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Biology and Immature Stages of the Aberrant Bee Genus *Meliturgula* (Hymenoptera, Andrenidae)

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The Panurginae are diversified, having undergone extensive and probably rapid evolutionary radiation in various parts of the world. This evolution has resulted in numerous extant genera. I tentatively assigned the main ones to groups, on the basis of a preliminary study of the male genitalia (Rozen, 1951). Since 1951, I have investigated the biology and immature stages of representatives of most of these groups, in an attempt to elucidate the phylogenetic relationships within the subfamily. The only group of which the biology and immature stages have not been studied contains the single African genus *Meliturgula*, in some respects the most aberrant panurgine of all. The present paper records details of the life history and descriptions of the egg, larvae, and pupa of a member of that genus, *Meliturgula braunsi* Friese. Heretofore, only Brauns (1913) has made observations on the biology of the genus; his account, also of *M. braunsi*, contributed several significant facts that are discussed below in appropriate places.

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FIG. 1. Nesting site of *Meliturgula braunsi* Friese, 17 miles northwest of Grahamstown, Republic of South Africa. The burrow entrances were near the figures. The pollen plant grew abundantly in the semi-barren areas on each side of the road.

BIOLOGY

DESCRIPTION OF NESTING AREA: The nesting site was on the shoulder of a dirt roadway 17 miles northwest of Grahamstown, Cape Province, Republic of South Africa (fig. 1). Discovered on November 21, 1966, it was studied over a five-day period. Only three nests were found, within $1\frac{1}{2}$ feet of one another, on a slightly sloping, well-drained area. Brauns (1913) observed colonies on flat, hard ground, presumably near Willowmore. Although the road near Grahamstown was moderately traveled, the shoulder was not disturbed by vehicles. The surrounding vegetation consisted primarily of low shrubs and herbs, and the few tall bushes did not shade the nest entrances. The pollen source was an aizoaceous plant, *Ruschia uncinata* (Linnaeus) L. Bolus,¹ which grew abundantly over a wide area on both sides of the road. The surface soil consisted of 3.5 to 4.0 cm. of loose, dry earth, with numerous stones and small pebbles.

¹ Kindly identified by Mrs. A. Jacot-Guillarmod.

Below, the soil was moist and hard-packed, with few stones. Although easily excavated near the surface, it was much harder farther down and appeared to consist primarily of decomposed rock. Excavation with a knife was quite difficult at the lower levels.

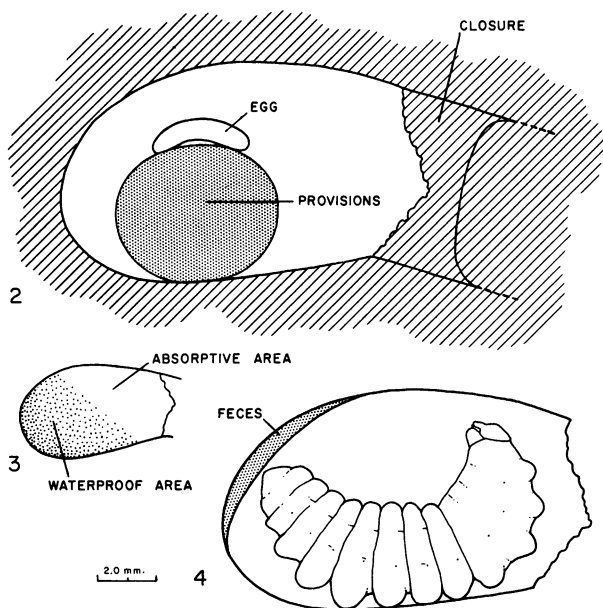
NESTING ACTIVITY: As Brauns (1913) pointed out, *Meliturgula braunsi* is a colonial bee. I found that one nest was occupied by at least two females, another by at least three males (all fresh and presumably just emerged) and 36 females, and the third by perhaps one female. The nests were "composite" (Malyshev, 1935), and there was no indication of division of labor among the females. The entrances were not "hidden" near prominent objects on the ground or surrounded by tumuli or by turrets. When first discovered at 2 P.M., they were open, but at 10:15 the next morning all were closed with soil, though they were again opened before noon, at which time the adults were entering and departing. The closing in the night may be a protective action against the entering of the nest by parasites and predators.

As with most of the panurgines, the main burrow, approximately 6.0 mm. in diameter, meandered downward. In the largest nest the main tunnel branched at a number of places, and each branch, also about 6.0 mm. in diameter, descended in a winding fashion. In some places the wall appeared to be coated with a thin layer of material, probably soil excavated from below. The wall was dull, non-waterproof, and did not possess any other sort of special lining. One branch descended 56 cm., and the female was still digging at the bottom. Probably other branches of this nest descended considerably farther in view of the fact that few recently completed cells were found in the area excavated compared with the numerous females provisioning the nest.

