had been preserved as they were hatching. This closely parallels the recent study of hatching spines (Rozen et al., 2017) among a diverse group of bees reporting that in those bees the first instar's exuviae is cast with the chorion as the second instar emerges and starts to feed for the first time. As a result, the first instar feeds on little or no pollen and thus simply seems a vehicle for the development and emergence of the second and following feeding instars. Unfortunately, the two specimens of *P. gloriosa* were too fragile to be studied successfully with an SEM in order to detect a row of hatching spines just above the spiracular line on both sides of the first instar. Such spines are predicted to play an important role in the first instar bee scenario described here, with the consequence that the first instar does not exist free of the chorion. If future studies of this species were to confirm the presence of hatching spines, this would be the first proof of this form of eclosion in the Andrenidae. Although the presumed first instar of *P. gloriosa* was described by Rozen (1964), that specimen was likely a second instar, since, in the scenario described above, the first instar does not exist free of the chorion. Accordingly, Hurd and Linsley's (1976) description of the first instar would also apply to that of the second instar.

After consuming provisions, the mature larva defecates, placing most of its feces on the upper surface of the cell wall where it meets the closure. Feces often tend to mold over time. Quiescent postdefecating larvae rest on the apex of the 10th abdominal segment (fig. 18) with their long axis paralleling the long axis of the cell, a position they maintain through the approximate 10 months of the diapause. They spin no cocoons.

The only cleptoparasite known to attack *P. gloriosa* is *Triepeolus kathrynae* Rozen (1989), the mature larva of which was reported earlier as *Triepeolus* species B (Rozen, 1966) and collected from the same locality (5 miles east of Sahuarita, Pima Co., Arizona) and at the same time as the larvae of the host were collected by Cazier and Mortenson. The diapausing larva of this cleptoparasite, like that of the host, rests on the apex of its abdomen against the lower end of the vertical cell while its dorsum leans against the wall, with the result that it appeared to be vertical in the cell when observed.

An interesting observation regarding the females of *P. gloriosa* was noted in August 2016 east of Bowie, Cochise Co., Arizona, where numerous adults of these fast-flying, seemingly aggressive bees were encountered visiting flowers alongside the roadway. Females, when picked up by hand from flowers, made no attempt to sting. Although it is generally known that female Andrenidae do not sting, one would assume that a female would still attempt to curl its metasoma as if to sting when handled. One wonders if this will be found characteristic of the subfamily.

The only other species of *Protoxaea* mentioned in the literature is *P. texana* (Fries), which is now regarded as *Mesoxaea texana* (Fries). Cockerell (1933) allowed that a nesting aggregation of 80,000 occurred in Texas in an area of 5000 m², in which nest tunnels 12 mm in diameter were "several feet deep."

OXAEA: The first important treatment of the biology of this genus is that of Roberts (1973) based on his discovering two nests of *Oxaea flavescens* Klug in central Colombia, South America. His account was of a nest possibly containing 40 cells, which presumably represented those of previous generations as well as current ones, some at depths of 2.5 m. These facts suggest that it might have been a multigenerational nest. Some current cells contained diapausing larvae, while other cells were being freshly provisioned by adults. Although he provided numerous illustrations of a last larval instar, the specimen he used was either a predefecating form or at least one that has not yet advanced into a fully formed diapausing individual, as pointed out below in the section on last larval instars. Although he did not describe the larva, he verbally described and illustrated its pupa. Fortunately, he deposited a sampling of these larvae in the collections of the American Museum of Natural History, which has allowed its treatment below. He also deposited larval specimens of the parasitic bee *Thalestria* sp. (Apidae: Epeolini) simultaneously collected from the site. Because the larva of that genus has not been described, its description is appended below.

As portrayed by Roberts, the nest of *O. flavescens* had the same architectural configuration as that of *P. gloriosa*: descending, somewhat curving main burrow at the bottom of which had been constructed an array of closed laterals radiating more or less horizontally in all directions, with the main burrow open as well as one lateral leading to an open cell. The nest differed from that of *P. gloriosa* in that the main burrows were deeper (cells ranged in depth 195–245 cm), and laterals tended to be much longer (20–50 cm). (See table 1 for additional nest statistics as reported by him.) Roberts' estimation of the total number of cells based on the partial distribution of those counted yielded an estimated total of 40 cells. This gives support to the hypothesis that *Oxaea* and *Protoxaea* sometimes may have multigenerational nests, occupied by subsequent generations (as hypothesized by Roberts), thus accounting for the absence of large entrance tumuli, and possibly by more than one female at a time. It would not be surprising if other deep-nesting taxa have evolved similar strategies. Hence at this time, the main differences between nests of *P. gloriosa* and those of *O. flavescens* seem to pertain to lengths of main burrows and laterals.

Bertoni (1911), reporting on nests of *O. austera* Gerstaecker in Paraguay, stated the main burrows, some of which "curved," were vertical and descended as much as one meter. One nest contained two females. He also saw the cleptoparasite *Thalestria* sp. (Epeolini) entering nests. Truxal (1962) found seven nests of *Oxaea* sp. in Peru but did not excavate them.

As stated in the introduction, Sarzetti et al. (2014) recently substantially expanded the information regarding nesting of *O. austera* and presented information that supports the hypothesis presented in the treatment of *P. gloriosa* that nests of members of the Oxaeinae may be communal. The paper also offers much information on nests and nesting biology that parallels what is known concerning *P. gloriosa*. However, it also states that cells of *O. austera* appear to be found arranged in a row beneath a lateral tunnel, a situation that has not yet been documented for *P. gloriosa*. The study does point out that the antechambers and cells of *O. austera* "closely resemble the fossil bee cells included in the ichnognus *Palmiraichnus* from the early Eocene Asencio Formaton of Uruguay," thereby suggesting the occurrence of a subfamily member there at that time.

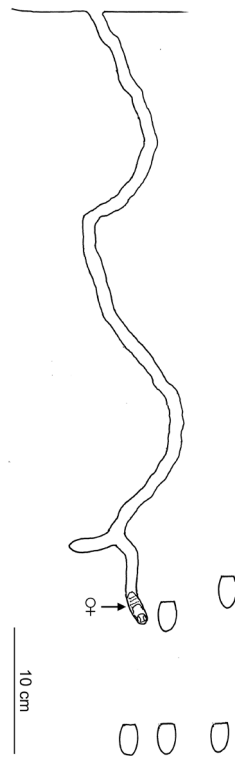


FIGURE 28. Diagram of nest of *Mesoxaea nigerrima*. Chamela, Mexico, 1986, with five cells and a possible short quarry excavation, below which is a branch containing a dead adult female, as indicated.

MESOXAEA: Linsley and Michener's (1962) account of a single nest of *M. nigerrima* found 14 mi south of Cuernavaca, Mexico, consisted of a vertical main tunnel, 10–12 mm in diameter extended 58 cm down, at which point it gave rise to laterals, one of which was open, leading to a cell that was being provisioned. The two cells encountered were vertical and seemingly identical to those described below for the first time.

A number of nests of *M. nigerrima* found along Eji Central, Chamela, Mexico, by Ricardo Ayala and J.G.R. were studied for several days starting November 11, 1986. The main burrow of one nest descended along an undulating path slanting at about 45° and terminated near four vertical closed cells at a depth of 32 cm; two of these cells contained postdefecating larvae. Elsewhere a single vertical open cell (fig. 14) with a 12.1 mm diameter was connected 7 cm from a main burrow by a lateral that curved upward just before the cell and then downward to meet the cell, as typical of *P. gloriosa*. Yet another vertical cell held very moist, soupy pollen and a young instar, and it had a distinct spiral closure. The nest diagrammed (fig. 28) with five cells had two of them at about the depth of 45 and 48 cm while three other cells were at 58 cm deep. The short side branch may have been a source of cell closure material, and a descending short terminal branch held the body of a dead female, as indicated. Cell 1 contained an active larva, cells 2 and 3 postdefecating larvae, and cells 4 and 5 mold.

