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The Biology and Immature Stages of *Melitturga clavicornis* (Latreille) and of *Sphecodes albilabris* (Kirby) and the Recognition of the Oxaeidae at the Family Level (Hymenoptera, Apoidea)

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Michener (1944) divided the andrenid subfamily Panurginae into two tribes, the Panurgini and Melitturgini, with the latter containing the single Old World genus *Melitturga*. This genus was relegated to tribal status apparently on the grounds that the adults, unlike those of other panurgines, bear certain striking resemblances to the essentially Neotropical Oxaeinae of the same family. In 1951 Rozen showed that the male genitalia of *Melitturga* are unlike those of the Oxaeinae and are not only typical of those of the Panurginae in general but quite like those of the *Camptopoeum*-*Panurgus*-*Panurginus*-*Epimethea* complex within the subfamily. On the basis of this information, Michener (1954a) abandoned the idea that the genus *Melitturga* represents a distinct tribe of the Panurginae. Recently evidence in the form of the larva of *Protoxaea gloriosa* Fox (Rozen, 1965) suggested that the Oxaeinae were so unlike other Andrenidae that they should be removed from the family unless some form inter-

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mediate between the two subfamilies is found. In spite of the structure of the male genitalia, *Melitturga* is the only known possible intermediary. Consequently it was of considerable interest to investigate the biology and larva of *Melitturga clavicornis* (Latreille) to see if data could be uncovered that would elucidate the interrelationships of *Melitturga*, the other Panurginae, and the Oxaeinae. The results of this study are divided below into three parts. The first records the observations on the ethology and nesting activities of *Melitturga clavicornis*. The second provides taxonomic descriptions of the immature stages of *M. clavicornis* and its halictid cleptoparasite, *Sphecodes albilabris* (Kirby) [= *fuscipennis* (Germar)].¹ In the light of the first two parts, the third discusses the relationship of *Melitturga* with the other Panurginae and the Oxaeinae and re-evaluates the taxonomic status of the Oxaeinae.

This investigation was made possible because of the generous assistance and warm hospitality of Prof. J. de Beaumont, Lausanne, Switzerland, who not only led me to the nesting site of this species but joined me for several days in the field, when the observations for this paper were carried out.

BIOLOGY OF *MELITTURGA CLAVICORNIS* (LATREILLE)

The biology of this species has been treated by a number of workers in the past: Mocsary (1884), Friese (1891, 1922–1923), Malyshev (1925, 1935), and Bischoff (1952). Only the studies of Friese (1922–1923) and Malyshev (1925) attempt to be complete, and the latter alone stands as a reasonably well-rounded, accurate account. Ferton's (1920) informative paper presumably reports on *M. clavicornis* in Africa, but the species identification is questionable, as *clavicornis* may not occur there. The following description is given, both because new information is included which will be important for a comparison of *Melitturga* with other panurgines at a later date and because certain discrepancies between Malyshev's and Friese's works can be clarified.

DESCRIPTION OF HABITAT: The nesting site (fig. 1) of this species has been known to de Beaumont since 1930. It is on the nearly horizontal field of a public campground in the Rhone River valley just east of the small town of Sierre in the canton of Valais in Switzerland. The site is exposed to the sun for almost all of the day, and the small trees border-

¹ The adults of this large-sized species were identified by comparison with named specimens kindly lent by Prof. J. van der Vecht, Rijksmuseum van Natuurlijke Historie, Leiden, the Netherlands.



FIGS. 1-3. *Melitturga clavicornis* (Latreille). 1. Nesting area near Sierre, Switzerland. Burrows were found over most of the field. 2. Several burrows before excavation. 3. Partly excavated burrow penetrating the column of a filled scarab tunnel.

ing the field do not shadow the area. The field, which is well drained and approximately 200 feet square, is so sparsely covered with low grasses and clover several inches high that barren ground separates the clumps of plants. Although the soil is hard and compact on the surface, it is easily excavated, fine, and contains few stones. Numerous other Hymenoptera were encountered nesting in the field, the most common one being the bee wolf, *Philanthus triangulum* (Fabricius) (Sphecidae). The following observations were made on July 3 and 5, 1964.