Only three open laterals, circular in cross section and of the same diameter as the main burrow, were discovered in the largest nest. They extended from the main branches in a meandering fashion and rose 1.0–2.5 cm. before widening into newly excavated empty cells. Two laterals were 6.0 cm. long and the other lateral was 10.0 cm., but some closed cells with filled laterals were found as close as 5.0 cm. from branches and others seemed removed as far as 20.0 cm. from known branches. However, because laterals and perhaps even main branches were filled with soil after the cells were closed, they could not be followed easily.

The cells ranged in depth from 7.0 to 40.0 cm. below the loose layer of surface soil, and, as indicated above, they undoubtedly occurred at greater depths. Cells seemed to be found both singly and clustered by twos or threes, at the end of laterals. There was no indication that

newer cells were at lower depths, whereas older cells were closer to the surface. Young larvae as well as pupae seemed randomly dispersed at all levels. Horizontal or tipping to the rear at most 10 degrees from the horizontal, each cell (fig. 2) was bilaterally symmetrical, the floor being slightly flatter than the roof. In spite of the variation in the size



FIGS. 2-4. Cells of *Meliturgula braunsi* Friese. 2. Freshly provisioned cell, side view. 3. Diagram of cell, side view, showing waterproof and absorptive areas on cell wall. 4. Cell with postdefecating larva, lateral view, showing feces. Scale refers to figures 2 and 4.

of the provisions, the cells were apparently nearly uniform in size—12.0 to 13.0 mm. long and 7.0 to 7.5 mm. at the maximum diameter. The cell wall was exceptionally thick (approximately 2.0 mm.) and rigid for that of a panurgine bee. It was apparently not “built in” but was produced by the adult’s impregnating the cell surface with some liquid. This impregnated layer readily absorbed water. The inner surface of the wall was coated with a thin, shiny, transparent, silklike substance that could be peeled off in strips from a fresh cell. This coating was waterproof and apparently varied in thickness; a droplet of water placed on the floor of the cell to the rear was not absorbed, whereas a droplet placed near the closure was absorbed quite readily. The rate of absorp-

tion in various places in a cell indicated that the rear of the cell and the floor about two-thirds of the way forward were the most waterproof, whereas the anterior two-thirds of the ceiling was quite absorbent to water (fig. 3). This variable absorption rate held for all cells tested (four or five) and should be checked with that of other panurgines.

The cell closure was a tight spiral, concave on the inside, and composed of about six or seven ridges to the radius. The outer surface of the closure was specially worked, being smooth and concave. The inner face absorbed droplets readily, but the outside was somewhat more waterproof. The thickness of the closure at the periphery was 3.0 mm. in one case and at the center, 1.25 mm.; other closures measured about the same. This instance is the first known in the Panurginae of a specially worked outer surface of the cell closure, a feature that now should be rechecked in other members of the subfamily.

PROVISIONING: The female of *Meliturgula* transported pollen as a very large moist mass attached to the anterior surface of each hind tibia. Completed provisions in cells were dull orange, homogeneously moist, and moderately hard. They were not coated with a waterproof material, as is the case with *Calliopsis* and *Nomadopsis*, nor were they covered with a thick, very moist layer of pollen as with some species of *Pseudopanurgus*. The provisions varied in shape and size from being almost spherical and small to being large and flattened. However, most of the pollen masses were large and decidedly flattened, so that their vertical diameter was 4.5 to 4.75 mm. and their horizontal diameter, 5.5 mm. (measured as in Rozen, 1967, fig. 5). The smallest had a vertical diameter of 3.3 mm. and a horizontal diameter of 3.8 mm. The small provisions probably account, in part, for the very small body size of some adult males, though, as discussed in the section on Sexual Dimorphism of Adults and Larvae, other factors may also influence the size of the males.

All the small food masses had eggs or larvae on top, a fact indicating that they were not shaped, incomplete provisions such as are found in *Calliopsis* and *Nomadopsis*. The provisions were placed toward the rear of the cell, though they did not touch the rear wall and did not change in consistency before being consumed. Two of the large-sized provisions were 1.5 and 1.75 mm. from the rearmost point in the cell.

OVIPOSITION: The eggs were placed on top of the provisions, perhaps slightly forward of center. The blunt anterior end of the egg was closest to the cell closure and in one case rose in the cell, and, in the second, touched the food mass as did the slightly more pointed rear end. The egg was curved, translucent white, and shiny. One measured 3.0 mm.

long and 0.75 mm. wide at the widest point (measured as in Rozen, 1967, fig. 5).

DEVELOPMENT: After hatching, the first instar occupies the same position as that of the egg on the pollen mass, presumably because the larva cannot crawl. At first the young larva eats the pollen beneath its head, but, when partly grown, it reorients, so that it rests on its dorsum and its head is closest to the rear of the cell.¹ The remainder of the pollen mass, cradled on the venter, is consumed. The larva, still on its back, then repositions itself in a manner similar to that of other members of the Panurginae (Rozen, 1967), so that its head is closest to the cell closure. Shortly thereafter, the larva defecates, applying the feces as a smooth patch flush with the rear upper end of the cell. The meconial mass, about 6 mm. long, reaches at its lowest point the rear-most part of the cell (fig. 4).