Cells of the species were all vertical or nearly so; nest dimensions are presented in table 1. Larvae deposited moist fecal pellets on the cell wall next to the cell closure, and postdefecating larvae with the front of the body curving forward stood erect with their 10th abdominal segment against the lower end of the cell. Cell walls were thick (2–4 mm) and hard like those of *P. gloriosa*, and they too extended upward to completely cover the junction of lateral and the cell itself. Cell wall surfaces were extremely smooth and slightly shiny. When surfaces were tested with a drop of water, the cell wall was waterproof, but the cell closure and the entrance tunnel walls immediately absorbed water. Hence, the cells of the *P. gloriosa* and *M. nigerrima* are nearly identical in all respects, though those of *M. nigerrima* appear slightly larger when the two are viewed side to side.

Dry pollen was found deposited at the bottom of one open cell suggesting that females start gathering “dry” pollen and later add nectar to form the completed provisioning food mass, which becomes very moist, not unlike that of *P. gloriosa*, since feeding larvae of both species were found partly submerged in the provisions while lying on their sides with the lower portion of their bodies submerged in the food. A single egg was only slightly curved possibly because it was about to hatch; it was 4.2 mm long and had a maximum width of 0.7 mm.

DISCUSSION OF NESTING BIOLOGY OF THE OXAEINAE

The known nesting biologies of the species in the Oxaeinae appear remarkably similar. All species examined are ground nesting with nests consisting of a long main burrow that descends following an irregular, somewhat twisting path. This burrow is open most of the way and varies little in diameter from one species to the next. Burrow walls are unlined. Cells of each species are grouped at the lower end of the burrow where they radiate out in various directions, each connecting to the main burrow by a more or less long, subhorizontal lateral tunnel. The laterals are soil filled in each case after the female oviposits on the provisions stored in the bottom of the vertical cell and seals the cell with a spiral closure.

Cells of all species are elongate, about twice as long as their maximum diameter and are oriented with their long axis vertical, anterior end up. Connecting side tunnels usually first curve upward and immediately afterward curve downward as they join with cell entrances (figs. 20–23). With all species known, newly deposited provisions quickly become moist, so that by the time the larva is even half grown it lies on its side with its lower side submerged in the liquid provisions.

Few biological differences between taxa have been detected. The known nests of *Oxaea flavescens* with long laterals and an extremely long main burrow (table 1) are noteworthy. Furthermore, the possibility that a single nest seems to accommodate 40 cells according to Roberts (1973) is also unknown among other oxaeine taxa. However, future studies may reveal that such a large number of brood chambers may merely indicate that a nest has been simultaneously or consecutively inhabited by more than one female, a situation that has been postulated here for several nests of *P. gloriosa*.

DESCRIPTIONS OF IMMATURE STAGES OF THE OXAEINAE

EGG OF *PROTOXAEA GLORIOSA*

Figures 19, 29–32

Eggs of only *P. gloriosa* were available for study.

DESCRIPTION: Form (fig. 19) elongate, strongly curved, sausage shaped; length 3.75 to 4.0 mm (average 3.84 mm) and 0.75 to 0.875 mm (average 0.83 mm) in maximum diameter, nearly parallel sided, with front and posterior ends similar in appearance except front end slightly smaller when viewed with stereoscope. Chorion surface smooth, faintly shiny, and mostly transparent, thereby revealing off-white color. Micropyle area not identifiable even under maximum stereoscopic magnification; with SEM, this structure small, low bulge (figs. 29, 30) on narrower front end of egg surrounded by radiating lines in chorion; bulge bearing numerous small porelike indentations, some of which presumably penetrate chorion. Under very high magnification chorion appears to be composed of wrinkled interconnecting fibers of changing thicknesses (fig. 31), features that have not been observed in other bee eggs by this author. Various views of chorion seem to demonstrate that fiber density responsible for various surface textures shown in micrograph (fig. 29).

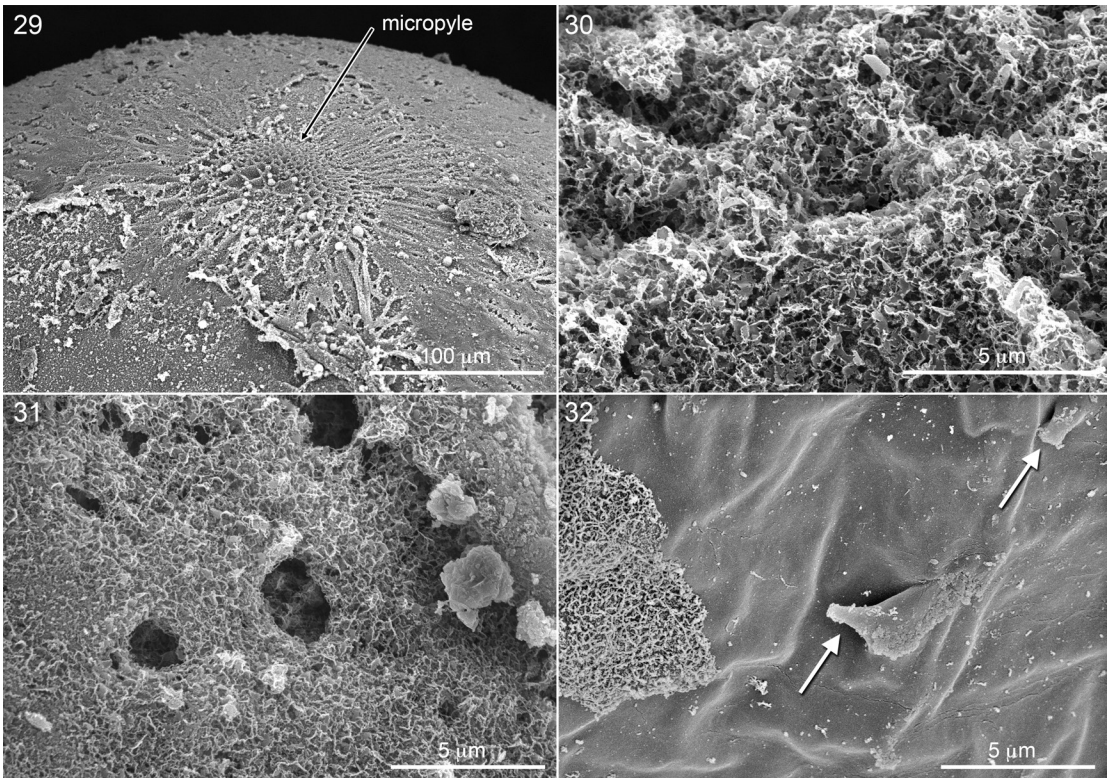
MATERIAL STUDIED: Three eggs: NEW MEXICO: Hidalgo Co., 1 mi north of Rodeo, VIII-20-1970 (J.G. Rozen).

DISCUSSION: What appeared to be a partly eclosed egg (fig. 32) revealed the underlying integument of the presumed first instar seems to have possessed stout spicules resembling those termed “hatching spines” found in a number of families of bees (Rozen et al., 2017). If this can be confirmed, this would be the first evidence of these structures being involved with eclosion in the Andrenidae.