MATING BEHAVIOR: Although no actual copulations were noticed, the behavior reported here is obviously associated with mating. On the first day, which was warm and clear, males were first seen around 9 A.M., were common by 10:30, and then had decreased in abundance by 4:00 P.M., with one or two visible on the field by 4:45. During the heat of the day numerous males could be seen hovering slowly at nearly ground level to 15 feet or more in the air. Their slow flight was suggestive of that of a syrphid fly. Suddenly a male darted extremely rapidly up, down, or horizontally, apparently toward a female. Occasionally a group of males (up to seven or eight individuals) converged and rapidly pursued a female. Often one or more males followed a female loaded with pollen as she approached her nest. In an apparent attempt to avoid an encounter, she dashed off and then in a short time returned to the area after she had presumably outdistanced her entourage. Premating behavior high in the air has not been observed in other panurgine bees. Because no individuals *in copulo* were seen, we can probably assume that copulation is brief.

NESTING ACTIVITY: Burrow openings were found scattered over a wide area of the field and were situated either in the barren stretches between the clumps of low vegetation (fig. 2), at the edges of the clumps, or actually in such clumps. Ordinarily there is but a single female to a nest, though one nest with two main tunnels that met near the surface had a female in each branch.¹ Always open, the entrances of active burrows are usually without tumuli (fig. 2) though occasionally a tumulus was found either on one side of an opening or surrounding it. Malyshev (1925) always found the entrances without tumuli.

The main burrow descends in a somewhat meandering fashion, in contrast to the drawings and description by Friese (1922–1923). Circular in cross section and with a diameter of from 7 to 8 mm. (in close agreement with the figures given by Malyshev, 1925), the main tunnel is without a built-in hard wall, and I saw no indication that saliva had been applied to it, as reported by Friese. Often, though apparently not always, the soil surrounding the tunnel is soft though otherwise of the same appearance and texture as the surrounding substrate. It is sufficiently consolidated that the surrounding earth can be chipped away, leaving it intact as a cylindrical column (fig. 3), perhaps 12 to 18 mm. in diameter. The column is penetrated either in the center or on the side by

¹ Dr. William P. Stephen (*in litt.*), who studied the same nest site shortly after my visit, concluded that "most of these nests [nine examined] had a distinctly branched main burrow with the females each occupying one half."

the descending burrow and is apparently the filled exit burrow of a scarab, for several cast larval skins of the beetle were taken at the bottoms of the columns. Whether the *Melitturga* fills in the old tunnel or merely avails itself of the softer soil of the already filled tunnel was not determined.

Malyshev (1925) apparently found somewhat the same phenomenon, though he interpreted it differently. He stated that the walls of the main burrow (but not of the side tunnels) were always covered with a thin layer of sand. "This seems to indicate that the bee does not throw out the rubbish, but even takes the necessary material from the surface near the opening. The soil here [Gotnya, Russia] is coarse-grained, black

TABLE 1
DIMENSIONS OF POLLEN MASSES AND CELLS OF
Melitturga clavicornis (LATREILLE)

	Number of Samples	Average	Range
Cell length	8	17.0 mm. ^a	15.0–18.0 mm. ^a
Cell diameter	9	10.0 mm. ^a	9.0–10.0 mm. ^a
Cell depth	10	10.5 cm. ^b	7.0–16.0 cm. ^b
Shortest diameter of pollen mass	3	5.5 mm. ^a	5.0– 6.0 mm. ^a
Longest diameter of pollen mass	3	7.5 mm. ^a	6.5– 8.5 mm. ^a

^a To the nearest half millimeter.

^b To the nearest half centimeter.

earth covered with a thin layer of sand." This passage suggests that the "thin layer of sand" may be the same as the soft fill of the scarab burrow. It further suggests that the fill comes from the surface and not from the excavations of the side tunnel. A full understanding of this situation should develop as soon as observations are made when nest construction first begins.

The bee burrow is usually open, though one was found late in the afternoon with a septum of soil below which was the female. On the morning of the second day, which was cloudy and cool, burrows were occasionally encountered that were filled with very soft soil below the open entrances. This fill was softer than the core of the scarab burrow. Unlike Ferton (1920), I saw no indication that burrows were plugged

with soil as the female departs. The side tunnel connecting the cell to the main burrow is always filled with soil after the cell is provisioned and closed. This tunnel, which in a few cases measured 1.5 to 4.5 cm. in length¹ (contrary to the extremely short tunnels reported by Friese, 1922–1923, fig. 53, pl. 5) and 6.0 mm. in diameter, was unlined and was not found in the filled scarab burrow (as also reported by Malyshev, 1925).