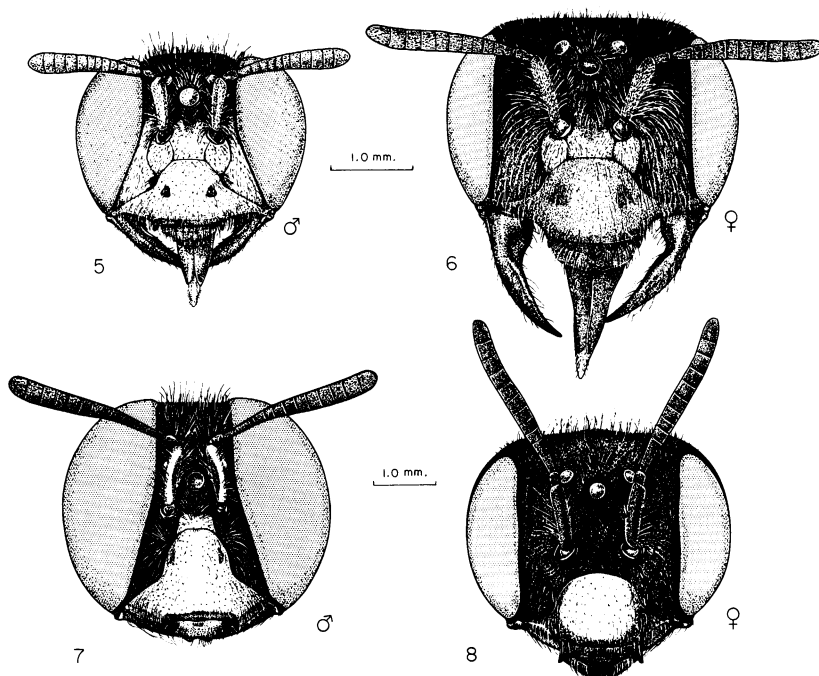
The postdefecating larvae are not totally quiescent. Even 11 months after excavation, the surviving larvae were still capable of slowly curling and uncurling and of moving the abdomen slightly from one side to the other. However, at that time they were not able to move their mouth parts or any other area of the body. Some pupae were found in the cells at the time of excavation, and other larvae pupated in the laboratory.

The species is multivoltine and the generations are not synchronized to the extent that both pupae and freshly provisioned cells were found at the time of excavation. Judged by the length of time larvae survived in the laboratory, the bee apparently passes through inclement seasons as a mature, postdefecating, but still active, larva. Because of the size of the nest and because old vacated cells were associated with it, the largest nest had obviously existed for a considerable period of time.

POLLEN-COLLECTING ACTIVITIES: The females of this species gather pollen from *Ruschia uncinata* during the heat of the day, when the flowers are open. On a cool day the females started foraging around 11 to 11:30 A.M., but on the following warmer day the nest was already open at 10:30, a fact indicating that females were visiting flowers. Pollen-laden females were noted still returning to the nest at 3 P.M. and may have continued to do so even later.

As a female left the nest, it undertook an orientation flight by swinging back and forth low over the entrance in a swift meandering flight. The range of each pass increased until the female flew toward the

¹ Only in one case among the numerous cells examined was a larva observed resting on its back, pollen cradled on its venter, and with its head nearest the cell closure.



FIGS. 5-8. Front view of heads of males and females. 5, 6. *Meliturgula braunsi* Friese. 7, 8. *Meliturgula clavicornis* (Latreille). Male and female of each species drawn to same scale.

flowers. On returning, some females landed at the nest entrance and crawled in immediately; others, perhaps disoriented by our activities in the area, flew swiftly over the vicinity for a considerable time and landed occasionally, presumably either to rest or to explore apparent nest entrances.

MALE ACTIVITIES: Although no instances of copulation were seen, males were found on bare patches in the vicinity of the pollen plant. On the cooler days they sat on the ground, often with their metasomas slightly raised. They suddenly flew up extremely swiftly and chased other insects (perhaps other individuals of *Meliturgula*). They then returned to the same bare area, hovered in one spot, and finally settled. Occasionally two males fought over a bare patch, a combat that lasted for a few seconds, until one of them departed. At times, males departed and gathered nectar from the pollen plant. On warm days the males landed less frequently and hovered longer, $\frac{1}{2}$ foot above the ground.

This territorial behavior is more pronounced than I have seen in

other panurgine bees. As discussed below, the large, dorsally converging eyes of the males are suggestive of those of *Melitturga* and probably are important in enabling the male to see oncoming insects. Brauns (1913) claimed that the males can be found in the evening on dried plants where they spend the night.