MATURE LARVAE OF THE OXAEINAE

The following description is based on the known postdefecating larvae of *Protoxaea gloriosa*, *Oxaea flavescens*, and *Mesoxaea nigerrima*. References to predefecating larva are those of *Protoxaea gloriosa* and *Mesoxaea nigerrima*. The single pale larva of *Oxaea flavescens* was actually an early stage postdefecating form and is described separately. Because mature larvae are so similar, individual formal descriptions of each are not presented although important features are discussed for each species, as are differences between pre- and postdefecating forms.

DIAGNOSIS: The following unique characteristic of the larvae of the Oxaeinae not shared with any other bee taxa are: mandibles apically bladelike, positioned so bladelike apices can cross one another like two blades of a scissor; and labrum with pronounced median apical cleft, so that lower apical edge bituberculate in frontal view, with each apex bearing cluster of sensilla. In addition, spiracle of postdefecating larva reveal that the subatrium and primary tracheal opening are laterally compressed (fig. 46), so that when viewed from the exterior the primary tracheal opening appears as a long linear slit formed by the compressed lips of the tracheal



FIGURES 29–32. SEM micrographs of egg of *Protoxaea gloriosa*. **29.** Anterior end showing apical mound of micropyle. **30.** Close-up of micropyle. **31.** Close-up of pits in micropyle demonstrating texture of chorion. **32.** Close-up of partly eclosed egg showing spiculelike structures suggestive of hatching spines (arrows).

opening (figs. 43, 44) encircled by an oval tracheal rim. This slit is perpendicular to the long axis of the body segment. While the above are thought to be a unique feature of the postdefecating larvae of this subfamily, certain other features are unusual though not unique among mature bee larvae: extremely dark pigmentation of postdefecating integument and extensive stiffening of flexible intersegmental and integumental membranous areas of predefecating forms, including compression of abdominal segment 10. This gives the very dark, quiescent larva a strong, stiff image accentuated by the series of small protuberant, shiny spiracular tubercles stretching along each side of the slender, rigid figure. On close inspection, the head is unusual in profile because of the greatly recessed and reduced labiomaxillary region overridden by the large projecting mandible with a large base and tapering long apex (fig. 38).

HEAD (Rozen, 1964: figs. 2–4): Integument surface of head capsule and mouthparts of postdefecating and predefecating larva wrinkled (see discussion for possible adaptive significance); integument of postdefecating larva moderate brown except mandibles, internal head ridges, and palpi tending to be darker. Integument of predefecating larva smooth to weakly wrinkled, mostly colorless except for heavily sclerotized areas such as mandibular apices and internal head ridges, which are faintly pigmented. Tentorium complete, but moderately thin, moderately pigmented; posterior tentorial pit below junction of posterior thickening of head

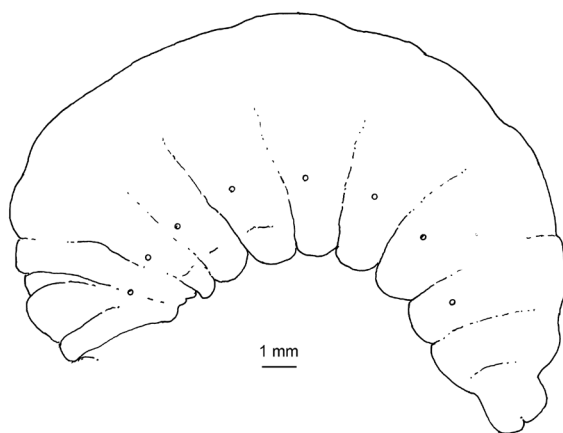
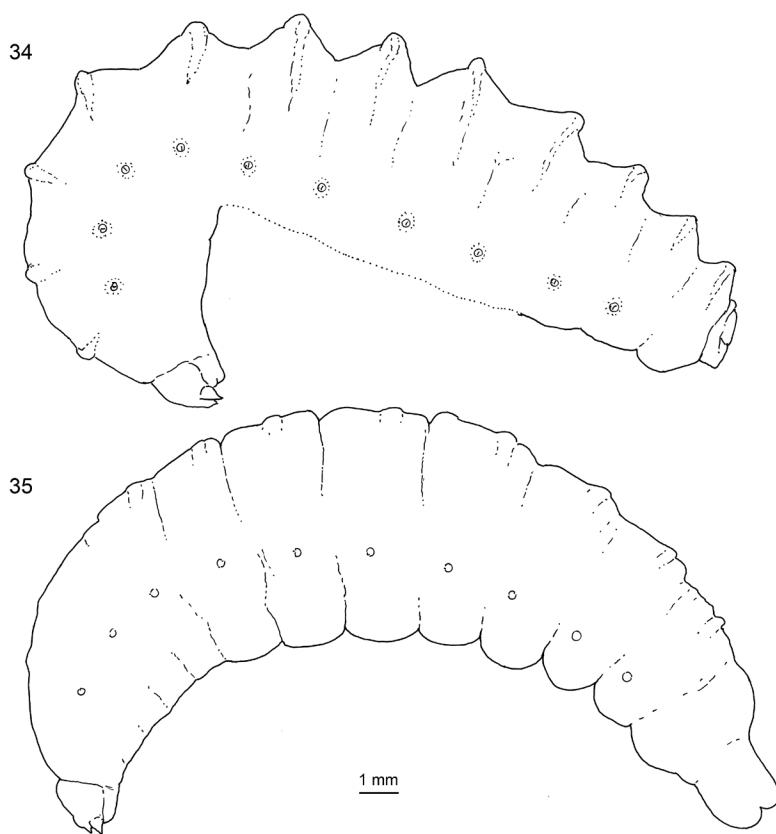


FIGURE 33. Abdomen of predefecating larva of *Protoxaea gloriosa*, lateral view.