All cells, the shape of which is depicted in figure 4, are arranged singly and are usually inclined at about 20 degrees from the horizontal, with the open end always being the higher. Only one cell dipped about 45 degrees, whereas Friese (1922–1923, fig. 53, pl. 5) showed all cells to be inclined at least this much. Malyshev (1925) claimed that the slope was 45 degrees “or even less” and Ferton (1920) stated that the cells are horizontal. The cell wall is several millimeters thick (as indicated by Malyshev and not as thick as depicted by Friese) and harder than the surrounding soil and is not “built-in.” It has an inner smooth surface that is coated with a visible waterproof lining, as stated by Friese and Malyshev. The closure is a spiral and has been carefully described by Malyshev; I did not have time to confirm his observations.

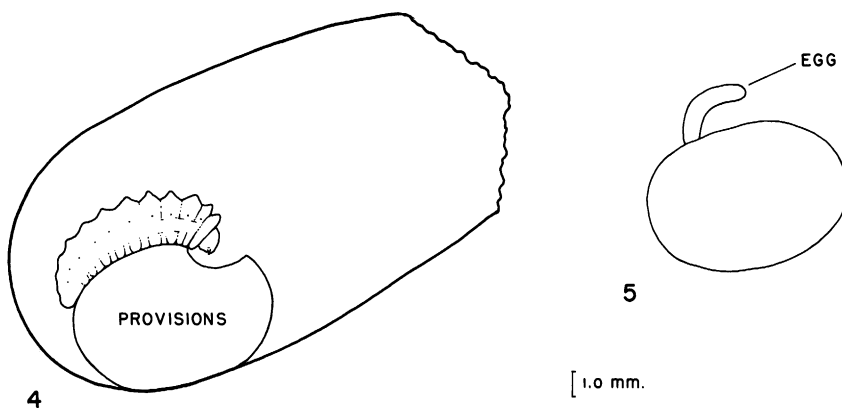
Table 1 gives the dimensions of the nests and the pollen masses of this species. The cell size is slightly larger than that (length, 15–16 mm.; diameter, 8 mm.) given by Malyshev (1925). In general, the nest configuration seems to be rather similar to that of *Nomadopsis anthidia* (Fowler) (Rozen, 1958, fig. 63) and to that of *Melitturga “clavicornis”* as described by Ferton (1920). It does not, therefore, resemble closely the nest plan drawn by Friese (1922–1923).

The female transports the pollen in a moistened condition and does not shape it into a spheroid form in the cell until she has gathered the entire provisions for the cell. The bracelet of pollen shown by Friese (1922–1923, pl. 5) is characteristic of many of the Panurginae. Cells with incomplete provisions contain adhering masses of the moist pollen on the floor toward the posterior end of the chamber. The completed mass takes the shape of a flattened sphere (figs. 4, 5), not a complete sphere as indicated by Ferton (1920), which is moist but firm, homogeneous throughout, and without a coating of any sort. The sphere rests toward, but does not touch, the posterior part of the cell. Its under surface often seemed somewhat moist, as if a droplet of nectar had been placed there by the female. The egg is attached by its posterior end to the top of the pollen mass (fig. 5; and Malyshev, 1925, fig. 1; it is not so far for-

¹ Stephen (*in litt.*) states that some laterals were as long as 7.5 mm.

ward as shown by Friese, 1922–1923, pl. 5). It rises into the lumen of the cell and has its anterior end closest to the closure. Curved, whitish, and without reticulations on the chorion, the egg is approximately 3.0 mm. long and 0.65 mm. thick.

The few young larvae encountered faced the cell closure. As with other panurgine bees, they did not move about on the pollen mass but ate the food beneath their heads (fig. 4). Mature or nearly mature larvae were found resting on their dorsa, so that we can probably assume that the larvae re-orient during the active period of eating as do those of *Nomadopsis* (Rozen, 1958) and many other Panurginae. In any event, the one



FIGS. 4–5. *Melitturga clavicornis* (Latreille). 4. Cell containing spheroid provisions and young larva. 5. Provisions and egg.

nearly mature larva encountered held the pollen on the middle of its venter, as do those of most North American Panurginae, and did not take the position shown by Friese (1922–1923, pl. 5). However, Ferton (1920) believed that the pollen sphere is consumed in a different fashion.

The larvae defecated a few days after finishing the provisions and then entered a quiescent stage. It would seem, therefore, that *Melitturga clavicornis* overwinters as a mature, postdefecating larva and that it has a single generation a year. As Friese stated, and my observations confirm, this bee does not spin a cocoon.