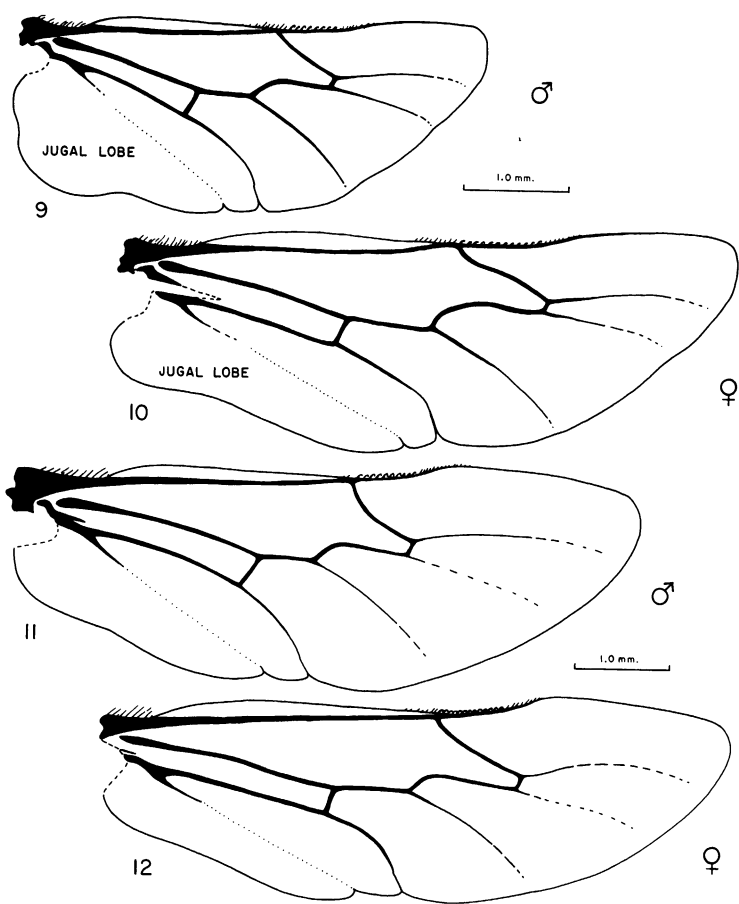
PARASITISM: No cuckoo bees or other parasites were found in association with the nests.

SEXUAL DIMORPHISM OF ADULTS AND LARVAE

Adult panurgine bees display considerable sexual dimorphism, involving, among other things, color pattern, body shape, and special modifications of the legs, not to mention the genitalia and the presence or absence of scopae. Most differences are obviously adaptive, and many are probably fundamentally concerned with sex recognition and mating. The fact that so many of these dimorphic characters provide excellent taxonomic features for species recognition indicates that they are often sexual isolating mechanisms.

The adults of *Meliturgula* exhibit many of the sexual dimorphic features referred to above. In addition, they display others that are not commonly encountered in the Panurginae or even in the Apoidea. The compound eyes (fig. 5) of the male are unusually large in relation to the rest of the head, and the inner orbits converge above, so that the upper part of the face is quite narrow. In contrast, the eyes of the female (fig. 6) are normally small, the inner orbital margins are subparallel, and the face is broad. The apical part of the flagellum of the male is slightly enlarged, somewhat clublike, whereas the female antenna appears normal. Similar but even more pronounced modifications (fig. 7) are found with respect to the head and the antennae of the males (but not the females, fig. 8) of *Melitturga*. From biological studies on *Meliturgula braunsi* and on *Melitturga clavicornis* (Latreille) (Rozen, 1965), I believe that the enlarged eyes and perhaps the clublike antennae are special adaptations enabling the males to detect oncoming flying insects. In both groups, the male rests on the ground or hovers slowly in the air; when it spies an approaching airborne insect, it darts swiftly in pursuit of mate or interloper, as the case may be.

In *Meliturgula braunsi* (figs. 9, 10) and *Melitturga clavicornis* (figs. 11, 12) the hind wing of the male is broad by comparison with its length, in contrast to the more elongate hind wing of the female. However, in *M. braunsi* alone the hind wing of the male is provided additional breadth by the greatly enlarged jugal lobe. The breadth of the hind wing is apparently a special adaptation, assisting the male bee either



FIGS. 9-12. Right hind wings of males and females. 9, 10. *Meliturgula braunsi* Friese. 11, 12. *Meliturgula clavicornis* (Latreille). Male and female of each species drawn to same scale.

in its hovering flight or in its ability suddenly to dart swiftly. Similar traits are associated with the unusually broad hind wing of the male of the oxaeid bee *Protoxaea gloriosa* (Fox).

There is an interesting difference in the sizes of the adult males and females of *Meliturgula braunsi* that I collected at the time the biological observations were made. The females tend to be nearly uniform in size, whereas the males are much more variable and average smaller than the females. The over-all body size is reflected in the easily measured maximum width of the head capsule of each individual. Table 1 gives

the pertinent statistics. These figures indicate that there is a highly significant statistical difference in the mean width of the head between the sexes. In spite of the small sample size of the males, the values for the standard error confirm that the males have a significantly greater range in the width of the head capsule than do the females.