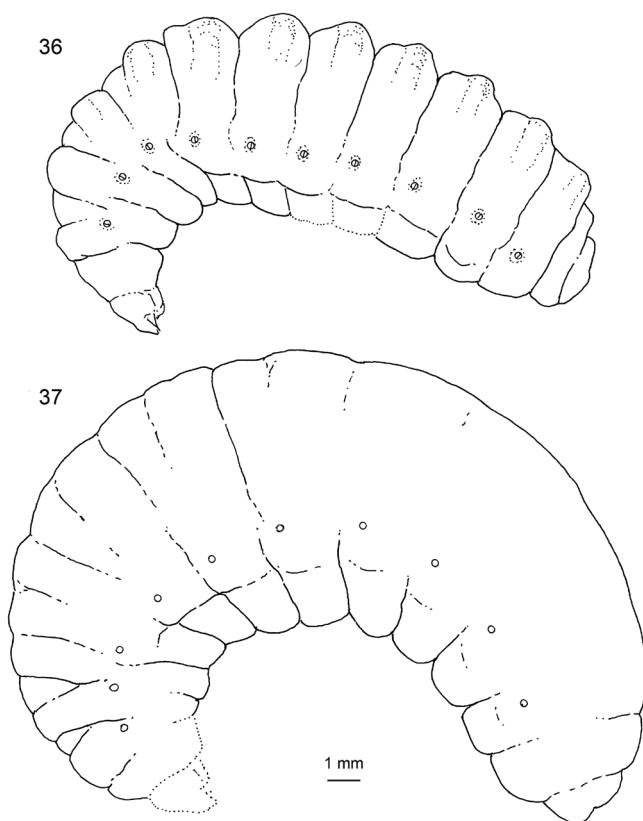
and hypostomal ridge but connected to posterior thickening by ventral extension of posterior thickening (alternatively, hypostomal ridge splitting posteriorly, with dorsal ramus extremely strongly developed and ventral ramus now completely lost); anterior tentorial pits just above epistomal ridge; epistomal ridge between anterior tentorial pits complete (contrary to Rozen, 1964, not "interrupted medially"); longitudinal thickening of head capsule absent; parietal bands unusually well defined. Vertex non protuberant and clypeus scarcely protuberant viewed laterally. Antenna not arising from prominence; antennal papilla small, shorter than basal diameter, bearing small cluster of sensilla. Labrum with pronounced median apical cleft, so that lower edge bituberculate in frontal view; in addition, front surface of labrum bearing pair of large, lateral, apically acute tubercles directed downward, passing laterad of tubercles of lower apical edge. Mandible in adoral view extremely broad basally but gradually tapering rapidly to very thin, elongate bladelike apex, created by dorsal surface becoming the leading edge of the blade identified by a series of large, sharp, apically pointed teeth and the ventral edge becoming thin outer edge of blade; under surface blade covered with large field of fine teeth; this surface facing obliquely downward and almost certainly homologous with apical concavity of apically broader more normal mandible; mandibular apex with apically projecting subapical tooth that is more slender than mandibular apex;² this subapical tooth lacking in previous instar. Mandibular apices of many mandibles found to be broken on preserved specimens. Labiomaxillary region of postdefecating larva darkly pigmented throughout; integument seemingly thick with surface wrinkled, without soft membranous articulating regions between structures, which therefore seem fused; mouthparts recessed in lateral view so that apices of maxillae and labium extending little beyond mandibular bases in lateral view (Rozen, 1964: fig. 3); articulating arm of stipes not evident; comparison of apical elements of labiomaxillary region of these three taxa suggesting that when additional specimens become available, features may be discovered to separate individual taxa. Salivary opening a small median transverse slit approximately halfway between top of hypopharynx and level of small labial palpi.

² Not known for *O. flavescens* because mandibular apices broken on all available specimens.



FIGURES 34, 35. Last larval instars of *Oxaea flavescens*, lateral view, postdefecating form and early stage postdefecating form, respectively.

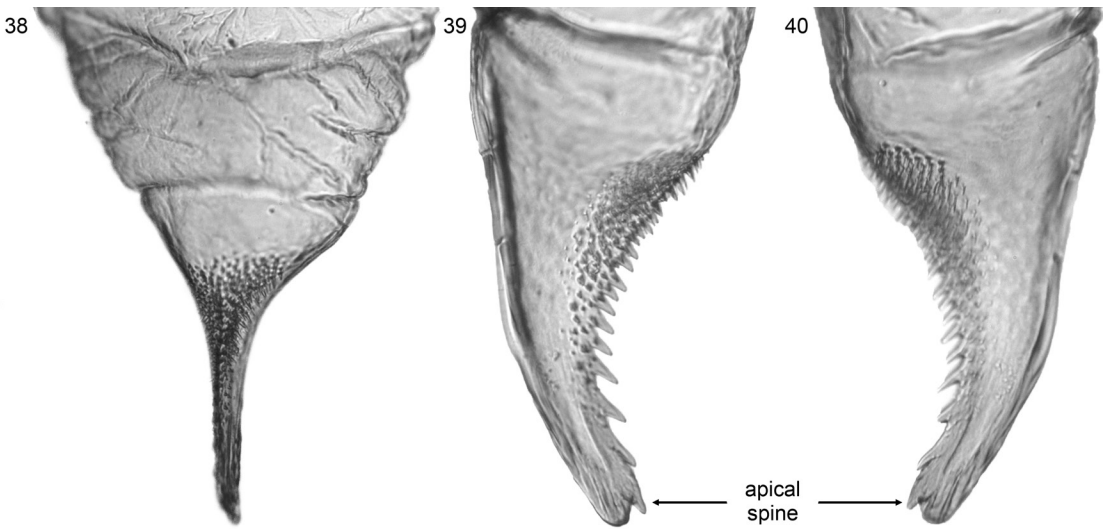
BODY: Integument of postdefecating larva minutely, evenly, transversely wrinkled (fig. 42), yellowish brown in color except spiracular tubercles somewhat darker, shiny, and not wrinkled; background shade varying in intensity from pale to dark, probably depending on age of instar. Integument of predefecating larva colorless, faintly, transversely wrinkled except for area around spiracles. Form of postdefecating larva: head and thorax bending forward from long axis of abdomen (figs. 34, 36). Thorax tending to have intersegmental constrictions less pronounced than those of abdomen; thoracic segments with postcephalic annulets bearing elevated narrow transverse dorsal ridges with distinctly granular surfaces flecked with darker pigments; these ridges briefly interrupted medially especially toward rear of abdomen; abdominal segment 10 very short in lateral view (fig. 34) (in sharp contrast with that of predefecating form) with posterior ridge tending to circumscribe flared anal surface. Ventral surface of most abdominal segments membranous, without even intersegmental lines except on terminal abdominal segments. Form of predefecating larva: intersegmental constrictions along posterior surface and dorsal surfaces swollen forcing larva to be curved along long axis; transverse dorsal ridges of postdefecating forms scarcely noticeable on predefecating form. Abdominal segment 10 of predefecating larva fully extended (fig. 33). Spiracular tubercles of postdefecating larva



FIGURES 36, 37. Last larval instars of *Mesoxaea nigerrima*, lateral view, postdefecating form and predefecating form, respectively.

strongly expressed as shiny, sclerotized, projecting, integumental blister with basal diameter about twice that of atrial rim; spiracular tubercles of predefecating larva not expressed; spiracles with atrial rims darkly pigmented, faintly oval; peritreme present; atrial wall densely covered with uniform, concentrically directed spines; subatrium moderately short, consisting of approximately seven annulations decreasing in size, melding, and fusing inward with flexure; entire subatrium compressed laterally, so that in postdefecating larva primary tracheal opening forming elongate linear slit bordered on both sides by projecting rim of primary tracheal opening forming projecting lip-like configuration that is almost as long as diameter of atrium (see Diagnosis and figs. 43–45 for further description); projecting lips beset with spines appearing to interlock, presumably guarding opening; because these spines slightly darker than atrium, they are often faintly visible under high magnification; compressed lips of primary tracheal opening forming visible line within spiracle perpendicular to long axis of its body segment. In predefecating larva pigmentation of atrium almost absent and primary tracheal opening far less compressed and flexure expanded.

MATERIAL STUDIED: See species descriptions.