PARASITES AND PREDATORS: Time did not permit a careful survey of the parasites and predators of this species. *Ammobatoides abdominalis* (Eversmann), a nomadine bee, has been recorded in the literature as a cleptoparasite of *Melitturga clavicornis*, but it was not encountered at this site nor does it occur in Switzerland according to de Beaumont. Several

times a large female of the halictid *Sphecodes albilabris* (Kirby) was noted entering *Melitturga* burrows, and once it remained there for eight minutes. Two mature larvae of this halictid were recovered from another nest on July 5; one pupated on July 7 and emerged as an adult on July 25. This species, like other halictines, does not spin a cocoon. Its larva and pupa are described below. All the adult *Sphecodes albilabris* collected at the nesting site were extremely worn in contrast to the adults of *Melitturga*, which were usually in a fresh condition. The fact that the *Sphecodes* larva pupated soon after capture whereas the *Melitturga* larvae entered the hibernating stage suggests that the seasonal cycles of the two species are dissimilar. Although the bee wolf was nesting throughout the field, it was never seen transporting *Melitturga* to its nest.

The females of *Melitturga* emit the oil-of-lemon odor so commonly encountered among the Panurginae and other bees when they are rolled between the fingers.

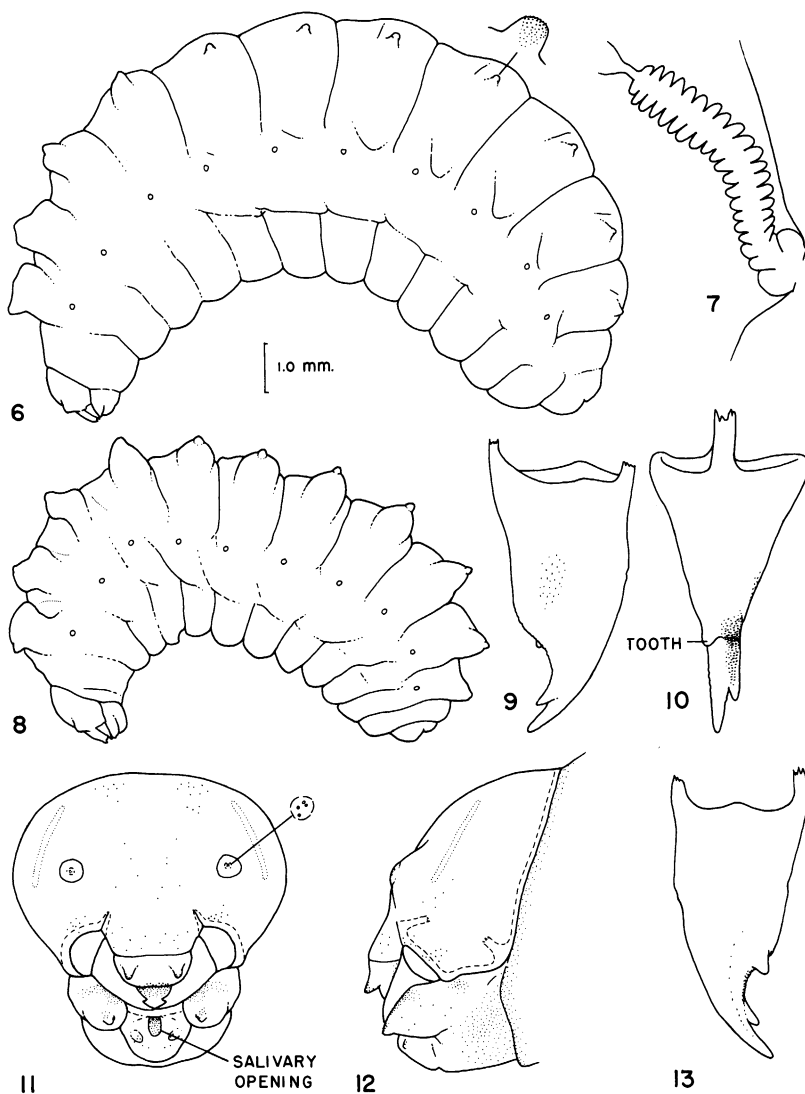
IMMATURE STAGES OF *MELITTURGA CLAVICORNIS* (LATREILLE) AND *SPHECODES ALBILABRIS* (KIRBY)

MATURE LARVA OF *Melitturga clavicornis* (LATREILLE)

Figures 6-13

The following description is comparative with a forthcoming treatment by me of the larvae of a number of genera of North American Panurginae. The larva of this species, unlike that of any other member of this subfamily, possesses a large tooth near the mandibular cusp.