Nielsen and Bohart (1967) pointed out that the sexes of larvae can be identified on the basis of the location of the paired imaginal discs of the genitalia and on the basis of the modified cuticle underlying the discs on the venter of the ninth abdominal segment. In the case of preserved larvae of *Meliturgula braunsi*, the discs of mature predefecating

TABLE 1
MAXIMUM WIDTHS (IN MILLIMETERS) OF THE HEAD CAPSULE OF ADULTS OF *Meliturgula braunsi* FRIESE COLLECTED 17 MILES NORTHWEST OF GRAHAMSTOWN, REPUBLIC OF SOUTH AFRICA

	Males	Females
No. in sample	11	50
Mean	2.25	2.55
Standard deviation	0.15	0.07
Standard error	0.05	0.01

larvae and of penultimate larvae are easily visible as white spots against a somewhat grayer background just beneath the ventral integument. In the female, the paired discs of the ninth segment appear paramedially in the anterior half of the segment; they are separated by a distance of nearly twice the width of a disc. The discs of the eighth segment are similar to those of the ninth except they are separated by a greater distance; the discs of the seventh segment, also similar, are separated by an even greater distance. The cuticle is somewhat modified below the discs of the ninth segment but is only very faintly modified beneath the other discs. Each modification is a nearly circular, clear scar, of about the same diameter as the disc, on cuticle stained with lignin pink. Preserved male larvae have only a single pair of contiguous imaginal discs, found on the posterior half of the ninth segment. The cuticular modification beneath them is greater than that of the female and appears as a transverse figure eight, similar to that of *Nomadopsis anthidius* (Fowler) (Nielsen and Bohart, 1967). There is no pronounced invagination of the cuticle.

The imaginal discs are also present on preserved postdefecating larvae but are more difficult to observe because the background tissue is also white. Although I had only female postdefecating larvae alive at

the time that I studied the sex of the larvae, I could identify the six females when I knew exactly where to look for the discs.

There is also a distinct sexual difference in the size of the last-stage larvae (and perhaps others). Table 2 shows that the maximum width of the head capsule of mature male larvae is significantly smaller than that of the females.

The size of the head capsule of insects does not, of course, increase during a stadium; young last-stage individuals of *Meliturgula* have the same head capsule width as postdefecating forms. Hence size difference in the head capsules of last-stage larvae are determined at the begin-

TABLE 2
MAXIMUM WIDTHS (IN MILLIMETERS) OF THE HEAD CAPSULE OF LAST-STAGE LARVAE OF
Meliturgula braunsi FRIESE COLLECTED 17 MILES NORTHWEST OF GRAHAMSTOWN,
REPUBLIC OF SOUTH AFRICA

	Males	Females
No. in Sample	8	12
Mean	1.21	1.35
Standard deviation	0.04	0.03
Standard error	0.01	0.01

ning of the stage, before the provisions have been consumed. Therefore, the amount of food does not control the size of the head capsule, as might have been expected when one considers the variation in the size of the pollen masses. Unless some qualitative difference can be found between the provisions of the two sexes, the difference in head size would seem to be genetic.

Though apparently not affecting the size of the head capsule of the larvae, the quantity of food consumed by the larvae must, nonetheless, have some effect on the body and head size of adults, in view of the pronounced variation in the dimensions of the provisions. It seems obvious that the large adult females, as larvae, cannot have fed on the small provisions or that the small males could have consumed the large provisions. To what extent the small average size of the adult male is nutritionally, as opposed to genetically, determined cannot be ascertained without experimentation. Similarly we also do not know whether the greater *variation* in body size of the male is genetic, nutritional, or (most likely) a combination of both.

The size of adult males is apparently seasonal. Brauns (1913) noted that males at the end of the season were only half as large as "normal" (i.e., earlier) ones.