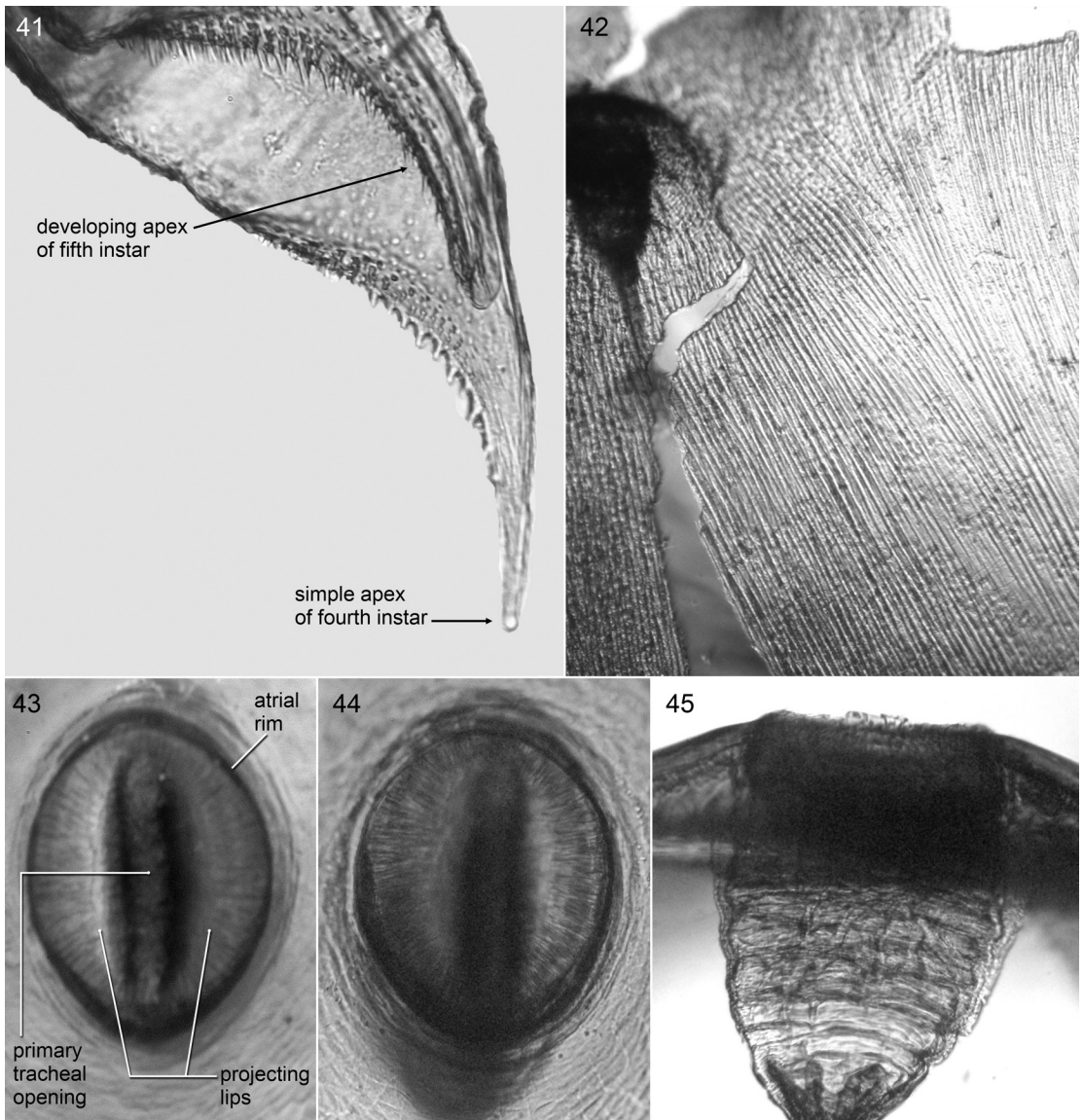


FIGURES 38–40. Microphotographs of right mandible of predefecating larva of *Protoxaea gloriosa*. **38.** Entire mandible, inner view of entire mandible demonstrating broad base with sides tapering as it extends to long, incurving, bladelike apical section. **39, 40.** Apical part of mandible, dorsal and ventral views respectively, showing curvature, large sharp, parallel-directed teeth of dorsal apical edge, with most apical spinelike tooth directed parallel to mandibular apex, and dense, broad field of spines possibly homologous with cuspal teeth subapically.

DISCUSSION: Although the anatomy of all larval stages of this subfamily is understood, how parts of it function remains to be discovered. Using the available larval instars of *P. gloriosa*, the species that is best known, the shape of the mandible with a broad base and long, thin tapering apex would scarcely seem to be the correct instrument to push a soupy pollen-nectar mix into the digestive track. The curved tapering blade of the mandible in the known larval instars of the species might be an adaptation to deal with parasites although the dentate inner edge would be hard to explain. Similarly the prognathous head capsule with a weakly developed labiomaxillary region might be a defense mechanism against parasites, although the cleptoparasitic threat to the subfamily does not appear to be excessive. In addition, the apically projecting subapical tooth known to occur both in *P. gloriosa* and *M. nigerrima* and very likely in *O. flavescens* is found only in the last larval instar, though it was detected developing through the exoskeletons of two late-stage fourth instars of *P. gloriosa* (fig. 41). Its use by the last stage larva remains a mystery. What is the adaptive function of the fifth instars mandibular apices? It is hoped that future fieldwork will explain these matters.

Limited material suggests variation in the expression of the apical structures of the labiomaxillary region between these taxa. These matters need further exploration when more material becomes available.

The presence of the small but blisterlike spiracular tubercles of the postdefecating larva at first appeared to be the result of loss of body volume resulting from defecation, that is, after the larva defecates, its soft integument shrinks, and folds in along the transverse parallel wrinkles of the membranous areas (fig. 42), which is most of the postcephalic integument. It was



FIGURES 41–43. Microphotographs. **41.** Right mandibular apex of 4th instar of *Protoxaea gloriosa* enclosing developing apex of 5th instar. **42.** Integument of postdefecating form of *Oxaea flavescens* showing minute parallel wrinkles that presumably allow integument to shrink as body size reduces with onset of postdefecating form. **43.** Spiracle of *Protoxaea gloriosa*, exterior view, showing oval atrial rim enclosing perpendicular line created by paired lips of primary tracheal opening. FIGURES 44, 45. Microphotographs of spiracle of postdefecating larva of *Mesoxaea nigerrima*: **44.** Outer (exterior) view, again showing: perpendicular line created by lips of primary tracheal opening. **45.** Spiracle from the front, with part of surrounding integument removed.

reasoned that because each spiracle is surrounded by sclerotic integument that does not shrink while the integument surrounding it does, the projecting tubercle is formed. However, this explanation alone is not completely adequate since in the case of *O. flavescens* the early stage postdefecating larva lacks spiracular tubercles (fig. 35) though they are clearly present in the fully established postdefecating larva (fig. 034). Although it seems unlikely that the shrinking of the membranous integument is entirely responsible for darkening the integument of the postdefecating larva, it may contribute to it. Integumental shrinkage almost certainly leads to decreased flexibility of the postdefecating form, which immediately enters diapause.

In the description of the head, reference is made to the extensive wrinkled condition of the heavily sclerotized surface of the cranium. This exists on both post- and predefecating forms and is a different phenomenon from the parallel wrinkling of soft integument in that the cranial wrinkling is multidirectional. Other studies have suggestion that wrinkling of sclerotized integument may be associated with distribution of water-deterrent waxes that are thought to prevent desiccation of body moisture during diapause (Mello et al., submitted).

An unexplained observation is the large number of mature larvae that experienced broken mandibles. Although breakage was perhaps not excessive in *P. gloriosa* and *M. nigerrima*, all seven postdefecating specimens of *O. flavescens* as well as the single early-stage postdefecating specimen had both left and right mandibular apices broken off.

POSTDEFECATING LARVA OF *PROTOXAEA GLORIOSA* (FOX)

This larva was described and illustrated by Rozen (1964), resulting in the format of the description used throughout this manuscript.

MATERIAL STUDIED: In addition the specimens listed in the 1964 treatment, mature larvae have been amassed from: NEW MEXICO: Hidalgo Co., VIII-18-25-1970 (J.G. and K.C. Rozen); ARIZONA: Pima Co., 5 mi east of Sahuarita, VIII-27-IX-5-1987 (J.G. Rozen and J.L. Foster); Cochise Co.: 8 mi northeast of Portal, VIII-31-1990 (J.G. and B.L. Rozen).