HEAD (FIGS. 11, 12): Integument with scattered sensilla; head capsule very faintly pigmented except parietal bands, palpi, and lateral arms of epistomal ridges more darkly pigmented; vertex moderately produced on each side above antennae, less so than in *Pseudopanurgus* but more so than in *Perdita*; antenna arising from moderately produced prominence. Tentorium complete and well developed; as in all Panurginae, each posterior tentorial pit situated at juncture of hypostomal ridge and posterior thickening of head capsule; posterior thickening of head capsule moderately well developed; hypostomal and pleurostomal ridges well developed; epistomal ridge and sulcus well developed laterad of anterior tentorial pits but absent mesiad of pits; parietal band well developed. Antennae low convexities, each bearing four sensilla. Labrum not cleft apically, bearing two prominent tubercles. Mandibles (figs. 9, 10, 13) slender in adoral view; dorsal surface with scattered, sharp-pointed spicules; upper inner edge with conspicuous subapical tooth as in *Pseudopan-*



FIGS. 6-13. Mature larva of *Melitturga clavicornis* (Latreille). 6. Freshly killed predefecating larva, lateral view. 7. Spiracle. 8. Live postdefecating larva, lateral view. 9. Left mandible, dorsal view. 10. Same, adoral view. 11. Head, frontal view. 12. Same, lateral view. 13. Left mandible, ventral view.

Scale refers to figures 6 and 8.

urgus; lower inner edge defined apically by inconspicuous teeth; apical concavity with band of very fine, rounded teeth (fig. 10) extending basad of subapical tooth and, unlike mandible of other Panurginae, with large tooth in middle near cusp. Hypopharynx spiculate. Maxillae large, projecting beyond labium; each palpus large, spiculate dorsally; integument spiculate dorsally. Labium perhaps inconspicuously divided into prementum and postmentum; posterior part of labium densely spiculate laterally; labial palpi much smaller than maxillary palpi; salivary opening a curved slit surrounding densely but very finely spiculated region.

BODY: Form robust (figs. 6, 8). Integument of postdefecating form yellowish and rigid, that of predefecating and postdefecating forms densely spiculate in many areas. Dorsal tubercles (figs. 6, 8) faintly pigmented apically, with those of thoracic region being similar in shape to, but more pronounced than, those of *Pseudopanurgus*; abdominal segments II to VII with tubercles conical (that is, not transverse), rather small on predefecating form (fig. 6) but large on postdefecating form (fig. 8); each tubercle beset with pigmented spicules apically; terminal segment without median tubercle. Spiracles (fig. 7) moderately small, situated on unsclerotized projections of body wall; atrium projecting very slightly above body wall; atrial wall without teeth; peritreme thin; primary tracheal opening with collar.

MATERIAL STUDIED: Three mature larvae, Sierre, Valais, Switzerland, July 5, 1964, J. G. Rozen, Jr. These specimens, together with younger forms, are in the collection of the American Museum of Natural History.

MATURE LARVA OF *Sphecodes albilabris* (KIRBY)

Figures 14-22

Because the following treatment is based on a single specimen that was about to pupate, some of the characters cannot be described with certainty.

HEAD (FIGS. 15, 16): Integument with scattered sensilla; head capsule not pigmented; vertex strongly produced above and mesiad of each antenna; antennae arising from well-developed prominences. Tentorium incomplete in this specimen, though perhaps present in specimens that are not about to pupate; each posterior tentorial pit situated at juncture of hypostomal ridge and posterior thickening of head capsule; posterior thickening of head capsule moderately developed; hypostomal and possibly pleurostomal ridges moderately thin, perhaps owing to fact that specimen was about to pupate; epistomal ridge well developed laterad of

anterior tentorial pits but not evident mesiad of them; coronal thickening absent; parietal bands well developed. Antennae large, low convexities,¹ one with three, the other with four, sensilla. Labrum bearing at most indistinct, paired tubercles. Mandibles (figs. 17–19) slender in adoral view and, unlike those of most halictids, with single apical tooth; upper and lower inner edges serrate; cusp only moderately developed and multi-dentate; dorsal surface with spicules. Hypopharynx spiculate, projecting beyond labium (as seen in lateral view), and separated from labial region by deep groove. Maxillae short, not projecting as far as labium and hypopharynx and with apices not bent mesiad; integument spiculate dorsally; palpi apparently obsolete.¹ Labium with prementum and postmentum not clearly separated, at least in this specimen; salivary opening situated well below labio-hypopharyngeal groove; opening a small crescent in this specimen; palpi apparently obsolete.¹