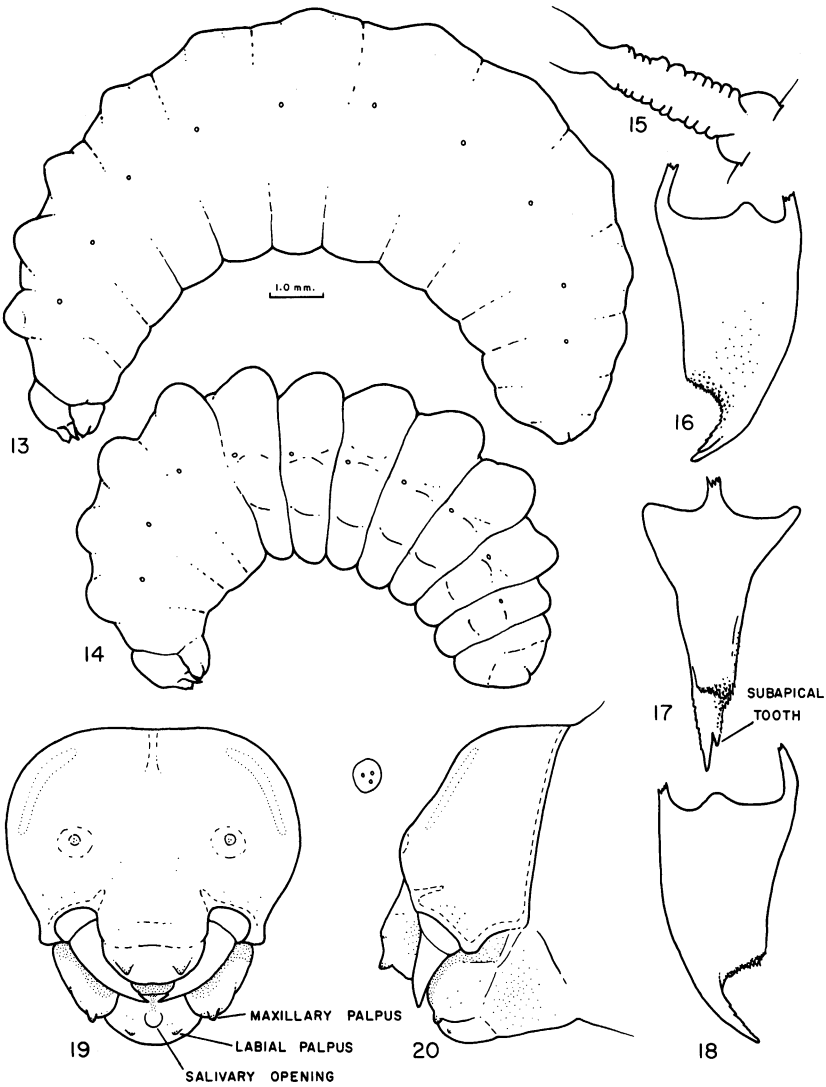
MATURE LARVA

Figures 13-20

Mature larvae of *Meliturgula braunsi* agree in almost all respects with those in the description of the subfamily in Rozen (1966). They differ primarily in that the paired dorsal tubercles are not present on most abdominal segments, at least of a fully fed individual. This feature is, perhaps, not very significant in view of the fact that certain other genera, discussed below, have greatly reduced tubercles.

Although the mature larva of *Meliturgula braunsi* will not key out in Rozen (1966), it is distinctive and can be distinguished from all known panurgine larvae (Rozen, 1965, 1966; Rozen and Rozen, 1966). The absence of paired dorsal tubercles on most abdominal segments separates it immediately from *Pseudopanurgus*, *Melitturga clavicornis*, *Calliopsis*, *Nomadopsis*, and *Perdita*. *Panurgus* and *Panurginus* have greatly reduced dorsal tubercles on the abdomen and in that respect appear similar to *Meliturgula*. The abnormally elongate clypeus and lack of hypopharyngeal groove (at least in *P. dentipes* Latreille) of *Panurgus* and the prominent antennal prominences, greatly recessed labium, and complete epistomal ridge of *Panurginus*, however, are features not found in *Meliturgula braunsi*.

HEAD (FIGS. 19, 20): Integument without setae though with widely scattered sensilla; integument unpigmented except for mandibles and except for palpi which are faintly and indistinctly pigmented. Vertex produced only moderately on each side above antennae; antennae arising from moderately low prominences; clypeus normally short; gena produced into low, rounded tubercle just above anterior mandibular articulation, as in *Pseudopanurgus*. Tentorium complete and well developed; each posterior pit situated at juncture of hypostomal ridge and posterior thickening of head capsule; posterior thickening of head capsule well developed; hypostomal ridge well developed; pleurostomal ridge well developed; epistomal ridge below anterior tentorial pits moderately developed, mesiad of pits absent; parietal bands faint. Each antenna a low convexity on nearly flat disc; antenna with three or four sensilla. Labrum bearing two prominent tubercles; epipharynx spiculate. Mandible (figs. 16-18) moderately slender; upper margin with sub-apical tooth, posterior to which are numerous fine serrations; lower apical margin with sharp-pointed serrations; cusp very strongly produced and dentate but without large tooth, such as found in *Melitturga*. Maxilla moderately large but not elongate so that it extends only short distance beyond labium, as seen in lateral view; apex scarcely, if at all, bent mesiad; palpus moderate in size and not curved strongly down-



FIGS. 13-20. Mature larva of *Meliturgula braunsi* Friese. 13. Predefecating larva, lateral view. 14. Live, postdefecating larva, lateral view. 15. Spiracle. 16-18. Left mandible, dorsal, inner, and ventral views. 19, 20. Head, front and lateral views. Scale refers to figures 13 and 14.

ward; integument of maxilla distinctly spiculate on dorsal surface but not on palpus; sclerotized cardo and stipes very faintly evident (these

structures are faintly discernible on certain other genera of panurgines, contrary to Rozen, 1966). Hypopharynx distinctly spiculate; hypopharyngeal groove present. Labium moderately projecting, unlike that of *Panurginus*; labium divided into prementum and postmentum; much of area between maxilla and labium spiculate, as seen in lateral view; labial palpus smaller than maxillary palpus, but distinct. Salivary opening an almost circular slit surrounding smooth, non-spiculate integument; very finely spiculate band extending from top of salivary opening to hypopharyngeal groove.