PREDEFECATING LARVA OF *PROTOXAEA GLORIOSA* (FOX)

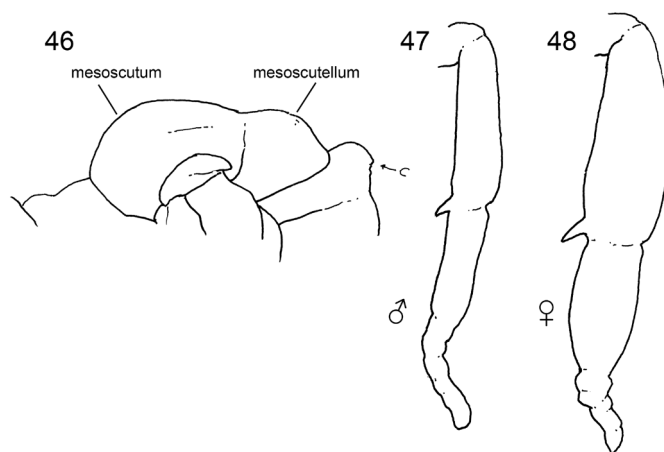
Figure 33

Because the postdefecating larva of *P. gloriosa* was previously described and illustrated, only the predefecating form is treated here.

HEAD: As described for postdefecating form (Rozen, 1964) except for following: integument scarcely pigmented; epistomal ridge complete, not interrupted medially.

BODY: As described for postdefecating larva except for following: form extremely robust, curved (fig. 33); posterior segments extruded, not telescoped, so that abdominal segments 8-10 fully exposed with segment 10 being as long as or longer than preceding segment. Spiracles with faintly pigmented atrial rims.

MATERIAL STUDIED: See Material Studied under postdefecating larva, above.



FIGURES 46–48. Pupae of *Protoxaea gloriosa*. 46. Lateral dorsal outline of thorax, anterior end toward left. Mid- and hind tibiae and tarsi of 47. male and 48. female.

POSTDEFECATING LARVA OF *OXAEA FLAVESCENS* KLUG

Figure 34, 42

Although Roberts illustrated the larva of *O. flavescens*, he did not describe it. Furthermore, we now know that the larva of this species illustrated by him (Roberts, 1973: fig. 1) was a specimen that had not yet fully developed many of the features of a postdefecating form as identified in the description of the subfamily above. Most notable was the protruding terminal body segment (fig. 35), contrasting with that of the postdefecating specimen (fig. 34) illustrated here.

The description of the subfamily, above, corresponds to that of the specimens examined here.

MATERIAL STUDIED: Seven postdefecating larvae: COLOMBIA: Meta: near Puerto Lopez, Hacienda Mozambique, December 1, 1971 (R.B. Roberts).

DISCUSSION: Roberts (1973: 443) reported that “nine of the 13 prepupae recovered from the excavation were mummified and their integument was very dark.” He suggested that some may have been from a previous generation, but it is uncertain whether he thought they had died before collection. The seven darkly colored larval specimens that he donated to the American Museum of Natural History were somewhat desiccated in shape in that the anterior part of the body was abnormally strongly bent beneath the posterior part. Furthermore, the ventral surface of the posterior part of the postcephalic region was unusually flat (possibly also from desiccation). All specimens seemed well preserved otherwise and dorsal surfaces were not distorted. While they may or may not have been alive when preserved, their anatomical integrity was trustworthy.

The single white-colored larva (fig. 35) among the donated material was likely one from “two cells containing large larvae but no pollen or feces” (Roberts, 1973: 443), as was the specimen he illustrated (Roberts, 1973: 438, fig. 1) and termed “pre-defecating.” Although I first assumed that this specimen was a predefecating form, I discovered on

dissecting it that the alimentary track no longer contained feces, the abundance of fatty material kept the integument plump (contrasting with that of fig. 34, here), and the flexures of all spiracles had constricted, indicating that the larva had started its diapause. This suggests that the transformation from a predefecating to postdefecating form is more or less gradual since this specimen exhibited little integumental darkening, and abdominal segments 9 and 10 were not compressed in sharp contrast to the dark postdefecating specimens (fig. 34). This specimen is here termed early stage postdefecating larva. There is no way to confirm whether the larva figured by Roberts (1973: fig. 1) is the same specimen and/or stage as fig 35) herein.

EARLY STAGE POSTDEFECATING LARVA OF *OXAEA FLAVESCENS* KLUG

Figures 35

A predefecating last larval instar of this species had not been preserved, but the single early-stage postdefecating larva was available. Because it had defecated, its more slender shape was obviously not characteristic of a predefecating form though its lack of pigmentation was. Assuming that the closing of spiracular flexures marks the start of diapause, the flexures on this specimen were already closed, indicating it had entered the very early stage of hibernation. Most of its other features were still in the prehibernation condition. Head capsule and several body segments were stained with Chlorazol Black E after being cleared.

HEAD: As described for postdefecating form except for following: integument mostly unpigmented, but mandibular apices and some of epipharyngeal surface darkly pigmented; labrum faintly pigmented. Much of internal tentorial structure missing, but surface ridges and short lengths of tentorial arms clearly present.

BODY: Integument unpigmented, with extensive coarse surface wrinkling, but without fine, deeply set, transverse wrinkling of postdefecating form. Form in lateral outline (fig. 35) nearly identical to that in Roberts (1973: fig. 1, lateral view) with body segmentation moderately expressed in sharp contrast with that of postdefecating form (fig. 34, lateral view) in which most body segments dorsally projecting, forming elevated transverse ridges contrasting with much lower intersegmental lines; abdominal segments 8, 9, and 10 much more elongate than those of postdefecating form; abdominal segment 10 longer than basal diameter; dorsal transverse abdominal ridges only faintly expressed, but on cleared, stained specimens integument of ridges appearing as pronounced transverse marks suggesting thicker integument. Spiracular protuberances faintly expressed, lacking pigmentation; spiracle form as described for postdefecating larva but without natural pigmentation.

MATERIAL STUDIED: One specimen with collection data as for postdefecating form, above.

DISCUSSION: The elongate terminal segments of the early stage postdefecating larva of *O. flavescens* contrasts (fig. 35) with the much shorter ones of the postdefecating larva (fig. 34). Rozen (1964: 227), noting the short terminal segments of the postdefecating larva of *P. gloriosa*, attributed this compression to "the larva's resting on the tip of its abdomen in a vertical cell."

POSTDEFECATING AND PREDEFECATING LARVAE OF
MESOXAEA NIGERRIMA (FRIESE)

Figure 36, 37, 44, 45

MATERIAL STUDIED: Two postdefecating and two predefecating larvae: MEXICO: Jalisco, Chamela, XI-10-1986 (J.G. Rozen).

PUPAE OF OXAEINAE

Figures 45–47

Roberts (1973) described and illustrated the pupa of *O. flavescens*, and Rozen and Rozen (2010) described the male and female pupae of *P. gloriosa*. Pupae of the two taxa are obviously very similar. Indeed, all of the minute tubercles identified by letters on the pupa of *O. flavescens* can also be observed on pupal *P. gloriosa* except for “h,” a feature of questionable homology. The pupae of the two taxa can be distinguished because in *P. gloriosa* the dorsal surface of mesothorax in lateral view (fig. 45) has the scutellum projecting dorsally beyond the curvature of scutum, unlike the even curvature of the mesothorax of *O. flavescens* (Roberts, 1973: fig. 7). With pupae of both taxa, the midlegs of females (fig. 46) have tibiae and basitarsi much thicker than those of males (fig. 47). Because of the close agreement of known mature larvae of the three oxaeine genera as well as that of pupae of *P. gloriosa* and *O. flavescens*, the pupa of *M. nigerrima* will likely be similar to those already known.