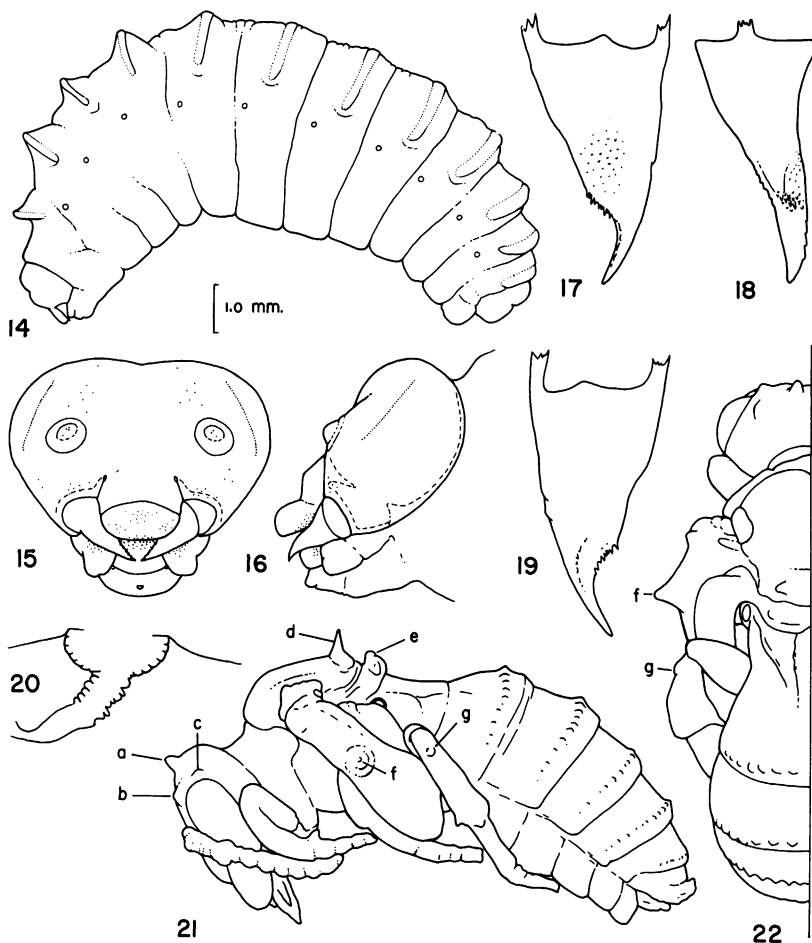
BODY: Integument rather soft, spiculate in various areas but without setae. Pronounced paired dorsal tubercles (fig. 14) present on most segments; these tubercles transverse, nearly meeting dorsally, extending nearly to level of spiracles, and with integument on apexes apparently more rigid than that of rest of body; ninth abdominal segment somewhat protuberant ventrally; terminal segment unmodified and with anus situated apically. Spiracles (fig. 20) with atrium projecting slightly above body wall; inner surface of atrium with rows of spines; peritreme flat and narrow; primary tracheal opening apparently without collar; subatrium rather short, possibly because specimen was nearing pupation.

MATERIAL STUDIED: Two mature larvae (one of which was allowed to reach adulthood), Sierre, Valais, Switzerland, July 5, 1964, from nest of *Melitturga clavicornis*, J. G. Rozen, Jr. One larva and the adult that developed from the second larva are in the collection of the American Museum of Natural History.

As can be seen from the above description and from the illustrations, the mature larva of *Sphecodes albilabris* agrees in most details with the larvae of the halictines treated by Michener (1953). It apparently can be distinguished from them on the basis of its mandible which has a simple apex but which lacks the slender projecting cusp of *Augochlora* (*Augochlora*) *pura* (Say).

Although larval *Sphecodes* have not been described before, Michener

¹ Contrary to Michener's (1953) interpretation of the antennae of halictids, I believe that the antennal papillae of this species and probably of the others are very large in diameter though low. There is a slight suggestion that the palpi are also very large, but, because they are so low, they are difficult to detect.



FIGS. 14-22. Immature stages of *Sphecodes albilabris* (Kirby). 14. Live postdefecating larva, lateral view. 15. Head of larva, frontal view. 16. Same, lateral view. 17-19. Left mandible of larva, dorsal, adoral, and ventral views. 20. Spiracle of larva. 21, 22. Live pupa, lateral and dorsal views.

Scale refers to figures 14, 21, and 22.

(1953) described a specimen supposedly of *Holcopasites* (as *Neopasites*) from a nest of *Calliopsis andreniformis* Smith. It does not agree at all with larvae of several species of *Holcopasites* that have recently been collected. Because this specimen has many characteristics of a halictid, it may be a *Sphecodes*.