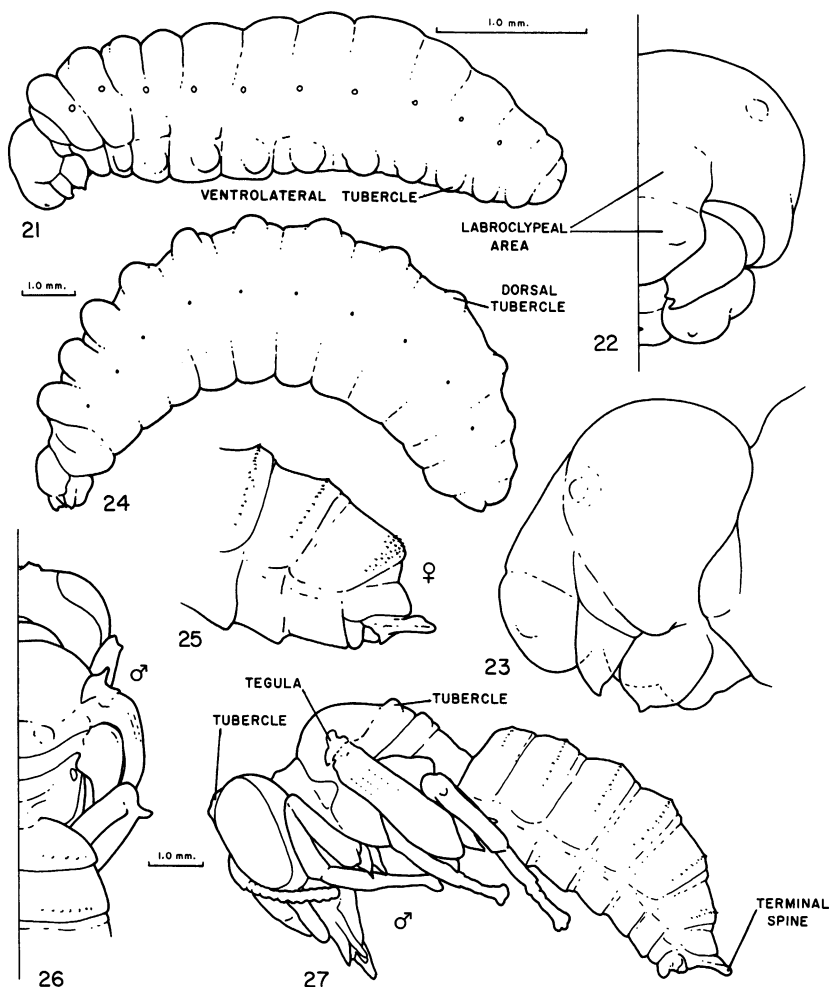
BODY (FIGS. 13, 14): Live postdefecating larva yellowish, with body wall turgid but apparently not particularly rigid; much of integument spiculate; tenth abdominal segment with spicules ventrally but these spicules not pigmented, inconspicuous, and like those on other segments. Paired dorsal tubercles low, present only on first four body segments; apices of tubercles, as seen on predefecating specimens, slightly duller than surrounding integument; pleural regions of most abdominal segments somewhat produced on postdefecating larva; intersegmental lines between abdominal segments on postdefecating larva very deeply incised, more so than those of other known Panurginae. Spiracles (fig. 15) with atrium projecting above body wall; atrial wall without teeth; peritreme present; primary tracheal opening with collar; subatrium moderate in length and wide in relation to diameter of atrium. Differences between male and female larvae described in section on Sexual Dimorphism of Adults and Larvae.

MATERIAL STUDIED: Numerous postdefecating and predefecating larvae, 17 miles northwest of Grahamstown, Cape Province, Republic of South Africa, November 22–24, 1966 (J. G. Rozen and D. Brothers).