MATERIAL STUDIED: *Protoxaea gloriosa*: one male and one female: Arizona: Pima Co.: 5 mi E. Sahuarita, VII-27 & V-5, 1989, as postdefecating larvae, pupated VI-23-1990 (J.G. Rozen and R.L. Foster). *Oxaea flavescens*: One male and one female: COLOMBIA: Meta: near Puerto Lopez, Hacienda Mozambique, December 1, 1971 (R.B. Roberts).

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The donation of immature specimens of *Oxaea flavescens* by Radclyffe B. Roberts to the American Museum of Natural History long ago was instrumental in broadening the comparison and interpretation with those of other taxa within the subfamily.

The author expresses his appreciation to Ricardo Ayala for his hospitality and assistance in the study of *Mesoxaea nigerrima* at the Estación de Biología Chamela, Jalisco, Mexico. He also acknowledges with thanks the field assistance of those who worked with him in the field studies of *Protoxaea gloriosa* listed in the text above.

Much of the information presented here was gathered while the author was in residence at the Estación de Biología Chamela and the Southwestern Research Station, Portal, Arizona. Curatorial Assistant Corey Smith is thanked for preparing the SEM micrographs presented herein and for proofreading and offering valuable suggestion resulting in improving the manuscript. Senior Scientific Assistant Stephen Thurston expertly arranged and labeled all plates.

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APPENDIX

POSTDEFECATING LARVA OF THE CLEPTOPARASITIC BEES *THALESTRIA SPINOSA*
(FABRICIUS) AND *TRIEPEOLUS KATHRYNAE* ROZEN (APIDAE: NOMADINAE: EPEOLINI)

The only known cleptoparasites that attack nests of the Oxaeinae are *Thalestria spinosa* (Fabricius) (= *T. smaragdina* Smith) hosted by *Oxaea flavescens* Klug and *O. austera* Gerstaecker and *Triepeolus kathrynae* Rozen, hosted by *Protoxaea gloriosa*. Both parasites belong to the Epeolini. The mature larva of *Thalestria spinosa* has not been fully described before, although its main morphological features based on specimens provided by Roberts were identified and interpreted in Rozen's (1996) phylogenetic analysis of the apid subfamily Nomadinae. These specimens of *T. spinosa* are illustrated and fully described below. The mature larva of *Triepeolus kathrynae* was extensively illustrated first by Rozen (1966: figs. 15–18) as *Triepeolus* species B and by Rozen (2001: figs. 7–13), but it too has not been verbally described until now. In the latter publication, both *T. kathrynae* and *T. spinosa* were differentiated in the key as representatives of their respective genera.

POSTDEFECATING LARVA OF *THALESTRIA SPINOSA* (FABRICIUS)

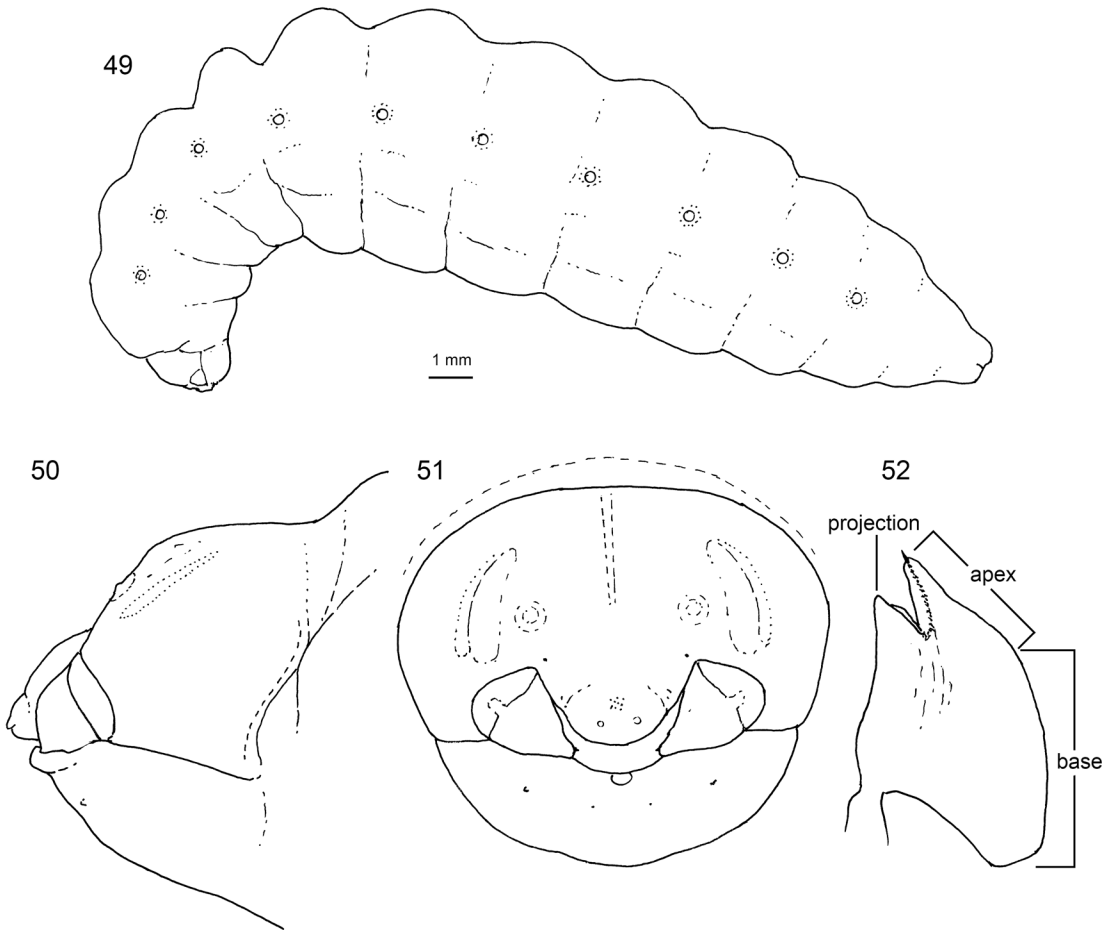
Figures 49–54

DIAGNOSIS: The postdefecating larva of *Thalestria spinosa* can be immediately differentiated from those of all known cleptoparasitic taxa on the basis of its very short mandible bearing an apically projecting tuberclelike structure from the adoral side of the base, which seems to run parallel to the mandibular apex in dorsal or ventral views (fig. 52). Another feature also serves well to distinguish this larva from that of its host: the simple pigmented circular atrial wall of its spiracle (fig. 54) combined with circular primary tracheal opening easily distinguishes it from that of its host with a more oval atrial wall and a distinctive linear primary tracheal opening (fig. 43).

DESCRIPTION: Length approximately 19–21 mm. **Head:** Moderately darkly pigmented, particularly noticeable on cleared head capsule, with inconspicuous sensilla; only hypopharyngeal surface spiculate.