PUPA OF *Sphecodes albilabris* (KIRBY)

Figures 21-22

The illustrations and description were made from a series of photographic slides of a single live female pupa. The following description is comparable to that of pupal halictids presented by Michener (1954b).

HEAD: Vertex with pair of pronounced protuberances (a) in position of lateral ocelli, with pair of lower protuberances (b) in front of upper ends of eyes, and with pair of very low protuberances (c) just above eyes; antenna with, at most, inconspicuous protuberances.

MESOSOMA: Mesoscutellum (fig. 21) with pair of high, pointed tubercles (d); metanotum with pair of low transverse protuberances (e); tegulae somewhat protuberant; each front wing with large protuberance (f) near middle and perhaps with inconspicuous one at base; spines of coxae, trochanters, and femora not studied; base of each hind tibia with low tubercle (g).

METASOMA: Terga with subapical tubercles.

The characters enumerated above, though incomplete, indicate the close relationship between *Sphecodes* and the other members of the Halictidae. The large tubercle near the middle of the front wing may be a diagnostic feature of the family.

COMPARISON OF *MELITTURGA* WITH THE PANURGINAE
AND THE OXAEINAE

The mature larva of *Melitturga clavicornis* agrees in almost all respects with larvae of the other Panurginae and possesses no characters that are oxaeine-like as opposed to panurgine-like, nor does it exhibit features that could be construed as intermediate between those of the two subfamilies.

Not only is the larva of *Melitturga* that of a typical panurgine, but it seems to be most similar to that of *Pseudopanurgus*. These two taxa agree in the pronounced and peculiarly shaped, anterior, dorsal body tubercles, which are most accentuated in *Melitturga*. Both also have a subapical dorsal tooth on the mandible and large, dorsally spiculate, maxillary palpi. These similarities would seem to contradict the groupings of panurgine genera based on the genitalia of the males (Rozen, 1951), for one would predict on the basis of the genitalia of the males that *Melitturga* larvae should be more similar to those of *Panurginus*. This apparent discrepancy emphasizes the fact that the interrelationships of the Panurginae need further study and refinement.

TABLE 2
COMPARISON OF THE PANURGINAE AND OXAEINAE BASED ON THE MATURE LARVA

Panurginae	Oxaeinae
Pigmentation moderately light to light	Pigmentation dark
Posterior tentorial pit at juncture of posterior thickening of head capsule and hypostomal ridge	Posterior tentorial pit below this juncture
Epistomal ridge absent, or nearly so, between anterior tentorial pits	Epistomal ridge well developed between anterior pits
Vertex moderately to strongly protuberant above antennae (except in <i>Perdita</i> ; see Rozen, 1965)	Vertex non-protuberant
Antenna on moderate to pronounced prominence (except in <i>Perdita</i> ; see Rozen, 1965)	Antenna not on prominence
Antennal papilla with three to four sensilla	Antennal papilla with numerous sensilla
Labrum not cleft apically	Labrum deeply cleft
Mandible not bladelike at apex and not abnormally wide at base	Mandible bladelike at apex and very wide at base when viewed adorally
Body tubercles prominent and conical	Body tubercles faint and transverse
Spiracles not on sclerotic plates, without spines, and with primary tracheal opening circular	Spiracles on sclerotic plates, with atrial spines, and with primary tracheal opening slitlike

The two columns in table 2, when compared, demonstrate the main contrasting features of the larvae of the two subfamilies. The first column is derived from the above description of *M. clavicornis* and a forthcoming paper reporting on the larvae of five diverse genera of North American panurgines that represent four of the five panurgine groups defined on the basis of the genitalia of the males (Rozen, 1951). The second column summarizes pertinent data presented in a recent study of the larva of *Protoxaea gloriosa* (Rozen, 1965). Because the Oxaeinae are a small and, as adults, homogeneous group, it is doubtful that the larvae of other oxaeines will be different from this species. Consequently table 2 probably can be considered a fairly stable indication of the marked distinctness of the larvae of the two groups.

A full comparison of the biology of *Melitturga clavicornis* with that of the other panurgines and that of the oxaeines is not possible as yet, because the necessary information is still fragmentary. In nest construction, provisioning, and egg deposition *Melitturga* agrees with the other Panurginae, as will be made evident in a forthcoming paper treating the biology of some of the North American Panurginae. The only unique feature of

Melitturga is the use of a scarab burrow for the main tunnel. With the exception of several papers (discussed below) on the mating habits of *Protoxaea gloriosa* and one (Linsley and Michener, 1962) briefly describing the nest of *P. nigerrima* (Friese), nothing has been written on the biology of the Oxaeinae. Cazier and Linsley are currently studying various aspects of the ethology of *P. gloriosa*; when published, the report should provide a means for comparing the biology of the two subfamilies.