YOUNG LARVAE

Figures 21–24

Although we cannot ascertain at this time the number of larval instars in *Meliturgula braunsi*, at least four are evident from a study of head-capsule size and anatomy. The first-stage larvae (i.e., those that have shed their chorion and are just beginning to consume pollen) (fig. 21) are linear in body form and lack distinct paired dorsal tubercles. Most body segments possess large and conspicuous ventrolateral tubercles well below the pleural regions. Similar tubercles have been noticed on the first instars of other panurgines. The head (figs. 22, 23) possesses an enlarged labroclypeal area and the antennae, labral tubercles, and at least the maxillary palpi are evident though small. The mandible already exhibits the large subapical tooth on the dorsal inner edge. Intermediate-



FIGS. 21-27. *Meliturgula braunsi* Friesie. 21. First instar, lateral view. 22, 23. Head of first instar, front and lateral views. 24. Early stage of last instar, lateral view. 25. Apex of metasoma of female pupa, lateral view. 26, 27. Male pupa, dorsal and lateral views. The three scales refer to figures 21, 24, and 25-27, respectively.

stage larvae still possess the ventrolateral body tubercles, but the labroclypeal region becomes increasingly smaller in relation to head size with each molt. Although distinct dorsal abdominal tubercles are not apparent on young larvae or on fully fed mature larvae, they are evident as low conical (as opposed to transverse) protuberances on the

penultimate instar and in the early stage of the last instar (fig. 24). The imaginal discs of the male and female genitalia are quite visible through the integument of preserved penultimate instars.

PUPA

Figures 25-27

The pupa of this species agrees with the description of the Andrenidae based on the pupae (Yager and Rozen, 1966). The only other panurgine group known to possess tubercles on the vertex is *Perdita*. However, the tubercles of *Perdita* are sharp-pointed and the terminal spine is greatly elongate, the mesoscutellum lacks tubercles, and the mesepisternum possesses a tubercle.

Length, 10.0 to 12.0 mm. Mandible of male without tubercle on ventral surface; mandible of female with small but distinct tubercle. Vertex with low tubercle above each lateral ocellus. Posterior lobes of pronotum not produced; mesoscutum without tubercles; mesoscutellum with pair of moderately rounded tubercles; mesonotum with only indistinct swelling; mesepisternum without tubercles. Tegula produced. All coxae and trochanters each with elongate apical spine; fore femur with rounded basal spine which is more developed on female than on male; hind tibiae with conspicuous tubercle near base but without apical protuberance. Metasomal terga I to VI (male) and I to V (female) with apical row of very small tubercles; some metasomal sterna with faint indications of very small apical tubercles; terminal spine rather short, rounded apically.

MATERIAL STUDIED: One male pupa, four female pupae, 17 miles northwest of Grahamstown, Cape Province, Republic of South Africa, November 23, 24, 1966 (J. G. Rozen and D. Brothers).

DISCUSSION AND CONCLUSIONS

In most respects the biology of *Meliturgula braunsi* is typical of that of the Panurginae (Rozen, 1967). However, only a few other genera have species in which females share a common nest, and no other panurgine nesting on a horizontal surface has such a deep nest. In the case of most panurgines, but not of *M. braunsi*, the burrow entrance is marked by a distinct symmetrical tumulus. The cells of *M. braunsi* have an unusually thick wall but otherwise are not distinctive, though the matter of symmetry and absorption rate on the cell wall should be investigated in other panurgines. The only feature of the provisions that appears atypical is the range of size of the pollen balls. As mentioned

elsewhere, the territoriality of the males is marked, and the mating behavior, though not fully studied, is apparently somewhat similar only to that of *Melitturga clavicornis*.

Perhaps the most outstanding difference between *Meliturgula braunsi* and other panurgines is the fact that the postdefecating, overwintering stage is apparently active, whereas in all the other genera this stage is totally quiescent. The basis for this difference is difficult to understand. However, physiological diapause is almost certainly an adaptation permitting individuals to pass unfavorable seasons with the minimal expenditure of stored energy; in the case of most univoltine panurgines, diapause occupies nearly 10 months of the year (Rozen, 1967). Possibly *Meliturgula* is essentially tropical, and, in the presence of year-round available food and favorable climate, the ancestral form lost its ability to undergo true physiological diapause.

The biology, larvae, and pupa of *M. braunsi* unquestionably confirm the fact that *Meliturgula* belongs to the subfamily Panurginae. Features of the immature stages and biology suggest, however, that the genus is not closely affiliated to other genera of which the life histories and larvae have been studied. The somewhat similar male premating behavior and concomitant similar adaptations of the male head suggest a relationship between *Meliturgula* and *Melitturga*. However, the features of the immature stages, particularly the mature larvae, of *Meliturgula braunsi* are not especially similar to those of *Melitturga clavicornis*. Likewise, agreement in biology between the two genera is not great. On the other hand, neither in the case of the immature stages nor in the case of biology are the differences between the two genera such as to exclude the possibility that *Melitturga* and *Meliturgula* had evolved from a common lineage that was already distinct from the other panurgine groups. After splitting, the two branches of the common lineage would have had to undergo considerable evolutionary change before the genera, as we now understand them, appeared.

In spite of the new data concerning the Panurginae presented in this paper and in other recent ones by Rozen (1958, 1963, 1965, 1966, 1967), Rozen and Rozen (1966), Shinn (1967), and Yager and Rozen (1966), our knowledge of the interrelationships of the panurgine genera is still incomplete. Perhaps the next major undertaking leading to an understanding of these relationships should be a revisional study of the adults. Such a study should be carried out at the generic level and should employ the biological data and the information on the immatures amassed in recent years.

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