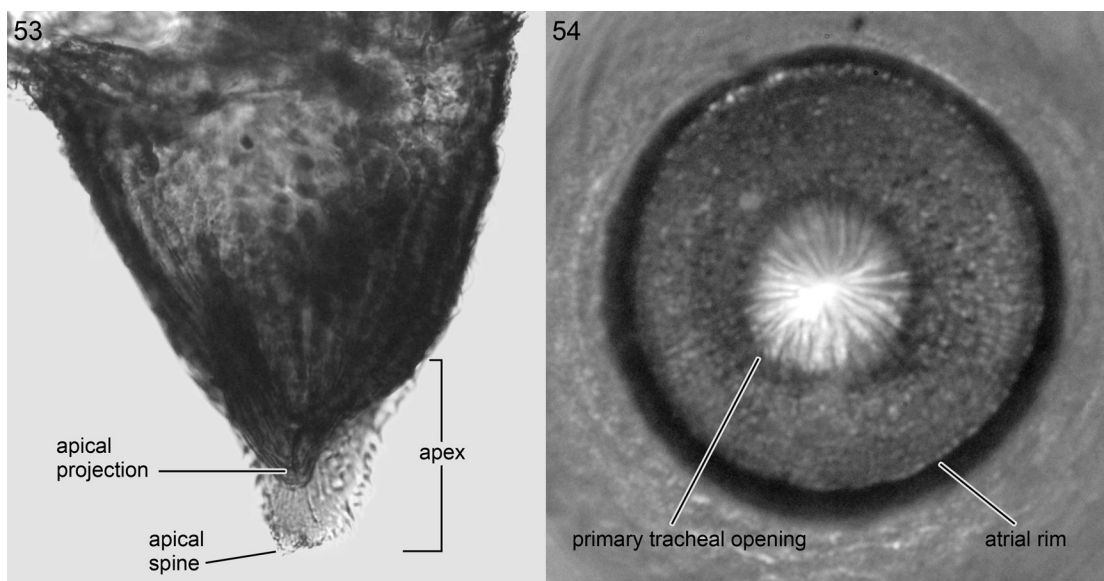
Head size small compared with elongate postcephalic region; head capsule broad in frontal view; head capsule in lateral profile gently curving to grade toward clypeus. Tentorium extremely thin; anterior tentorial pits inconspicuous, close to anterior mandibular articulation; posterior pits also inconspicuous at or close to confluence of hypostomal ridge and posterior thickening of head capsule which is weakly defined. Median longitudinal ridge of head capsule weakly expressed, fading below before reaching level of antennae. Hypostomal and pleurostomal ridges weak but quite evident because of dark pigmentation; epistomal ridge between anterior tentorial pits absent. Parietal bands conspicuous; surface immediately mesad of each but not extending to antenna, slightly elevated and uneven. Antennal prominence inconspicuous. Antennal disc indistinctly differential from papilla, which bears tight cluster of perhaps 6–7 sensilla. Clypeus broad basally in frontal view, narrowing apically to labrum; clypeus and labrum in lateral view projecting beyond frontal profile of head capsule. Labrum narrow relative to broad aspect of head in frontal view, bearing pair of small, rounded tubercles and median tight cluster of approximately 10 short setae basal to tubercles.

Mandible almost black, extremely short, resulting in head, frontal view (fig. 51), with mandibles widely separated; mandibular length close to basal width in outer or inner view (Rozen, 2001: fig. 74),



FIGURES 49–52. Diagram of postdefecating larva of *Thalestria spinosa*. **49.** Entire larva, lateral view. **50, 51.** Head, lateral and frontal views, respectively. **52.** Dorsal view of mandible showing apex and projection rising parallel to apex from adoral surface of base.

with sides of mandible converging to simple apex; in dorsal or ventral view, base of mandible massive; mandibular apex projecting as flattened, bladelike structure; in outer or inner view (fig. 52), dorsal and ventral apical edge of apex beset with numerous, fine, sharply pointed, curved teeth; in same view, dorsal edge nearly straight whereas ventral edge curving toward single apex, which bears single apical spine (fig. 53); adoral surface of mandibular base swollen with apical projection extending approximately parallel with mandibular apex in dorsal or ventral views (fig. 52); this projection simple with rounded apex (fig. 53; Rozen, 2001: fig. 74), with surface facing apex longitudinal sulcate; on mandibular closing, entire projection presumably assisting in directing food toward mouth by separating epipharyngeal and hypopharyngeal surfaces. Salivary opening darkly pigmented oval hole. Hypostomal groove poorly defined but hypostomal surface broad, strongly projecting well beyond labiomaxillary region below it and meeting apposed epipharyngeal surface of labrum. Entire labiomaxillary region a continuous globose surface except for hypostomal surface, with little differentiation of boundaries of maxillae and labium; maxillary palpi minute pigmented projections below (posterior to) base of mandibles; labial



FIGURES 53, 54. Microphotographs of postdefecating larva of *Thalestria spinosa*. **53.** Right mandible, adoral surface, showing thin but broad apex with fine sharp teeth on upper and lower margins and single larger apical projection. **54.** Spiracle on pigmented tubercle, showing pronounced circular primary tracheal opening and concentrically pointing atrial spines as well a circular shape of atrial rim.

palpus unpigmented, not projecting but faintly evident as pair of cuticular abrasions on labium slightly behind level of maxillary palpi in ventral view on cleared specimen.

Body (fig. 49): Integument without setae or spicules, very faintly wrinkled, lightly pigmented, except spiracular tubercles moderately darkly pigmented and atrial wall and primary atrial opening darkly pigmented. Body form elongate, slender, tapering evenly to narrow posterior apex, as seen laterally and in dorsal profile; segmentation clearly defined except abdominal segments 9 and 10 appearing nearly fused, tapering uniformly to apical surface bearing median transverse anus; dorsal intrasegmental lines defining separation cephalic and caudal annulets not expressed; dorsal tubercles absent although paired, sublateral dorsal apices of most segments faintly rugose, transverse, unpigmented bands. Spiracle (fig. 54) with moderately shallow atrium that projects beyond pigmented spiracular tubercle, with nearly circular rim and with narrow, unpigmented peritreme; inner surface of atrium densely covered with concentrically directed long spines; diameter of circular atrial rim almost twice that of primary tracheal opening; subatrium moderately long, consisting of about 10 chambers of approximately equal diameter; flexure collapsed.

MATERIAL STUDIED: Five postdefecating larvae: COLOMBIA: Meta: near Puerto Lopez, Hacienda Mozambique, December 1, 1971 (R.B. Roberts).

Postdefecating Larva of *Triepeolus kathrynae* Rozen

DIAGNOSIS: See Diagnosis of *T. spinosa*, above.

DESCRIPTION: (Figures: see Rozen, 2001: figs. 7–13.) Length approximately 12 mm. **Head:** As described for *T. spinosa*: except for following: condition of tentorium unknown. Median longitudinal ridge of head capsule scarcely expressed. Mandible dark brown, short but not as short as mandible of *T. spinosa*; mandible significantly different from that of *T. spinosa* in that mandibular apex (Rozen, 2001: figs. 9–11) fanglike, narrow, and tapering to single apical point rather than flattened; mandibular base

massive but lacking apically directed projection found in *T. spinosa*. Other mouthparts somewhat similar to those of *T. spinosa* except shape of maxillae and labium with somewhat more distinct boundary inflections; palpi slightly larger than those of *T. spinosa*; hypostomal surface continuous with anterior surface of labium, scarcely projecting beyond it so that lower hypostomal delineation vague (Rozen, 2001: fig.8).

Body: As described for *T. spinosa*; body size smaller.

MATERIAL STUDIED: one postdefecating larva: ARIZONA: Pima Co., 5 mi east of Sahuarita, IX-5-1989–VIII-7-1989 (J.G. Rozen and J.L. Foster) from cells of *Protoxaea gloriosa*: one postdefecating larva: NEW MEXICO: Hidalgo Co.: 1 mi N. Rodeo, no date (M.A. Cazier and M. Mortenson) nest of *Protoxaea gloriosa*).

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