TAXONOMIC AND PHYLOGENETIC CONSIDERATIONS

The Oxaeinae were regarded by Michener (1944) as a subfamily of the Andrenidae, primarily because of the presence of two pairs of sub-antennal sutures in the adults. He indicated, however, that, because of the distinctness of the subfamily, it was "a matter of choice whether one wishes to regard the Oxaeinae as a distinct family or not." Another seemingly cogent reason for including the oxaeines with the andrenids was the existence of the supposedly annectent form, *Melitturga*. As an adult, *M. clavicornis* and presumably the other members of the genus possess the following oxaeine-like features: body size large (though not so large as that of the Oxaeinae); compound eyes of male large and strongly converging above; ocelli, especially those of male, low on face; first flagellar segment as long as scape; other antennal segments short; thorax robust and in male with dense pile; wings strongly papillate.

However, the Oxaeinae differ from all the Panurginae, including *Melitturga*, on the basis of numerous characters. The features of the larvae and the genitalia have already been mentioned. Michener (1944) gave the following significant characteristics of adult oxaeines: apex of posterior femur of female enlarged and forming a plate; scopa abundant from coxa to basitarsus; pterostigma absent; and marginal cell narrow and elongate. To these should be added: clypeus strongly protuberant; labrum as long as, or longer than, broad; and mentum and submentum fused into a single plate.

It is important to point out that the Oxaeinae differ from the Andreninae on the basis of all the characters indicated above except that the andrenine larvae lack conical tubercles (though the transverse ones on the anterior end of the body are more pronounced than those of the Oxaeinae). Also females of the Andreninae have the scopa distributed from the coxa to the basitarsus, as in the Oxaeinae. However, both of these characters are almost certainly plesiomorphic, for they are found in the Colletidae and are thus not significant for a judgment of phylogenetic relationships.

In summary, the Oxaeinae possess numerous adult and larval charac-

ters that indicate that this subfamily is not at all similar to other Andrenidae nor do these features suggest that the two groups recently evolved from a common ancestor. One must conclude then that the similarities between the two are either homoplastic (probably convergent) or represent primitive (plesiomorphic) features that were found in the remote common ancestor of the two groups, or both. On close scrutiny, the similarities of the Oxaeinae and *Melitturga* may indeed be analogous rather than homologous. Although certainly striking, many of these characters seem to be referable to a single functional trait, namely, the premating and perhaps mating behavior of the males. Linsley and Michener (1962) and Cazier and Linsley (1963) have commented that male *Protoxaea gloriosa* "hover like flies . . . periodically darting aggressively outward and upward," a description that closely parallels Malyshev's and mine for *Melitturga clavicornis*. The enlarged converging eyes of the male are perhaps special adaptations for seeing the female as she flies by. The ocelli tend to be crowded just above the antennae, as a compensation for the enlarged compound eyes. The robust appearance of the thorax may be important for the musculature that permits the hovering flight. Although the adaptive significance of these structural modifications cannot as yet be proved, the suggestion is strong that the supposedly annectant *Melitturga* is not truly an intermediary but apparently owes most of its similarities with the oxaeines to evolutionary convergence of one behavior character with correlated morphological modifications.

Although the presence of four subantennal sutures in the adults was considered to be of much taxonomic importance earlier, this character seems to bear less significance now for several reasons. First, Michener (1944) has pointed out that some colletids of the subfamily Stenotritinae have two subantennal sutures immediately beneath each antenna. These sutures converge and fuse before reaching the clypeus, and as a result triangular subantennal areas are defined. Second, not all panurgines have two pairs of subantennal sutures. Males of several species of *Pseudo-panurgus*, such as *nanulus* Timberlake and *nebrascensis* (Crawford), exhibit only a single suture on each side. Lastly, even though there is only a single external suture on each side in many bees, an internal ridge represents the missing suture.

Because of the distinctness of the Oxaeinae and because of the lack of evidence indicating that they are recently related to the other Andrenidae, they are here assigned family status—the Oxaeidae. The main characteristics of the adults of this family are presented above. As pointed out by Michener (1944), this is a small, mostly Neotropical group consisting of only two genera, *Oxaea* and *Protoxaea*. Although it probably di-

verged early from the evolutionary lines that gave rise to the higher bees, its relationship with the other families can be ascertained only after other primitive derivatives are given further study.

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